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The Triassic Reptile *Procolophon* in Antarctica

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

ABSTRACT

A series of procolophonid fossils is described from the Lower Triassic Fremouw Formation of Antarctica. All the specimens are identified as *Procolophon trigoniceps* Owen, typically found in the *Lystrosaurus* Zone of the Beaufort Series in South Africa. The presence of this one species in Africa and Antarctica lends additional weight to previously published paleontological evidence (notably the distribution of the dicynodont reptile *Lystrosaurus* in Gondwanaland) indicating a close ligation between the two continents at the beginning of the Mesozoic.

INTRODUCTION

Among the fossil remains of Lower Triassic tetrapods discovered in Antarctica are about a dozen specimens of the cotylosaurian reptile *Procolophon*. These fossils, ranging from a beautifully preserved skull and skeleton to isolated jaws and fragments of skeletons, were all discovered in the vicinity of Shackleton Glacier in the Transantarctic Mountains during the austral summer field season of 1970-1971. With the exception of two specimens noted below all the fossils were collected by James Kitching during the course of an intensive search for Triassic tetrapods in this region.

The fossils described were contained in a fine-grained and rather hard matrix, so that considerable time and labor have been allotted to the preparation of the specimens for study. It has not been feasible to remove the fossils from the enclosing rock, but all have been sufficiently exposed for detailed study. The nature of the prepared specimens is indicated in some of the accompanying photographs.

Preparation of the materials was carried out for the most part by Mrs. Nova Young. The drawings were made by Miss Pamela Lungé and the photographs by Mr. Marc Gaede.

We wish to acknowledge the constant advice and help of Dr. David H. Elliot of The Ohio State University, leader of the field party at Shackleton Glacier. Also we are much indebted to the involved personnel of the United States Navy for logistical support.

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STRATIGRAPHIC RELATIONSHIPS

The Antarctic specimens of *Procolophon* were collected from the Lower Triassic Fremouw Formation, as have been other Triassic tetrapods discovered so far in Antarctica. These fossils all came from the vicinity of Shackleton Glacier, which is about 225 km., east by south of Coalsack Bluff, the locality at which Lower Triassic tetrapods were collected during the austral summer of 1969-1970. No fossils of *Procolophon* were found at Coalsack Bluff, which may be a result of the accidents of collecting, or may be a result of facies differences at the particular stratigraphic levels where fossils were collected. Dr. James W. Collinson of The Ohio State University, who made extensive stratigraphic studies of the Fremouw Formation, both at Coalsack Bluff and in the McGregor-Shackleton Glacier area, made the following statement in a personal communication. "The deposits at Mt. Kenyon (near McGregor Glacier) and Coalsack Bluff are amazingly similar, consisting of fining-upward cycles with coarse channel deposits at the base and fine floodplain deposits at the top. Bedding plane exposures of fine-grained sediments at McGregor made the real difference."

The stratigraphic setting of the fossiliferous Fremouw sediments has been outlined in a paper describing *Lystrosaurus* from Antarctica (Colbert, 1974, pp. 5-12), and particularly, in more detail, by Elliot, Collinson, and Powell (1972, pp. 387-392). Therefore no detailed description will be presented here.

There is no doubt that at Shackleton Glacier *Procolophon* occurs in stratigraphic association with *Lystrosaurus*, *Thrinaxodon*, and other forms typical of the *Lystrosaurus* Zone in South Africa.

We digress briefly on the stratigraphic relationships of *Procolophon* in South Africa, as this bears directly on the subject. This reptile was for many years assigned to a separate zone in the Karroo sequence, immediately above the *Lystrosaurus* Zone. Thus in Africa the Middle and Upper Beaufort beds were thought to have consisted of the *Lystrosaurus*, the *Procolophon*, and the *Cynognathus* zones. Indeed, this sequence is well established in the earlier literature.

During the past few decades, however, it has become increasingly apparent that *Procolophon* in South Africa does not occur within a separate stratigraphic horizon between the *Lystrosaurus* and *Cynognathus* zones, but rather within the *Lystrosaurus* Zone itself—in distinct facies or pockets. This was noted by Broom in 1932, after he had found fragments of *Procolophon* associated with *Lystrosaurus* in a sandstone. It was more definitely established by Hotton and Kitching in 1963, by Hotton in 1967, and especially by Kitching in 1968 and 1972.

It has been observed that *Procolophon* frequently occurs in the conglomerates at the base of the higher sandstones at many *Lystrosaurus* Zone localities. At some localities *Procolophon* is found in nodules well within the *Lystrosaurus* Zone. Furthermore, *Procolophon* has been recovered from the same horizon as *Lystrosaurus declivis* and *L. murrayi* in a road cutting at Lootsberg Pass, Graaff Reinet.

At some South African localities *Procolophon* is found in small localized exposures immediately above the upper *Lystrosaurus* Zone sandstone, within a light, gray-green or reddish purple mudstone, similar in texture to the mudstones below the sandstone. In the Queenstown, Cathcart, and Tarkastad districts it is evident that a number of these scattered deposits were laid down in erosion channels or depressions in the sandstone.

"With the presence of well-preserved specimens of the genus *Procolophon* in the *Lystrosaurus* zone (Kitching 1968) and the frequent occurrence of fragmentary remains in the upper sandstones and conglomerates of this zone there appears to be no doubt that this genus co-existed with *Lystrosaurus* during the deposition of these sediments" (Kitching, 1972, p. 311).

The undoubted association of *Procolophon* with *Lystrosaurus* in the Fremouw Formation of Antarctica reinforces the evidence of their contemporaneity in South Africa. Moreover, the association of these genera in the Lower Triassic sediments of both southern Africa and Antarctica adds still more evidence for a close geographic relationship between these regions at the beginning of Triassic history, a point that will be explored more fully later.

SYSTEMATICS

CLASS REPTILIA

ORDER COTYLOSAURIA

SUBORDER PROCOLOPHONIA

FAMILY PROCOLOPHONIDAE

PROCOLOPHON OWEN, 1876

Procolophon Owen, 1876, p. 25.

Type Species. Procolophon trigoniceps Owen.

Horizon and Locality. Lower Triassic, Middle Beaufort beds, *Lystrosaurus* Zone, South Africa.

Generic Diagnosis. Small, advanced cotylosaurs, with deep skull, triangular in shape. Orbits very large and elongated, and pineal opening large; nares almost terminal. Quadrate forward of occiput, with articulation well below level of teeth. Otic notch large; tabular and quadratojugal expanded and spikelike. Palate restricted and with elongate choanae. Lower jaw deep, with strong coronoid and elongated retroarticular process. Four premaxillary teeth and seven maxillary teeth, of which five or six are transversely broad and chisel-shaped. Nine dentary teeth, the last six chisel-like. Postcranial skeleton compact. Neural arches of vertebrae expanded, in cotylosaurian fashion. Ribs essentially single-headed. Girdles strong and limbs comparatively short. Feet broad, with full complements of carpal and tarsal elements. Tail short.

Procolophon trigoniceps Owen

Procolophon trigoniceps Owen, 1876, p. 25, pl. 20, figs. 4-7.
Procolophon minor Owen, 1876, p. 26, pl. 20, figs. 8-12.
Procolophon griersoni Seeley, 1878, p. 799, pl. 32.
Procolophon cuneiceps Seeley, 1878, p. 799, pl. 32.
Procolophon laticeps Seeley, 1878, p. 799, pl. 32.
Procolophon platyrhinus Seeley, 1905, p. 218, fig. 35.
Procolophon sphenorhinus Seeley, 1905, p. 218, fig. 36.
Procolophon baini Broom, 1905, p. 212.

Type. BMNH [British Museum (Natural History) London] R. 1726, a skull, from Donnybrook, Tarkastad, South Africa.

Diagnosis. See generic diagnosis above.

