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ABSTRACT

Labyrinthodont amphibians from the Lower Triassic Fremouw Formation of Antarctica are described. These consist of a fragment of a lower jaw collected at Graphite Peak in the Transantarctic Mountains in December, 1967, and various fossils from Coalsack Bluff (west of the Beardmore Glacier and some 140 km., or about 88 miles, northwest of Graphite Peak) during the austral summer of 1969-1970 and from near the junction of the McGregor and Shackleton Glaciers (about 100 km., or 60 miles, more or less, to the east and a little south of Graphite Peak) during the austral summer of 1970-1971. Two new genera and species are described. *Austrobrachyops jenseni* is a brachyopid showing resemblances to *Batrachosuchus* from the Lower Triassic of South Africa and to *Hadrokkosaurus* from the Middle Triassic of North America. *Cryobatrachus kitchingi* is a lydekkerinid related to *Lydekkerina* and *Limnoiketes* from the Lower Triassic of South Africa. In addition an isolated tabular bone from Coalsack Bluff represents a temnospondyl amphibian of possible capitosaurid or benthosuchid relationships. These fossils supplement the evidence of reptiles collected from the Fremouw Formation, to indicate a probable linkage between Antarctica and South Africa and paleozoogeographic relationships between Antarctica and other parts of Gondwanaland and even of Laurasia.

INTRODUCTION

The first fossil of a Triassic tetrapod found in Antarctica was discovered December 28, 1967, by Dr. Peter J. Barrett, then of the Institute of Polar Studies, The Ohio State University, Columbus, now of Victoria University, Wellington, New Zealand. The specimen, consisting of a fragment from a left mandibular ramus of a labyrinthodont amphibian, was collected in the Fremouw Formation, of early Triassic age, as exposed on the slopes of Graphite Peak in the Transantarctic Mountains, about 400 miles from the South Pole.

The specimen was submitted to the senior author for identification, and it has been described and figured in previous papers (Barrett, Baillie, and Colbert, 1968; Colbert, 1971c). It represents a rather large labyrinthodont amphibian

which, following further comparative studies, is identified in the present paper as a brachyopid.

The discovery of this specimen—an accidental event tangential to Barrett's study of the geology of the Transantarctic Mountains in the general region of the Beardmore Glacier—was the stimulus for a program of vertebrate paleontological collecting in Antarctica. An expedition under the auspices of the Institute of Polar Studies of The Ohio State University and the National Science Foundation went to the Beardmore Glacier area during the austral summer of 1969-1970 for the express purpose of searching for and collecting fossil tetrapods of Triassic age. Fossils were collected at Coalsack Bluff, about 35 miles east of the Beardmore Glacier during this field season. A second expedition during the austral summer of 1970-1971 collected fossils near the confluence of McGregor and Shackleton glaciers, some 90 miles or so west of the Beardmore Glacier, and about 60 miles west of the original discovery site at Graphite Peak. Amphibians were collected at both localities.

The purpose of the present paper is to give preliminary lists and descriptions of the fossil amphibians collected in Antarctica up to now.

The first season of field work at Coalsack Bluff was carried on by the senior author with William Breed of the Museum of Northern Arizona, Flagstaff; James A. Jensen of Brigham Young University, Provo, Utah; and Jon S. Powell of the University of Arizona, Tucson. The second season of field work at McGregor and Shackleton glaciers was done by James W. Kitching of the Bernard Price Institute of Palaeontology, University of the Witwatersrand, Johannesburg, Union of South Africa; with John Ruben of the University of California, Berkeley; and briefly Thomas Rich, then of Columbia University, New York. Both paleontological parties were sections of larger geological study units all under the leadership of David H. Elliot of the Institute of Polar Studies of The Ohio State University, Columbus. The work was done under the auspices of the National Science Foundation of the United States of America.

The fossils described herein were prepared by

Mr. David Lawler and Miss Camas Lott. The drawings (figs. 1-11, 13) were made by Miss Pamela Lungé of the Museum of Northern Arizona and Mr. William E. Loechel of the School of Medicine, Wayne State University. The photographs were made by Mr. Marc Gaede of the Museum of Northern Arizona. The work was supported in part by a grant from the National Science Foundation, no. GV-25431.

Abbreviations for Illustrations

Ang, angular
 c, corpus of the pterygoid
 cr. bpt, basiptyergoid crest
 cr. spt, suprapterygoid crest
 ept, platform for the epiptyergoid; broken base of the epiptyergoid
 F, frontal
 f.st, stapedial fossa
 fa. a, articular facet
 fo.ra., retroarticular fossa
 Ip, interparietal
 J, jugal
 L, lacrimal
 Mx, maxilla
 N, nasal
 P, parietal
 p. b, posterior border of the pterygoid corpus
 p. ra, retroarticular process
 p.b. eo, basal process of the exoccipital, sutural surface on the pterygoid for the basal process of the exoccipital
 Pa, prearticular
 Pin, pineal
 Pmx, premaxilla
 Po, postorbital
 Pof, postfrontal
 Prf, prefrontal
 Qj, quadratojugal
 r. as, ascending ramus of the pterygoid
 r. c, conical recess
 r. pl, palatal ramus of the pterygoid
 r. qu, quadrate ramus of the pterygoid
 s.a. ca, sulcus for the internal carotid artery
 Sa, surangular
 Smx, septomaxilla
 Sq, squamosal
 St, supratemporal
 T, tabular

STRATIGRAPHIC RELATIONSHIPS

The stratigraphic relationships of the Fremouw Formation at Coalsack Bluff and in the

McGregor-Shackleton Glacier region have been outlined in previous contributions on Antarctic Triassic fossils (Elliot, Collinson, and Powell, 1972, pp. 387-392; Colbert, 1974, pp. 5-12). Suffice it to say that the Fremouw beds, the lowest of the Mesozoic units in the Transantarctic Mountains, are composed of sandstones, shales, and siltstones of varying consistency and composition as is characteristic of freshwater continental deposits.

The sediments at Coalsack Bluff and at McGregor-Shackleton glaciers are cyclic, consisting of coarse, almost conglomeratic channel deposits at the base (Coalsack Bluff fossil beds) and fine floodplain deposits at the top (Mount Kenyon fossil beds), with intergradations between. The bedding-plane exposures of fine-grained sediments at McGregor and Shackleton glaciers account for the prevalence of skeletons or partial skeletons at this locality, as contrasted with the isolated bones found at Coalsack Bluff.¹

Thus we see the indications of two different habitats, at Coalsack Bluff and Shackleton Glacier, and these differences bear on the nature of the fossils. So far as the fossils are concerned, the differences as mentioned above are those between isolated bones and articulated specimens—the former easily freed from the somewhat coarse and friable sands containing them, the latter firmly enclosed in their matrices.

DESCRIPTIONS OF FOSSILS

CLASS AMPHIBIA

SUBCLASS LABYRINTHODONTIA

ORDER TEMNOSPONDYLI

SUPERFAMILY BRACHYOPOIDAE

FAMILY BRACHYOPIDAE

Brachyopids form a distinctive group of the Temnospondyli, highly specialized in certain features of cranial anatomy. Genera included in the

¹We are indebted to Professor James W. Collinson of The Ohio State University, for clarification of the sedimentary characters of the Fremouw Formation, as based on his studies in Antarctica. This corrects the discussion in Colbert (1974, pp. 2 and 11), in which it was implied that the differences in the fossils collected at the two Antarctic localities was due to local sedimentary differences rather than stratigraphic distinctions.

family range from the Late Permian into and probably through the Middle Triassic and encompass an exceptionally large geographic range. With the addition of the new material from Antarctica described below the family is now known from fossil assemblages on every continent, except South America. It has been extensively described, reviewed, and revised three times in recent years—by Watson (1956), Welles and Estes (1969), and Cosgriff (1969). These authors all discuss the contents of the family, its diagnostic morphologic characters, evolutionary relationships among the various genera and species, and stratigraphic and geographic occurrences.