ANTARCTIC SPECIMENS UNDER CONSIDERATION

AMNH[1] 9501–partial impression of a skull in rock; from Kitching Ridge.
AMNH 9506–well-preserved skull, mandible, and associated skeleton to and including twenty-first presacral vertebra; pelvis, hind limbs, and tail missing; from Kitching Ridge.
AMNH 9507–disarticulated lower jaws with a few associated skull fragments and postcranial elements; from Mount Kenyon.
AMNH 9508–front portion of a left dentary with eight teeth; from Kitching Ridge.
AMNH 9509–poorly preserved skull and partial skeleton; from Kitching Ridge.
AMNH 9510–right humerus, radius and ulna, and series of ribs; from Kitching Ridge.
AMNH 9511–right half of a small skull buried in matrix; from Kitching Ridge.
AMNH 9512–several ribs and other postcranial bones; from Kitching Ridge.
AMNH 9518–portions of two skulls and jaws in matrix, in cross-section; from Collinson Ridge, near Halfmoon Bluff.
AMNH 9533–badly crushed skull with some associated bones; from Collinson Ridge, near Halfmoon Bluff.

Kitching Ridge is on the east side of Shackleton Glacier, opposite its confluence with Logie Glacier and about 15 km. above the junctions of Baldwin Glacier on the east and McGregor Glacier on the west with Shackleton Glacier. Its position is approximately latitude 85° 13′ S and longitude 177° E.

Halfmoon Bluff and Collinson Ridge are directly across Shackleton Glacier about 15 km. east of Kitching Ridge. Their position is approxi-

[1] The American Museum of Natural History.

mately latitude 85° 13′ S and longitude 175° 30′ E.

Mount Kenyon is about 8 km. east of Halfmoon Bluff. Its position is approximately at latitude 85° 13′ S and longitude 174° 30′ E.

All localities are within the lower portion of the Fremouw Formation, of Early Triassic age.

All specimens were collected by J. W. Kitching, except AMNH 9509, collected by Thomas Rich, and AMNH 9510, collected by John Ruben.

General Remarks

Before proceeding to a consideration of the Antarctic fossils it should be pointed out that *Procolophon* is essentially a monotypic genus in Africa. As can be seen from the taxonomic listing above, several species were named by Owen and Seeley, but later authors have regarded the subsequent forms created by Owen and by Seeley as synonymous with the type, *Procolophon trigoniceps.* In 1905 Broom described *Procolophon baini*, based on a skull collected years earlier by J. M. Bain or his father, T. Bain, from an unknown locality. Broom distinguished this skull from typical *Procolophon trigoniceps* because the matrix is different from that associated with other South African specimens of the genus, as well as by the relatively small size of the quadratojugal, the relatively large size of the fourth premaxillary tooth, and the presence of eight, instead of seven, teeth in the maxilla. Because the anatomical characters of this supposed species are of such equivocal nature, and because its locality is unknown, it probably should be regarded as synonymous with the type species.

The specimens of *Procolophon* from Antarctica vary in completeness and in the state of preservation. Although the descriptions and conclusions presented here are based partly on the suite of materials, the evidence for much of what is written is found in the beautifully preserved skull and skeleton, AMNH 9506. This is one of the most completely fossilized specimens of *Procolophon* known, and as such it offers an opportunity for rather detailed comparisons with *Procolophon trigoniceps* from Africa.

Skull and Mandible

AMNH 9506 is a *Procolophon* of medium size in which the quadratojugal "horns" are not so strongly developed as in the large, supposedly male, specimens from Africa. The skull of the Antarctic specimen is only about half the length of a large skull in the Bernard Price Institute for Paleontological Research, Johannesburg (BPI 4248), distinguished by the very strongly developed quadratojugal projections (fig. 7). Likewise, the Antarctic skull is little more than half the length of the skull figured by Broom in 1936 (p. 387, fig. 1), a specimen with prominent quadratojugal "horns," considered by Broom as "probably" a male. The Antarctic skull is almost as large, however, as the skull of the skeleton figured by Watson in 1914, and considered by him as a male. These skulls are compared in figure 7. The skeleton figured by Watson (1914, p. 743, fig. 5) is one of two specimens that he described; the other was regarded by him as a female. According to Watson (p. 743), the two skeletons are of similar length, but the "female" is "much more lightly built, having narrower and more slender limb-girdles, and limbs which are less than three-quarters as long as those of the male skeleton and much less robust." Unfortunately Watson did not publish a figure of the supposed female skeleton for comparison with the supposed male specimen nor did he give comparative measurements.

The skeleton illustrated by Watson (fig. 24) can be compared with the skeleton from Antarctica (fig. 23). In addition to being of comparable size, the skulls in the two specimens show somewhat similar developments of the quadratojugal and tabular "horns." Therefore, if these are males, they may be considered as juvenile or partially grown individuals, not only because of their modest size, but also because of the modest development of the quadratojugal bones.

As is readily apparent from the comparison of the two skeletons, the skull of the Antarctic specimen is relatively smaller than that of the African specimen. How this difference is to be interpreted is open to speculation. Perhaps it is a matter of ontogenetic development; certainly the skull of the specimen figured by Watson appears to be more or less intermediate in its structure between the Antarctic specimen and the large skulls with laterally protruding quadratojugals, such as BPI 4248 (fig. 7), or the one figured by Broili and Schroeder (1936, fig. 4).

The skull of the Antarctic *Procolophon* is of triangular shape as seen in dorsal aspect, quite similar in this respect to skulls from Africa. The quadratojugal, although not so extended as in very large specimens known from Africa, is sufficiently developed (figs. 5, 6) to largely obscure the quadrate in lateral view–a character definitive for *Procolophon trigoniceps*. Also, as is typical of *Procolophon trigoniceps*, the quadrate articulation is well forward of the occiput, and although this skull is dorsoventrally flattened, it is quite apparent that the articulation is well below the level of the tooth row.

In the dorsal aspect of the skull (fig. 4) the squamosal is restricted, occupying a small area of the border of the otic notch between the large

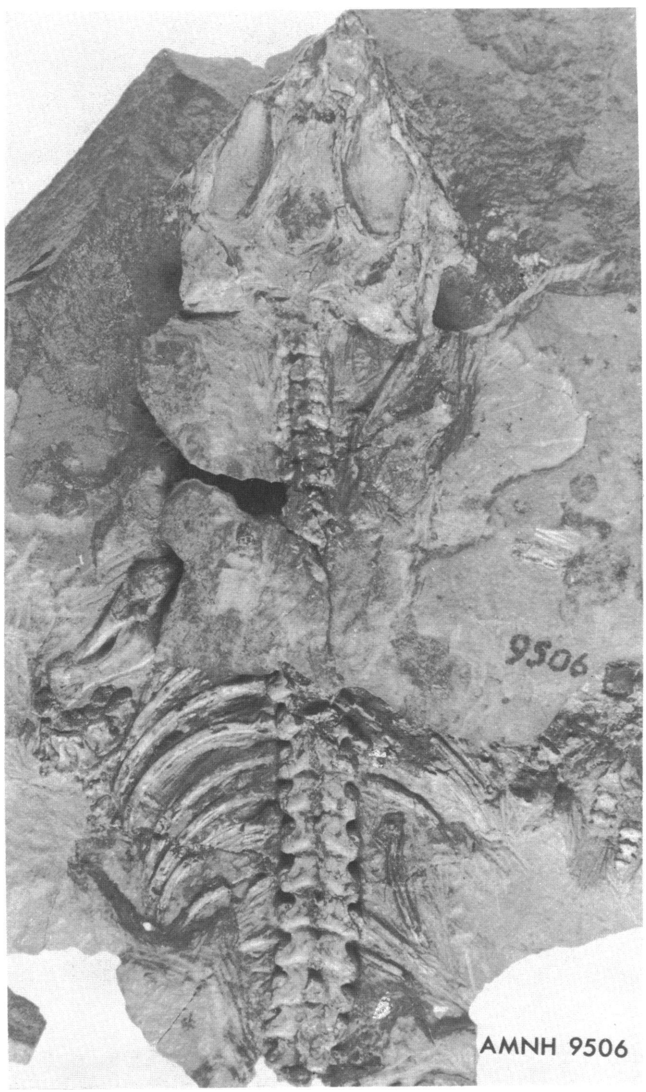


FIG. 1. *Procolophon trigoniceps* Owen. Partial skeleton from the Lower Triassic Fremouw Formation of Antarctica. Dorsal view. X1.