Contents of the Family

The taxonomic history of the Brachyopidae has been complex but the above cited authors concur in recognizing a central core of genera that is clearly distinct in morphology from other labyrinthodont groups. This central core, expanded by Cosgriff (1969) from Watson (1956), includes: *Brachyops laticeps* Owen, 1855, from the Lower Triassic Panchet beds near Mángali in Central India; *Tracheosaurus (Bothriceps) major* (Woodward, 1909) (referred to *Bothriceps australis* by Welles and Estes, 1969), from the Upper Permian Lithgow Coal Measures of New South Wales, Australia; *Bothriceps australis* Huxley, 1859, of uncertain provenance but probably also from the Lithgow Coal Measures; *Blinasaurus (Platyceps) wilkinsoni* (Stephens, 1887) from the Lower Triassic Gosford Formation of New South Wales; *Blinasaurus henwoodi* Cosgriff, 1969, from the Lower Triassic Blina Shale of Western Australia; *Batrachosuchus browni* Broom, 1903, and *Batrachosuchus watsoni* Haughton, 1925, from the Lower Triassic *Cynognathus* Zone of South Africa; *Hadrokkosaurus bradyi* Welles, 1947 (see also Welles and Estes, 1969) from the Middle Triassic Holbrook Member of the Moenkopi Formation of Arizona; and *Boreosaurus thorslundi* Nilsson, 1943, from the Lower Triassic Sticky Keep Formation of Spitzbergen. Welles and Estes (1969) also included *Batrachosuchus lacer* Shishkin, 1966, from the Lower Triassic Federov Horizon of European Union of Soviet Socialist Republics, and *Batrachosuchus* sp. from the *Cynognathus* Zone of South Africa, but excluded *Boreosaurus thorslundi*.

Two recent additions to the family from the Lower Triassic of Australia are: *Brachyops allos* Howie, 1971, from the Rewan Series of Queensland; and *Blinasaurus townrowi* Cosgriff (In press) from the Knocklofty Formation of Tasmania. The former species is based on a single skull and the latter on a fairly extensive hypodigm of skull, lower jaw, and postcranial material.

The new material from the Fremouw Formation that can be allocated to the Brachyopidae with certainty includes the original jaw fragment (AMNH¹ 9301) from Graphite Peak and an isolated pterygoid bone (AMNH 9346) from Coal-sack Bluff. The latter specimen is the more adequate for comparative purposes; it is distinct enough in several of its features to be nominated the holotype of a new genus and species. The former is listed with question as a referred specimen of the new taxon.

AUSTROBRACHYOPS, NEW GENUS

Etymology. Austro, from Latin australis = south; brachy from Greek brachys = short; ops, from Greek ops = face.

Diagnosis. A brachypoid in which the posterior edge of the ascending ramus of the pterygoid bone possesses a distinct angle in the middle of its course, giving the stapedial fossa a quadrangular shape. This angle on the ascending ramus is surmounted by a longitudinal suprapterygoid crest. The ventrolateral corner of the stapedial fossa is incised by a groove for the internal carotid artery. The posterior border of the pterygoid corpus is diagonal to the skull midline.

Type. *Austrobrachyops jenseni*, new species.

Austrobrachyops jenseni, new species

Etymology. Named in honor of Dr. James Jensen who found the type specimen.

Holotype. AMNH 9346, a left pterygoid bone lacking only a small part of its palatal ramus and its posterolateral corner and including the broken base of the epipterygoid bone fused to its dorsal surface.

Referred Specimen. AMNH 9301, a fragment of the articular region of a left lower jaw ramus

¹ AMNH, the American Museum of Natural History, New York.

is questionably referred to the species. It includes parts of the articular facet, the labial wall of the adductor fossa, and the retroarticular process that are formed by the articular, angular, surangular, and prearticular bones. Although it definitely derives from a brachyopid it was collected from a different locality than the holotype and means are lacking for a clear establishment of homotaxy between the two specimens.

Horizon. Lower part of the Fremouw Formation, Lower Triassic.

Locality. Coalsack Bluff, Transantarctic Mountains, at approximately latitude $84^{\circ} 15' S$, longitude $162^{\circ} 20' E$, for the type. Graphite Peak, Transantarctic Mountains, at approximately latitude $85^{\circ} 02' S$, longitude $172^{\circ} 30' E$, for the referred specimen. Antarctica.

Diagnosis. Same as for genus.

DESCRIPTION AND DISCUSSION

General Morphology of Brachyopid Pterygoid Bone

Detailed comparisons have been made between the holotype and pterygoids of *Batrachosuchus* sp. and of *Hadrokkosaurus bradyi*, two forms for which isolated pterygoid bones are also known. Two fragmentary right pterygoids (figs. 1, 3, 4) are included in a collection of disarticulated cranial and postcranial material made by C. L. Camp in the *Cynognathus* Zone at Bethal Farm in 1936. All of this material is numbered UCMP¹ 42856 and some of it, including skull fragments, vertebrae, and a humerus was described by Welles and Estes (1969, pp. 47-51, figs. 23-25). An isolated left pterygoid of *Hadrokkosaurus bradyi* (figs. 2, 6, 9) was collected at the Holbrook Quarry in the Moenkopi Formation, is numbered UCMP 36247, and was figured by Welles (1947, fig. 9).

The pterygoid bone of the Brachyopidae is a distinctive element that differs profoundly in overall shape and in the development of certain of its processes from the pterygoids of such "normal" temnospondyl families as the Benthosuchidae (Bystrov and Efremov, 1940, fig. 9), Capitosauridae (see, for example Watson, 1919,

figs. 11-16; Welles and Cosgriff, 1965, fig. 43), Metoposauridae (Wilson, 1941, figs. 1, 2), and Trematosauridae (Säve-Söderbergh, 1936, figs. 7, 9, 12, 15, 16, 20, 34, 37, 43). Fortunately, it is also a particularly massive element, resistant to erosion, which accounts for its having been found isolated for three different species.

The position of the pterygoid on the palatal and occipital surfaces of the skull of *Hadrokkosaurus bradyi* is shown in figure 11 (adapted from Welles and Estes, 1969, figs. 26b, 27c; pls. 1b, 2c). This view of the skull is also given for *Batrachosuchus watsoni* (*ibid.*, figs. 17b, 17d), for *Brachyops laticeps* (*ibid.*, figs. 15b, 15c), for *Bothriceps australis* (*ibid.*, figs. 16b, 16c), for *Batrachosuchus watsoni* (Watson, 1956, figs. 6, 7), for *Blinasaurus henwoodi* (Cosgriff, 1969, figs. 5a, b, 7a, b), and for *Brachyops allos* (Howie, 1971, figs. 1b, 2a; pls. XIVb, XVa). As shown in all of these, the pterygoid consists of a main portion that occupies most of the postero-lateral area of the palate and an ascending ramus that arises from the dorsal surface of the main portion and is exposed in greatest relief on the occipital surface. It is the posterior edge of this ascending ramus that is termed the "parotic part of the pterygoid" by Watson in his illustrations of *Batrachosuchus watsoni*, but consideration of the entire structure on the isolated pterygoid bones and comparison of these with pterygoids of species of other labyrinthodont families clearly shows that this "parotic part" is the highly modified and specialized homologue of the structure commonly termed the ascending ramus.

The main portion of the bone consists of three confluent areas—the corpus, the quadrate ramus, and the palatal ramus—all best delineated on the palatal surface.

The corpus forms the central part of the bone, lies on a horizontal plane parallel to the surface of the skull table, and is firmly joined on its medial edge by a long suture with the corpus of the parasphenoid bone that reaches from the interpterygoid vacuity to the posterior edge of the palatal surface. The posterior border of the corpus which lies lateral to this pterygoid-parasphenoid suture is invariably roughly straight but lies at a variable angle to the midline of the skull. The variation in this angle between species is a

¹ UCMP, University of California Museum of Paleontology, Berkeley.