FIG. 2. *Procolophon trigoniceps* Owen. Anterior part of skeleton from the Lower Triassic Fremouw Formation of Antarctica. Ventral view. X1.

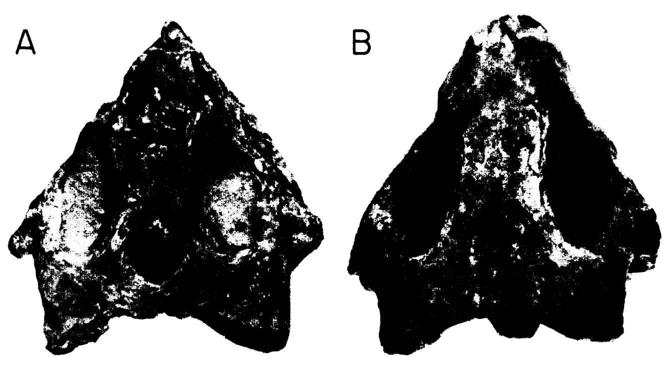


FIG. 3. *Procolophon trigoniceps* Owen. A. Skull from the Lower Triassic Fremouw Formation of Antarctica. B. Skull from the Lower Triassic *Lystrosaurus* Zone of South Africa. Dorsal views. X1.

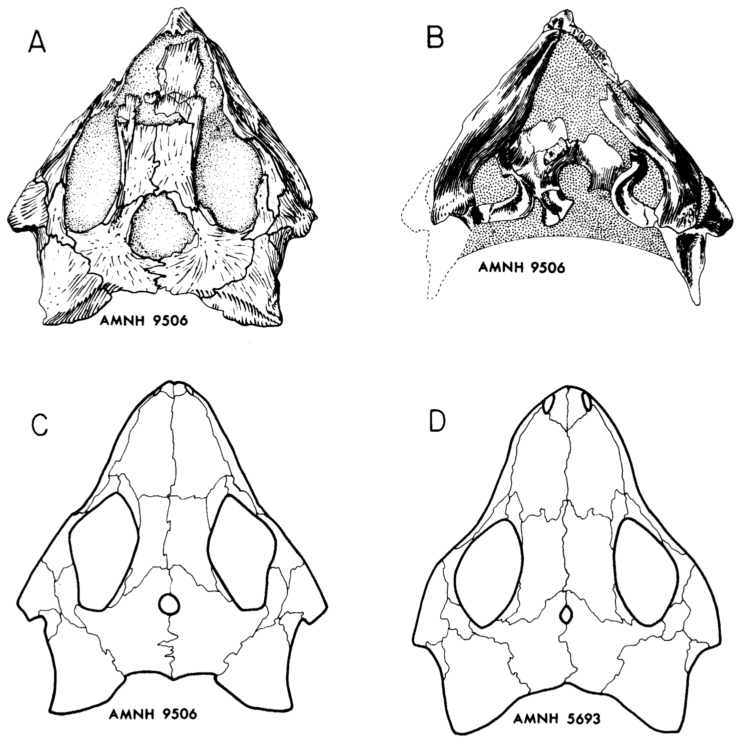


FIG. 4. *Procolophon trigoniceps* Owen. A. Skull and jaws from the Lower Triassic Fremouw Formation of Antarctica, dorsal view. B. The same, ventral view. C. Antarctic skull restored, dorsal view. D. South African skull restored, dorsal view. All X1.

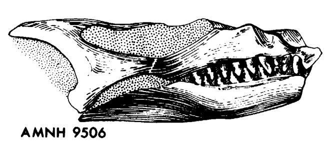


FIG. 5. *Procolophon trigoniceps* Owen. Skull and jaws, from the Lower Triassic Fremouw Formation of Antarctica. Right lateral view. X1.

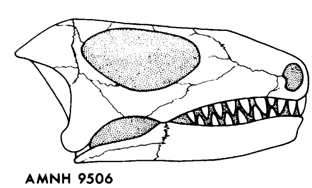


FIG. 6. *Procolophon trigoniceps* Owen. Skull and jaws, restored. Right lateral view. X1.

quadratojugal and the very large pointed tabular. The other bones of the skull roof show the characteristic *Procolophon* pattern: the nasals, frontals, and parietals are large; the prefrontals, lacrimals, postfrontals, and postorbitals are comparatively small. The jugals, as in *Procolophon trigoniceps*, form considerable portions of the borders of the large orbits, and their ventral surfaces are concave, in part as an adaptation to the high coronoids of the mandible and in part in configuration with the sweeping curve of the lower border of the quadratojugals. The premaxillae are not well preserved in the Antarctic specimen, but in dorsal aspect they appear to be small, and it seems likely that they curved around below the nares, as is typical for *Pro-*

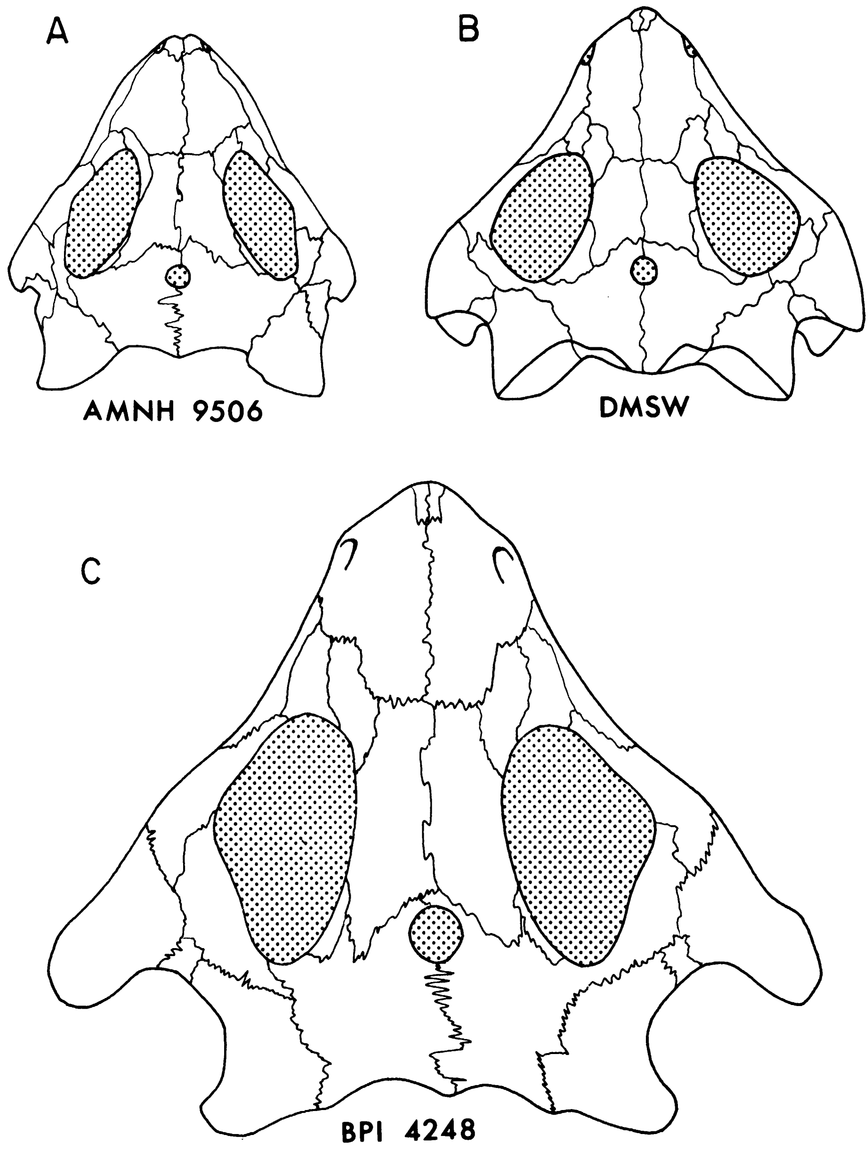


FIG. 7. *Procolophon trigoniceps* Owen. Comparison of skulls in dorsal view, showing successive stages in ontogenetic growth. A. From the Lower Triassic Fremouw Formation of Antarctica. B. From the Lower Triassic *Lystrosaurus* Zone of South Africa (figured by D. M. S. Watson). C. Also from the *Lystrosaurus* Zone of South Africa. All X1.

colophon trigoniceps. The maxillae are anteroposteriorly restricted.