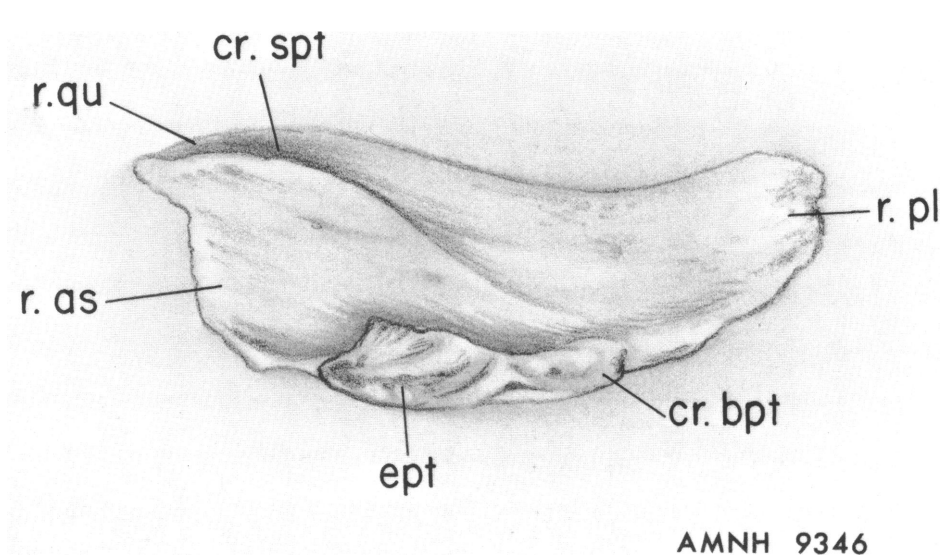


FIG. 1. *Austrobrachyops jenseni*, new genus and species. AMNH 9346, type, left pterygoid, dorsal view. X 1.

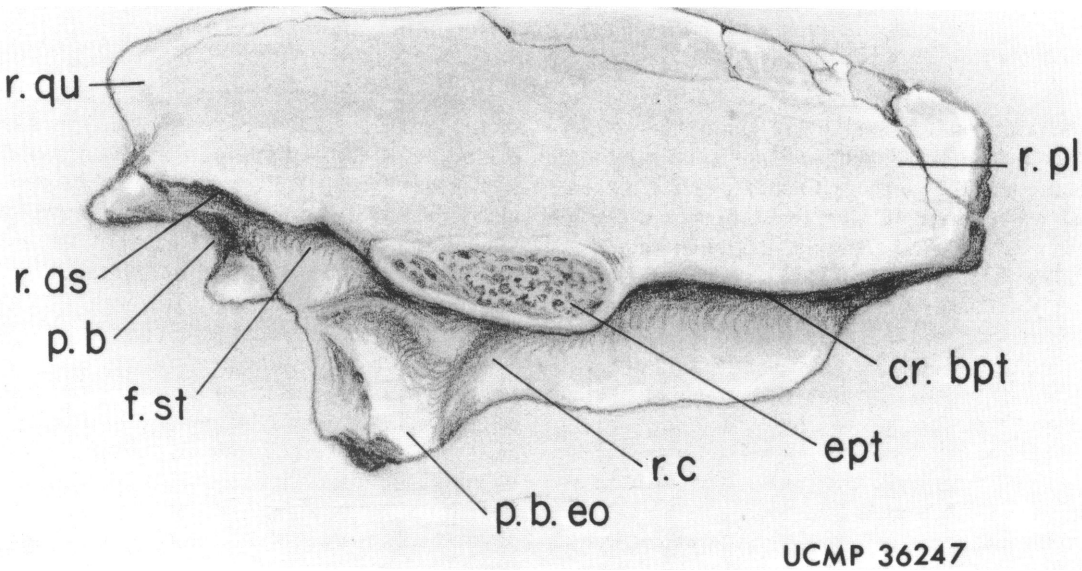


FIG. 2. *Hadrokkosaurus bradyi* (Welles). UCMP 36247, left pterygoid, dorsal view. X 1.

taxonomic character to be considered in the following comparative section.

The quadrate ramus, which lies lateral to the corpus, is typically bent down at a 45-degree angle to the plane of the corpus. This deflection is a

well-marked feature on all brachyopid pterygoids and one that is diagnostic of the family as a whole. The quadrate ramus forms the medial edge of the subtemporal fossa and its posteroventral corner is fused to the inner surface of the