The orbits in the Antarctic *Procolophon* are very large and quite elongated. This is a feature of the Procolophonidae, and it seems quite probable that such elongation provided a sort of pseudo-supratemporal opening to allow for the bulging of what must have been very strong temporalis muscles. These muscles would have occupied much of the posterior portion of the

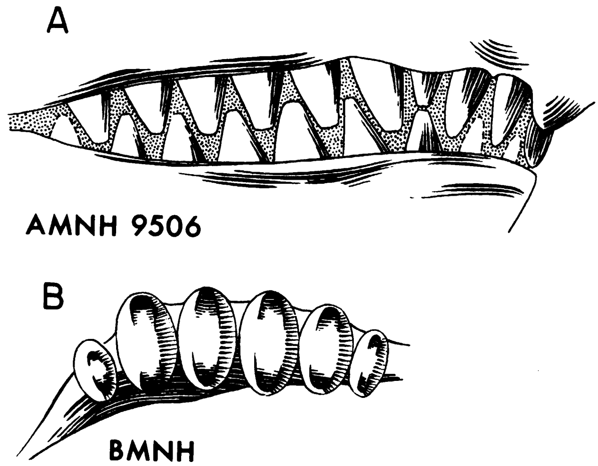


FIG. 8. *Procolophon trigoniceps* Owen. A. Upper and lower dentitions of Antarctic specimen, in occlusion, right lateral view. B. British Museum (Natural History) specimen from the Lower Triassic *Lystrosaurus* Zone, Trollip Siding near Rosmead, Cape Province, South Africa, right maxillary teeth in crown view. Both X4.

orbital opening, the eyeball with its attendant muscles being restricted to the anterior region of the orbit.

The Antarctic skull is especially noteworthy by reason of the unusually large pineal opening. It seems probable, however, that the great size of the opening in this specimen is not completely natural. Some parts of the border appear to be smooth, particularly on the left side, and thus have a rather natural look, but even here one cannot suppose that the border as preserved represents the actual limit of the opening. Very possibly the parietals in this region may have been to some degree cartilaginous (assuming that this was a young individual) so that those portions of the actual border of the opening that were not destroyed by erosion or abrasion may never have been fossilized. The pineal opening is restored to its normal size in figure 4.

The palate of the Antarctic specimen (figs. 2, 4) is only partially visible, but as exposed it accords closely with the palate in *Procolophon trigoniceps*. The pterygoids are rather heavy and enclose a broad interpterygoid vacuity—considerably broader than the vacuity as figured by Broili and Schroeder in 1936. In this respect, however, there is close correspondence to a specimen in the British Museum (Natural History) collected in 1933 from Trollip siding near Rosmead, Cape Province, a latex cast of which has been kindly lent us (together with casts of other British Museum specimens) by Dr. Pamela Robinson of the University of London. As is typical for *Procolophon*, there are small pterygoid teeth forming a row on each side of the interpterygoid vacuity but, as also is typical for *Procolophon*, the pterygoid flanges are toothless. A large tooth is present on the palatine, and presumably there were vomerine teeth. A curved pterygoid wing extends laterally to meet the quadrate. The ectopterygoid forms the lateral ridged border of the palate.

The parasphenoid-basisphenoid complex is missing in the Antarctic specimen, but it probably was short and broad, as in *Procolophon trigoniceps*.

The lower jaw, of characteristic *Procolophon* form, is heavy and deep, with a strong coronoid process and with a strong retroarticular process.

The marginal teeth in *Procolophon* are reduced in number and largely specialized in form. This is certainly true for the various specimens of *Procolophon* found in Antarctica. In AMNH 9506 (fig. 8), the lower jaws are tightly locked in place, as is also common among specimens of *Procolophon* found in Africa. Consequently it is difficult to be completely certain as to the number of teeth, above and below, in this specimen, but because of the close correspondence of the teeth to those in African specimens, it seems obvious that the dental formula was probably the same as for characteristic *Procolophon trigoniceps.* Two other specimens from Antarctica, AMNH 9507 (figs. 9, 10) and AMNH 9508 (figs. 11, 12), are mandibular rami with teeth, and although these specimens show some of the teeth rather clearly, they do not in either case contain the complete tooth row. No very helpful information concerning the dentition can be derived from AMNH 9509, a crushed skull with lower jaws.

In a specimen of *Procolophon trigoniceps* from South Africa, there are four premaxillary teeth of peglike form, of which the first is the largest and the fourth is the smallest. These are followed in sequence by seven maxillary teeth, of which the first is a small peglike tooth, the next five are large, transversely broad, chisel-shaped teeth, and the last tooth is reduced, somewhat intermediate in shape between the simple peg and the chisel form characteristic of the five teeth in front of it. Although the cutting edges of the large maxillary teeth are in the form of sharp transverse chisels, their bases are expanded anteroposteriorly as well as transversely. Consequently, there is a V-shaped space between each pair of teeth into which the similarly constructed lower teeth can bite.

Because of the interlocking of upper and lower teeth in the Antarctic fossil, it is possible to see them only in buccal and lingual views. It is quite clear, however, that they accord in most respects with the teeth of *Procolophon trigoniceps.* But there are some differences. Thus, although the premaxillary teeth of AMNH 9506 are peglike, they are almost all equally large.

FIG. 9. *Procolophon trigoniceps* Owen. Left mandibular ramus (above) and right ramus below it, with vertebra and other postcranial bones. From the Lower Triassic Fremouw Formation of Antarctica. X2.

An unexpected feature of this specimen is the large size of the first maxillary tooth (fig. 8). It is fully as large as the teeth that follow, and like them is chisel-shaped. Consequently there are six fully formed chisel maxillary teeth in this specimen, instead of the five seen in the African specimen with which it has been compared. It should be noted, however, that the specimen figured by Broili and Schroeder in 1936 shows the first maxillary tooth as a developed chisel, so it seems that this tooth varies considerably within the species. If there is a seventh maxillary tooth in the Antarctic specimen, as probably is the case, it is hidden because of the tight occlusion of the mandible upon the skull.

The Antarctic specimen, AMNH 9506, seems to have nine dentary teeth, as might be expected. The first three are peglike and quite large. The

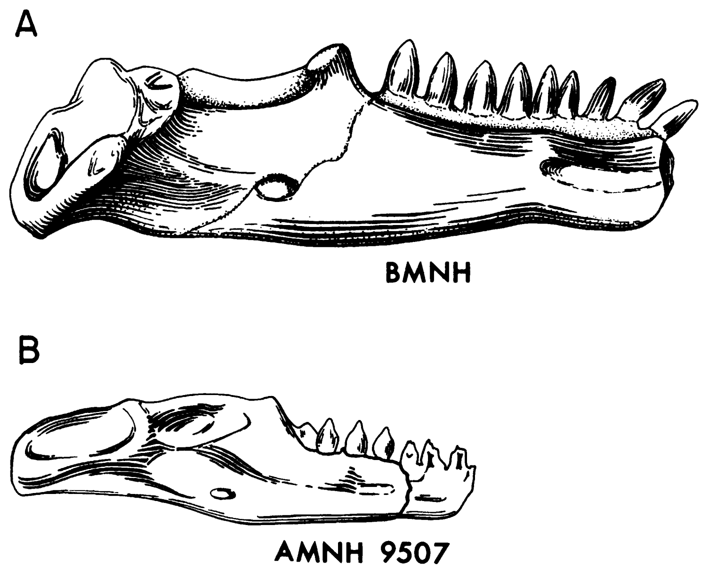


FIG. 10. *Procolophon trigoniceps* Owen. A. Left ramus in the British Museum (Natural History) from the Lower Triassic *Lystrosaurus* Zone, Trollip Siding near Rosmead, Cape Province, South Africa. B. Left mandibular ramus from the Lower Triassic Fremouw Formation of Antarctica. Both internal lateral views. X2.

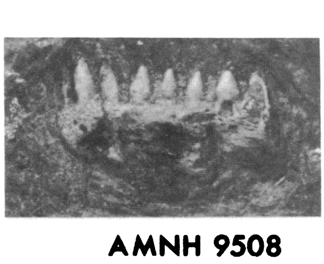


FIG. 11. *Procolophon trigoniceps* Owen. Front portion of a left dentary with eight teeth, from the Lower Triassic Fremouw Formation of Antarctica. X2.

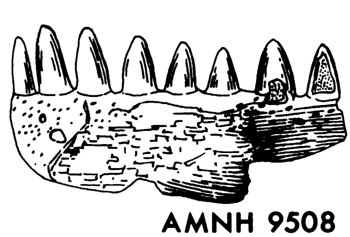


FIG. 12. *Procolophon trigoniceps* Owen. Front portion of the left dentary seen in figure 11. X3.

following teeth are clearly of the usual chisel-like form. Although the upper and lower teeth in this specimen are tightly occluded, it has been possible to expose a portion of what seems to be the last, or ninth, tooth of the dentary series on the right side. This tooth is clearly chisel-shaped, as is the last dentary tooth in *Procolophon trigoniceps.*

The Axial Skeleton

The best information concerning the postcranial skeleton in *Procolophon* from Antarctica is to be obtained from AMNH 9506 (fig. 1), in which the skeleton is preserved back to and including the twenty-first presacral vertebra. There is every reason to believe that there were 26 presacral vertebrae in this specimen, which is typical for *Procolophon trigoniceps* from Africa. In this specimen the atlas is missing, but its position in the series is retained. All the vertebrae preserved in this fossil are in sequence and articulated, with a slight amount of telescoping in the middorsal region. This, however, does not seriously distort the nature of the vertebral column. The ribs are in place, and are especially well preserved on the left side.

The vertebrae are of characteristic cotylosaurian form (figs. 13, 14), with expanded neural arches, especially in the more posterior portion of the column, where zygapophyses are broad. The neural spines are much abraded in AMNH 9506, but it appears that when complete they were relatively low. In describing *Procolophon*

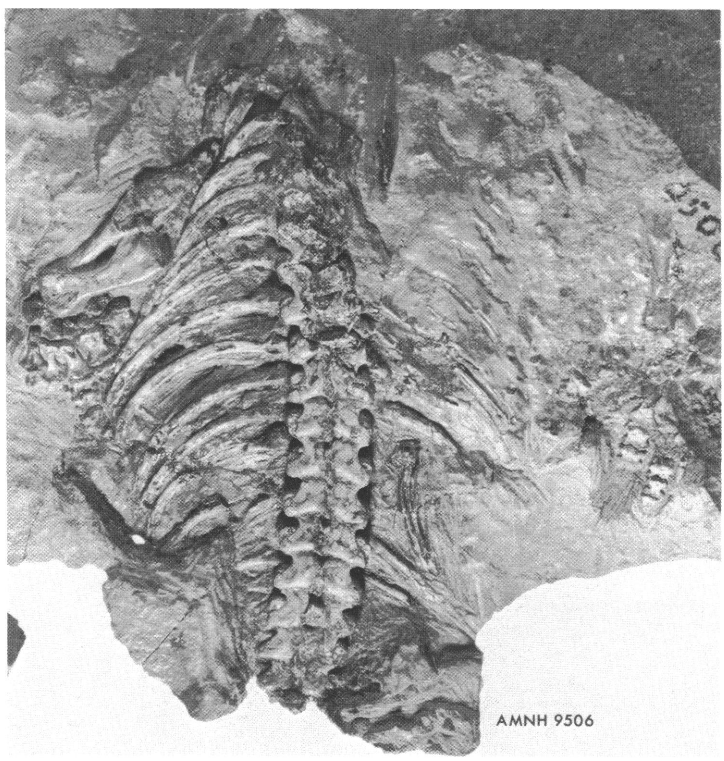


FIG. 13. *Procolophon trigoniceps* Owen. A portion of the articulated vertebrae column, with ribs, the left forelimb and a part of the right forelimb. (This figure shows some of the more anterior thoracic vertebrae and ribs, which are not visible in fig. 1.) Dorsal view. X1.

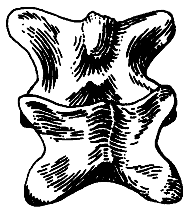


FIG. 14. *Procolophon trigoniceps* Owen. Two articulated thoracic vertebrae. Dorsal view. X2.

trigoniceps from Africa Watson (1914, p. 740) stated, "The neural spines are only represented by very short projections on the top of the swollen neural arch." This description certainly applies to the vertebrae in AMNH 9506. Unfortunately, the centra are not visible in this specimen.

The ribs are stout and flaring, indicative of a relatively capacious thorax in this little reptile. In his paper of 1914 on *Procolophon trigoniceps*, Watson described rib articulations as being "single-headed throughout." He described these articulations as joining to "single" articulations on the vertebrae, these vertebral facets being formed by both the arch and centrum. In the Antarctic specimen the proximal end of the rib consists of a conjoined capitulum and tubercle which, while forming in effect a single-headed rib, still retain clear indications of their identities (fig. 15). Such a conjunction would articulate quite closely with the type of conjoined vertebral facet described by Watson. However, the proximal end of the rib in this specimen is not quite so simple as might be inferred by describing it as a single-headed rib.

The Appendicular Skeleton

The pectoral girdle (fig. 16) consists of a scapula, two coracoids, and clavicle, with a median interclavicle. The scapula is rather short and widely expanded both proximally and distally, with a slightly constricted "neck" near the proximal end. The posterior edge of the bone is strongly concave, and it is this concavity that produces the constricted neck. Moreover, it appears that the vertebral edge is slightly curved. Thus the bone differs markedly from the rather rectangular-shaped scapula of *Procolophon trigoniceps* as figured by Watson (1914, fig. 4).

The two coracoids are imperfectly preserved. Although the anterior coracoid is partially missing an imprint in the rock shows what its shape would have been when complete. The bone is rather oval, its external border interrupted by a deeply incised coracoid notch. The posterior coracoid is only partially present, so that its shape must be inferred. It evidently was a large bone.

The interclavicle is of the characteristic T-shape, with a very long stem. The clavicles are large and strong.

Taken together, the bones of the pectoral girdle constitute a strong and well-developed girdle of characteristic cotylosaurian form. Figure 17 shows an attempted restoration of the pectoral girdle.

The front limbs in the Antarctic *Procolophon* show considerable differences from the front limbs of *Procolophon trigoniceps* as figured by Watson (1914, fig. 5). In brief, they are much heavier throughout than the African specimen here mentioned.

FIG. 15. *Procolophon trigoniceps* Owen. Proximal portion of a rib, showing the conjoined capitulum and tubercle. X2.