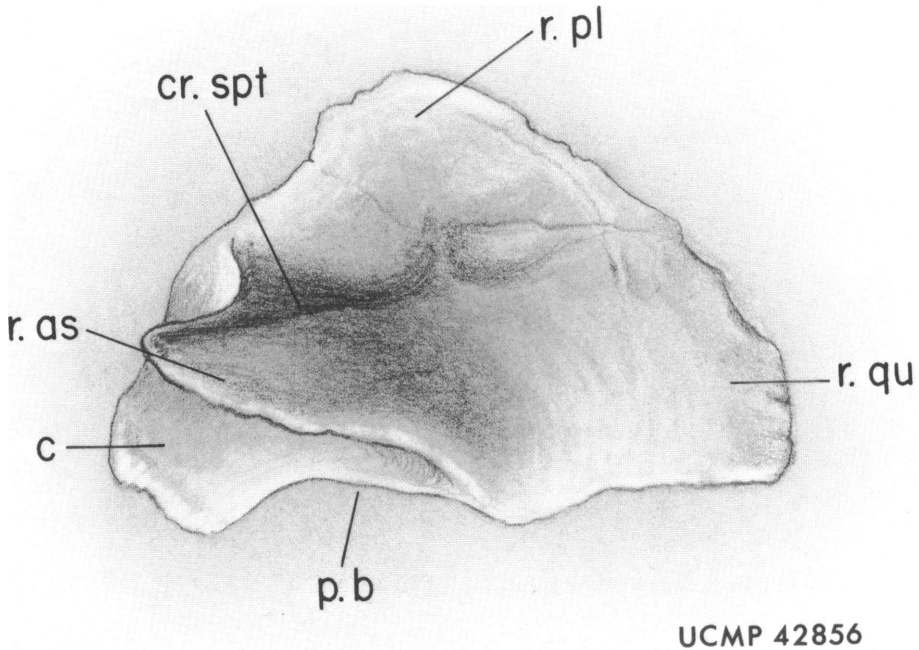


FIG. 3. *Batrachosuchus* sp. Composite illustration, made from two right pterygoids, both numbered UCMP 42856. Dorsal view. $\times 1$.

quadrate bone. In the living animal the entire outer surface of the ramus was overlapped by the palatoquadrate cartilage that extended between and was continuous with the two visceral ossifications of the skull-quadrate and epipterygoid.

The palatal ramus is an anterior extension of both the corpus and the quadrate ramus, continuing the horizontal attitude of the former on its inner portion and the ventrolateral slope of the latter on its outer portion. It forms part of the anteromedial border of the subtemporal fossa and part of the posterolateral border of the interpterygoid vacuity. Anteriorly it is sutureally joined to the ectopterygoid bone.

The ascending ramus of the pterygoid is one of the most diagnostic and characteristic features of the brachyopid skull. The dorsal, occipital, and medial views of the isolated pterygoid bones (figs. 1-10) show details of the construction of this ramus that are not visible on complete skulls described in the literature.

In dorsal view the ascending ramus is a massive, rounded structure that covers the entire dorsal surface of the corpus. The anteromedial area

of the ramus is a flat platform to which the base of the epipterygoid (partly retained in AMNH 9346) was fused. Anterior to this epipterygoid platform in two of the species (*Austrobrachyops jenseni* and *Hadrokkosaurus bradyi*) a high wall of bone runs forward toward the posterior edge of the interpterygoid vacuity. This wall of bone, here termed the basipterygoid crest, is parallel and just lateral to the pterygoid-parasphenoid suture. The dorsal surface of the pterygoid slopes gently and evenly away from the basipterygoid crest on its lateral side but drops sharply down to the pterygoid-parasphenoid suture on its medial side. In the living animal the basipterygoid crest undoubtedly marked the medial edge of the portion of the pterygoid that was overlapped by the palatoquadrate cartilage.

In occipital view the ascending ramus is deeply excavated by the stapedial fossa for which it forms an anterior wall and an overhanging roof. The floor of the fossa is excavated into the dorsal surface of the corpus. The posterior edge of the roof portion of the ascending ramus describes an arc from the angle where the quad-