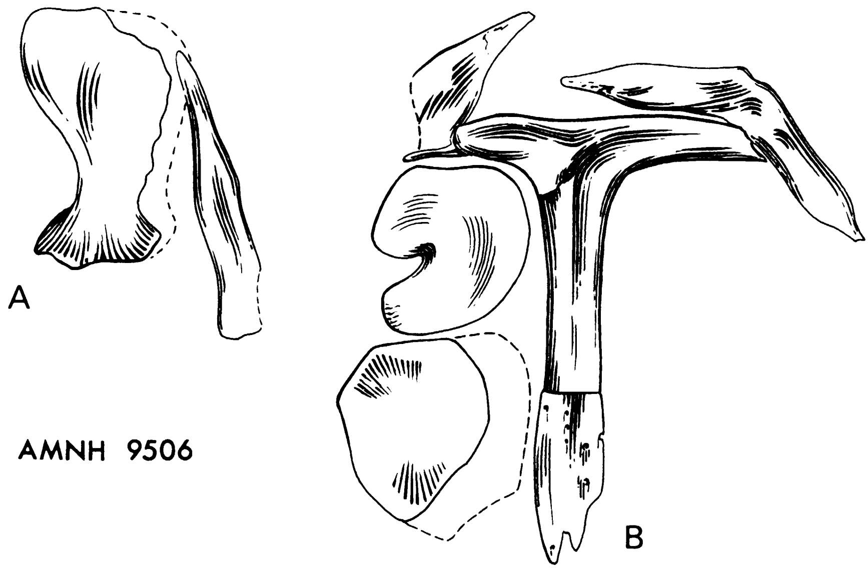


FIG. 16. *Procolophon trigoniceps* Owen. Pectoral girdle. A. Right scapula and portion of clavicle, lateral view. B. Interclavicle, portions of both clavicles and right coracoids, ventral view. X2.

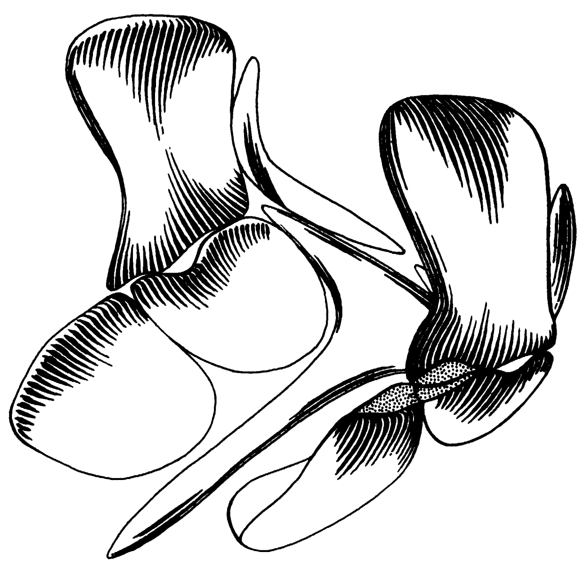


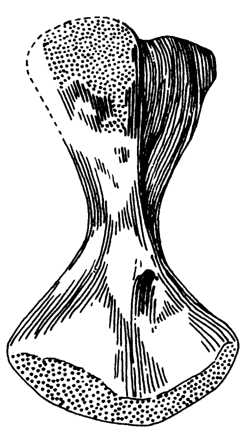
FIG. 17. *Procolophon trigoniceps* Owen. Oblique restoration of the pectoral girdle in AMNH 9506, showing the interrelationships of the constituent elements. Not to scale.

This is readily apparent in the shape of the humerus—a much heavier and broader bone than the humerus shown in Watson's figure. This bone in the Antarctic specimen (fig. 18) is generally of a form that would be expected in a primitive reptile humerus, with the proximal and distal ends widely expanded. There is, however, apparently less "twist" in the humerus, a feature that distinguishes the bone in many of the Procolophonia from the more primitive type of cotylosaurian humerus. Proximally the head of the humerus is rounded and heavy and set off from a prominent lateral tubercle. Distally there is an entepicondylar foramen, set within a prominent depression, but there appears to be no ectepicondylar foramen.

The ulna (fig. 19) is also a heavy bone, much heavier than the radius, and is expanded both proximally and distally. The radius also is expanded at each end, but its medial portion is rather slender.

Both forefeet are preserved, and they indicate that there probably was a full complement of carpal bones, but some of the proximal bones are not preserved (fig. 20). There is a well-developed row of five distal carpals articulating with the metacarpals, as shown in figure 21, and these may be interpreted as the four characteristic cotylosaurian distal elements, plus an ulnare. The fourth bone in the row of distal carpals articulates with both the fourth and fifth metacarpals, as would be expected. Lateral to this bone, and between the fifth metacarpal and the ulna is the large ulnare.

The heavy structure of the hands is especially noteworthy in the Antarctic *Procolophon*. This is apparent especially in the metacarpals and phalanges. The two innermost digits are very robust, and there is a progressive diminution in lateral dimensions of the bones as one proceeds toward the external side of the manus—as is clearly shown in figures 21 and 22. A *Procolophon* manus from Trollip Siding, near Rosmead, Cape Province, South Africa, is illustrated in figure 22 (the drawing was made from one of the latex casts of British Museum specimens lent us by Dr. Robinson). The African specimen is shown together with the manus of the Antarctic *Procolophon*, and the difference in the robustness of the bones comprising the manus of the two specimens is quite apparent. However such a difference is well within the range of individual, or perhaps sexual, variability of *Procolophon trigoniceps* from South Africa, as is shown by the partial manus of a specimen from Fern Rocks, Middleburg, Cape Province (BPI F. No. 2275) illustrated in figure 21. If Watson's speculation as to sexual dimorphism in the weight of the limbs in *Procolophon*, already mentioned, is valid, then the Antarctic specimen may be a male, as has been suggested in a previous paragraph. Certainly the heavy limbs and feet



AMNH 9506

FIG. 18. *Procolophon trigoniceps* Owen. Left humerus. Dorsal view. X2.

AMNH 9506

FIG. 19. *Procolophon trigoniceps* Owen. Left radius and ulna. Dorsal view. X2.

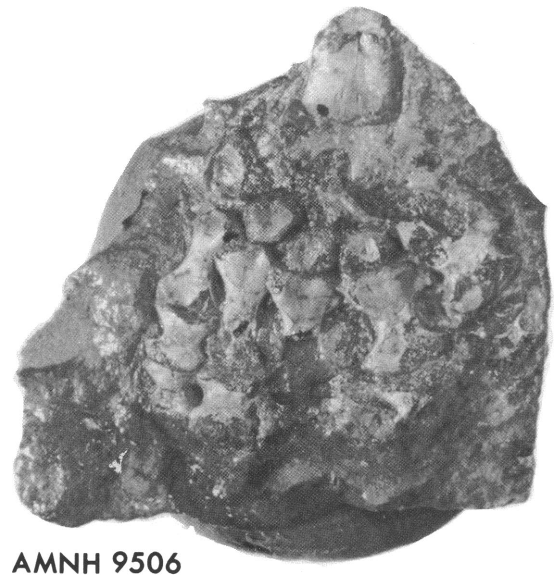


FIG. 20. *Procolophon trigoniceps* Owen. Right manus, ventral view. X3.

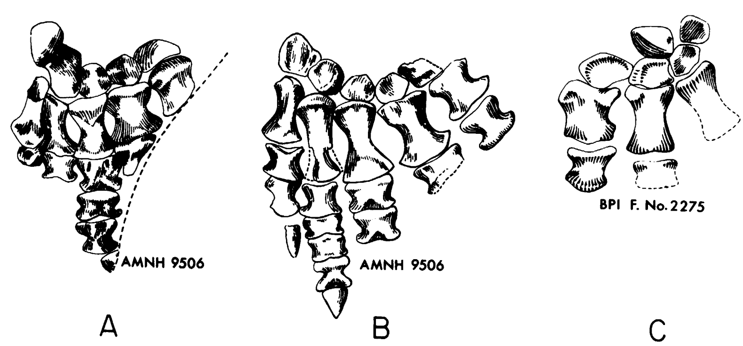


FIG. 21. *Procolophon trigoniceps* Owen. A. Left manus, ventral view. B. Right manus, dorsal view. C. Partial left manus from the Lower Triassic *Lystrosaurus* Zone, dorsal view. Note in all of these the very heavy internal digits. X2.

of the Antarctic specimen are no reason for considering it to be specifically different from the African form. Perhaps the broad inner digits represent an adaptation for digging more or less similar to the digging adaptations characteristic of the Cape Golden Mole *(Chrysochloris)*, or of some of the edentates.

SUMMARY OF COMPARISONS

It may be helpful to summarize briefly the manner in which the materials of *Procolophon* from Antarctica resemble or differ from the characteristic *Procolophon trigoniceps* from Africa.

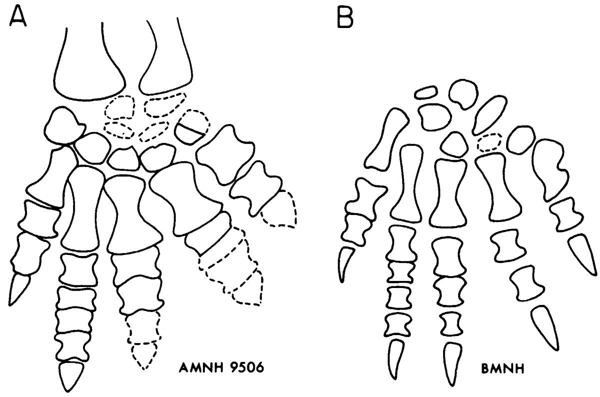


FIG. 22. *Procolophon trigoniceps* Owen. A. Restoration of right manus, from the Lower Triassic Fremouw Formation of Antarctica. B. Restoration of right manus of a slender-limbed individual in the British Museum (Natural History) from Trollip Siding near Rosmead, Cape Province, South Africa. Dorsal views. X2.

There seem to be no significant differences in size. The skeleton from Antarctica, AMNH 9506, apparently represents a partially grown individual, perhaps half as large as the largest *Procolophon* from Africa. That the Antarctic specimen probably is not fully adult is indicated by the small size of the quadratojugal "horns" which are small—even smaller than in the specimen figured by Watson. An interesting difference between the Antarctic specimen and the African specimen shown in Watson's figure is the relatively smaller skull of the former. One might suppose that such skull characters represent a female, but the heaviness of the limbs and feet in the Antarctic skeleton favor its identification as a male. Certainly these heavy limbs and feet cannot be used to separate the Antarctic fossil from the African *Procolophon trigoniceps*, because, as has been shown, African materials contain individuals with extremities fully as heavy as the Antarctic *Procolophon.* The elongated orbits in the Antarctic *Procolophon* are perhaps somewhat narrower than in large African skulls, but this is almost surely a factor of growth; the lateral expansion of the jugal region in *Procolophon* leads to some broadening of the orbits in their posterior portions.

There are some minor differences in the dentition between the Antarctic and some African specimens. For example, the premaxillary teeth are of about equal size and the first maxillary tooth is large and chisel-shaped in the Antarctic specimen, as contrasted with relatively smaller posterior premaxillary teeth and a peglike first maxillary tooth in certain African specimens. But these characters are not uniform in African fossils, so it seems evident that the differences are readily explained on the basis of individual variability.

The scapula is perhaps not quite so rhomboidal in the Antarctic *Procolophon* as in *Procolophon* from Africa. Likewise, the coracoids are seemingly somewhat more rounded in the Antarctic specimen than is shown in Watson's figure. But again, these are probably characters showing individual variation, perhaps affected in the Antarctic *Procolophon* by growth factors.

All the differences outlined above are of small import, and taken in conjunction with other characters they indicate, in our judgment, that no valid specific differences are to be seen between the specimens of *Procolophon* from Antarctica and the well-known fossils of *Procolophon trigoniceps* from Africa. The Antarctic *Procolophon*, like the African fossils, shows a restricted squamosal bone, a heavy pterygoid, a

TABLE 1
COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF *PROCOLOPHON TRIGONICEPS*

	AMNH 9506	AMNH 9507	AMNH 5693	From Watson (Figure)	BPI 4248[a]	
Skull						
Length	39.5	–	41.0	50.0	84.0	
Greatest width	41.0	–	39.5	57.0	108.5	
Width across quadrates	38.0	–	34.0	–	–	
Preorbital length	16.0	–	15.0	18.0	32.0	
Orbital length	16.5	–	14.7	18.4	33.0	
Breadth of palate	–	–	–	–	–	
						BMNH specimen
Mandible						
Length of ramus	32.0	32.5	33.0	44.0	63.0	45.0
Depth of ramus at last tooth	4.9	5.0	7.0	8.0	–	10.0
Presacral vertebrae						
Length	126.0	–	–	154.0	–	
Length of dorsals 10-20	60.0	–	–	70.0	–	
Humerus						
Length	20.5	–	–	32.0	–	
Distal breadth	13.8	–	–	13.0	–	
Radius						
Length	15.0	–	–	21.0	–	
					BPI F. No. 2275	
Metacarpals						
1st, length	4.3	–	–	5.6	4.9	4.7
Distal breadth	3.7	–	–	3.0	3.8	2.4
4th, length	5.9	–	–	7.2	–	6.5
Distal breadth	3.1	–	–	2.8	–	2.9

[a]From photograph.

broad interpterygoid vacuity, a forward position of the quadrate-articular joint, palatine and vomerine teeth, broad neural arches in the vertebrae, short neural spines, flaring ribs with essentially single-headed articulations, and short, cotylosaurian limbs.

Therefore the fossils of *Procolophon* from Antarctica are here identified as *Procolophon trigoniceps*.

Procolophon and Gondwanaland

If our identification of *Procolophon* from Antarctica is valid `(and we believe we have presented ample evidence to support validity), some significant paleogeographic implications must follow. *Procolophon trigoniceps* most assuredly was a reptile of thoroughly terrestrial habits, ecologically comparable with some of the modern lizards. Consequently the presence of a single species of a small land-living reptile in the Lower Triassic sediments of Antarctica and South Africa is presumptive evidence of a land connection between these two regions in early Triassic time. In view of the known geological and geophysical evidence, such a land connection very probably took the form of a ligation binding contiguous land masses that are now widely

TABLE 2
COMPARATIVE RATIOS AND INDEXES OF *PROCOLOPHON TRIGONICEPS*

	AMNH 9506	From Watson (Figure)	BPI 4248	
$\frac{\text{Skull length}}{\text{Skull width}} \times 100$	104	114	129	
$\frac{\text{Orbital length}}{\text{Skull length}} \times 100$	42	49	39	
$\frac{\text{Mandible}}{\text{Skull length}} \times 100$	81	88	75	
$\frac{\text{Skull length}}{\text{Presacral length}} \times 100$	31	28	–	
$\frac{\text{Humerus length}}{\text{Distal breadth}} \times 100$	67	40	–	
			BPI F. No. 2275	BMNH specimen
$\frac{\text{Metacarpal 1, length}}{\text{Breadth}} \times 100$	86	54	78	51
$\frac{\text{Metacarpal 4, length}}{\text{Breadth}} \times 100$	53	39	–	45

separated from each other. In short, *Procolophon trigoniceps* inhabited a range during early Triassic time that encompassed at least the southern portion of Africa and East Antarctica.

If Antarctica and Africa are joined according to a reconstruction of Gondwanaland that is widely accepted–that is, with the area of the Weddell Sea and the Princess Martha Coast of Antarctica contiguous with the border of southeastern Africa from the region of Durban to Mozambique–the localities at which *Procolophon trigoniceps* has been found in Antarctica and Africa are brought within about 2400 km. of each other. This is not out of line with the range of a single species of a small reptile. For example, the collared lizard of North America has a distribution extending from California almost to the Mississippi River below St. Louis in one direction, and from Oregon to northern Mexico in the other. This may be translated into a west to east range of about 3000 km. and a north to south range of about 2300 km.