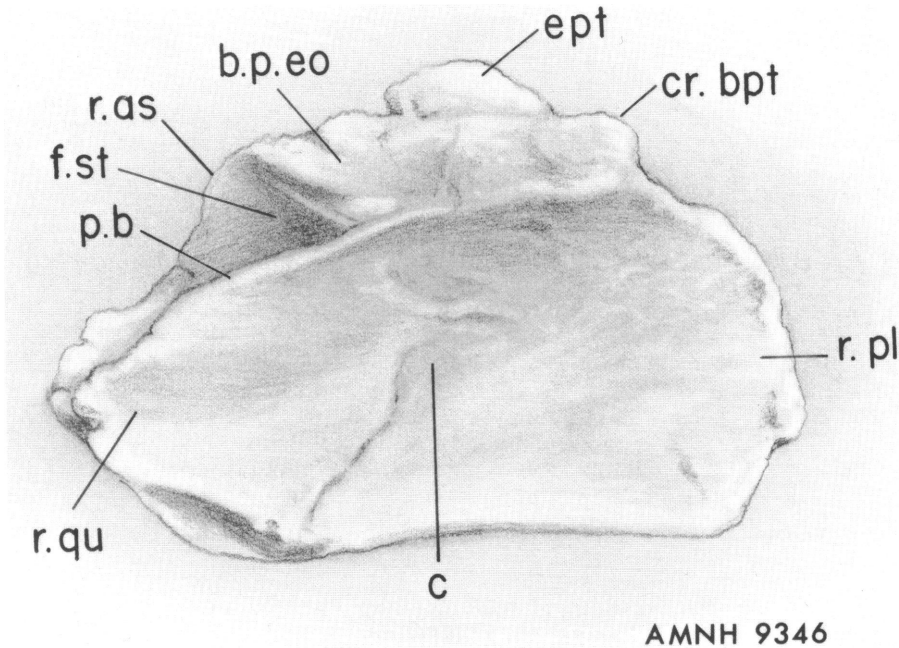


FIG. 4. *Austrobrachyops jenseni*, new genus and species. AMNH 9346, type, left pterygoid, ventral view. X 1.

rate ramus joins the corpus to a broad sutural area where it is fused to the basal process of the exoccipital bone.

In medial view the only important feature is the broad, flat sutural surface for the exoccipital basal process. This sutural surface, which is nearly vertical, is continuous anteriorly with the vertical surface of the area beneath the epipterygoid platform and the steep medial side of the basiptyergoid crest.

Particular Features of *Austrobrachyops jenseni*, AMNH 9346

The pterygoid bone from Coalsack Bluff is somewhat battered and chipped on all edges, damaged probably during water transport prior to burial. The only sizable portions that are missing, however, are the posterolateral corner of the quadrate ramus (the area in contact with the quadrate bone), part of the anterior edge of the palatal ramus (the area suturally joined to the ectopterygoid bone), and the anterior part of the basiptyergoid crest.

As seen in posterior view (fig. 8), the quadrate

ramus is strongly deflected ventrolaterally in typical brachyopid fashion, and the ascending ramus is deeply excavated by the stapedial fossa. The ascending ramus is massive as in other brachyopids but is unusual in that its posterior edge has a pronounced angle near its center. In consequence of this angularity the stapedial fossa is quadrangular rather than hemispherical as in other species of the family.

A large sulcus is incised into the angular junction of the ascending ramus with the dorsal surface of the corpus on the lateral edge of the stapedial fossa. This sulcus, probably for a portion of the internal carotid artery, runs forward along the edge of the stapedial fossa to end anteriorly near the triple junction of pterygoid, parasphenoid, and exoccipital. At this point it enters a foramen that, presumably, carried the internal carotid forward through a canal in the pterygoid to anterior parts of the braincase.

The angle on the middle of the posterior edge of the ascending ramus is surmounted by a sharp-edged ridge, best seen in dorsal view (fig. 1), that runs forward along the top of the ascend-