Furthermore, such a distribution as adduced for *Procolophon trigoniceps* is in accord with the distributions of the Lower Triassic dicynodonts, *Lystrosaurus murrayi* and *Lystrosaurus curvatus*, recently described from Antarctica (Colbert, 1974).

Procolophon trigoniceps in Antarctica supplements and reinforces the evidence of two species of *Lystrosaurus* to indicate the continuous distributions of tetrapod species across parts of a former Gondwanaland that now are far apart. Moreover, the presence of *Procolophon trigoniceps* in Antarctica and Africa, taken in conjunction with similar distributions for *Lystrosaurus* (Colbert, 1974) and labyrinthodont amphibians (Colbert and Cosgriff, 1974), as well as for other Lower Triassic tetrapods yet to be described, affords us the view of a well-

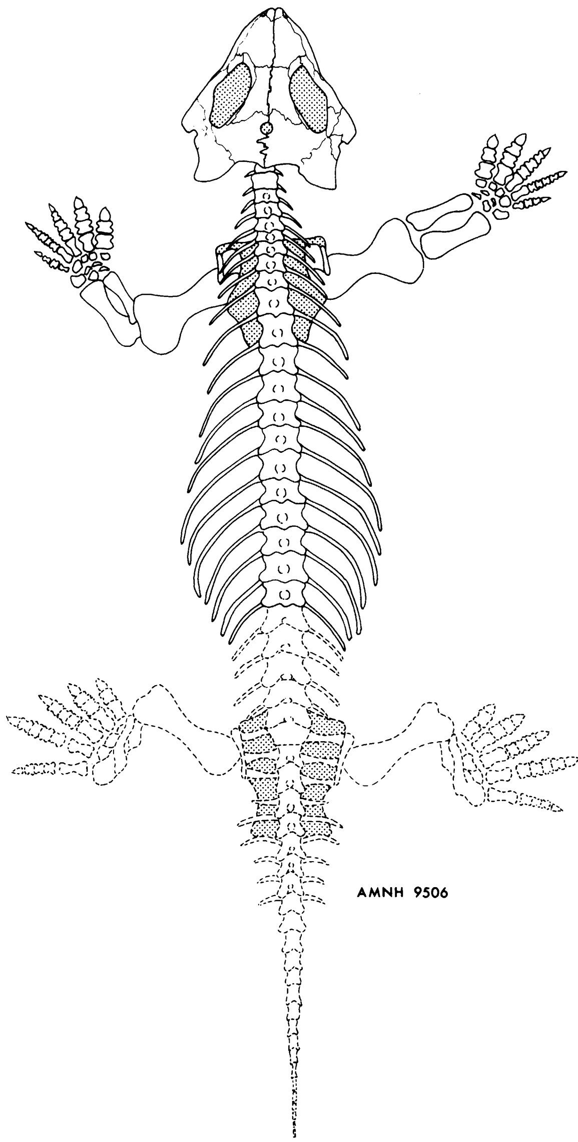


FIG. 23. *Procolophon trigoniceps* Owen. Restoration of skeleton from the Lower Triassic Fremouw Formation of Antarctica. X½.

defined tetrapod assemblage—the *Lystrosaurus* fauna—extending across a considerable extent of Gondwanaland.

How extensive the distribution of the *Lystrosaurus* fauna might have been during early Triassic time is a problem still to be resolved. None of the elements of the *Lystrosaurus* fauna have been found in South America, but this negative evidence may be due to the accidents of preservation and discovery. Some of the representatives of the *Cynognathus* fauna, the Lower Triassic tetrapod assemblage immediately above the *Lystrosaurus* Zone in South Africa, have been discovered in Argentina. So there is good

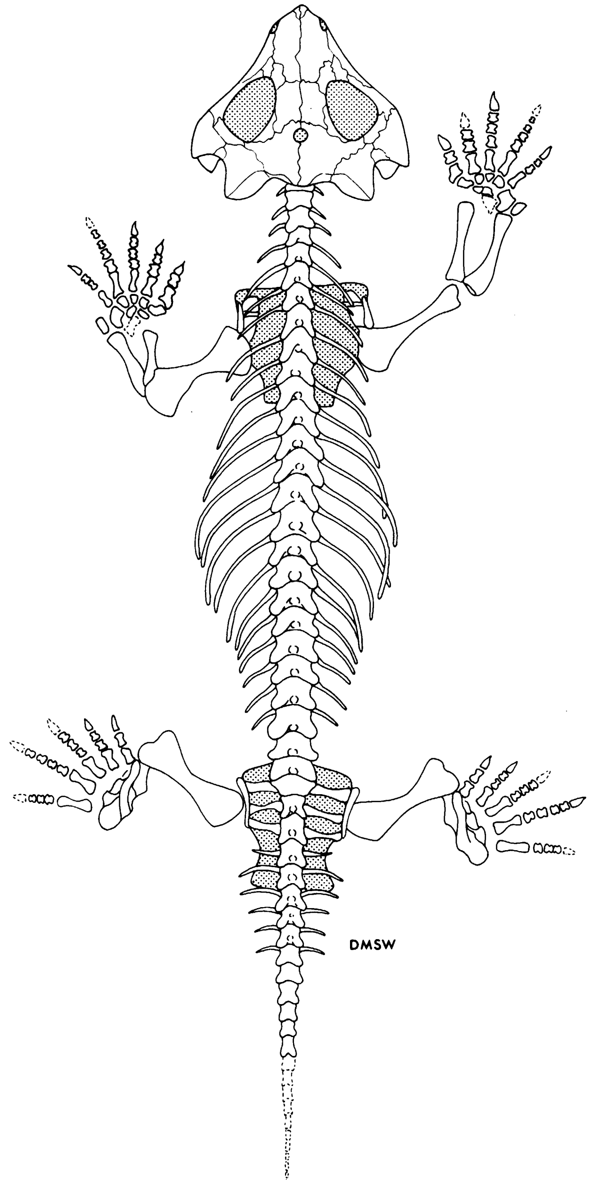


FIG. 24. *Procolophon trigoniceps* Owen. Restoration of skeleton, modified from D. M. S. Watson, from the Lower Triassic *Lystrosaurus* Zone of South Africa. X½.

reason to think that the *Lystrosaurus* fauna eventually may be discovered in South America.

Lystrosaurus and some other members of the *Lystrosaurus* fauna occur in India and in China. But *Procolophon* has not been found in these regions. Young (1957) described a procolophonid, *Neoprocolophon asiaticus*, from the Lower Triassic sediments of Shansi. Although this form, based on a single incomplete skull and jaw, is evidently close to *Procolophon*, Young was probably correct in assigning it to a separate genus. For one thing, the quadratojugal "horns" are much farther forward than they are in *Procolophon.*

Perhaps *Neoprocolophon* is a derivative genus descended from *Procolophon* as a migrant into early Triassic Laurasia, or even into a far corner of Gondwanaland, if one accepts the inclusion of a part of eastern Asia within Gondwanaland, as has been suggested by Hurley (1971) and Hurley et al. (1971).

In this connection mention should be made of a recent paper by Bartholomai and Howie (1970) describing a Lower Triassic vertebrate assemblage from Queensland, Australia. One of the specimens figured by these authors and identified by them as questionably a paliguanid reptile has the appearance of the front of a *Procolophon* skull and jaw. The possible extension of the range of *Procolophon* to the Australian segment of Gondwanaland is interesting but not surprising.

There is still much to be learned about the distribution of *Procolophon* as a constituent member of the *Lystrosaurus* fauna within Gondwanaland. In the meantime the presence of *Procolophon trigoniceps* in the Lower Triassic Fremouw Formation of Antarctica and in the Middle Beaufort *Lystrosaurus* Zone of South Africa offers evidence, additional to that already set forth, to demonstrate a faunal unity within the Antarctic-African portion of Gondwanaland during early Triassic time.

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