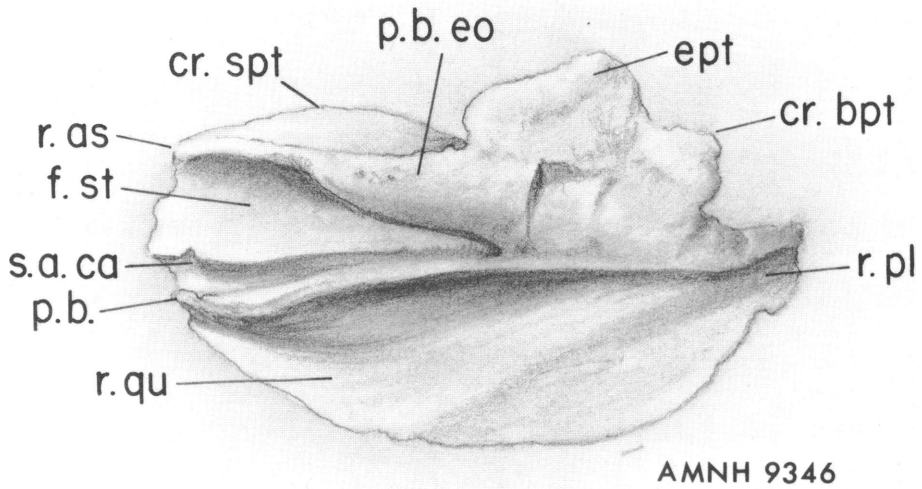


FIG. 5. *Austrobrachyops jenseni*, new genus and species. AMNH 9346, type, left pterygoid, medial view. $\times 1$.

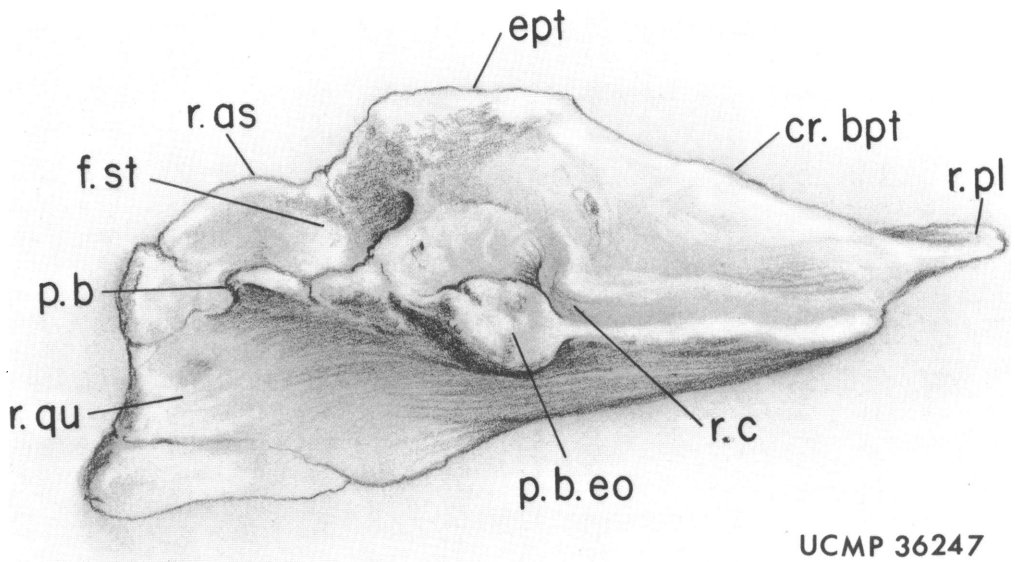
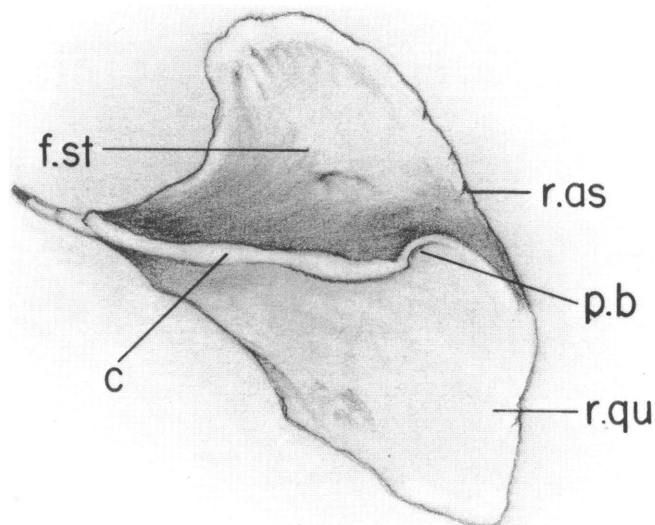


FIG. 6. *Hadrokkosaurus bradyi* (Welles). UCMP 36247, left pterygoid, medial view. $\times 1$.

ing ramus to end just medial to the base of the epipterygoid. This ridge, here termed the supra-ptyergoid crest, was probably in contact with the underside of the skull roof and probably served to brace the pterygoid during feeding activities.

In medial view (fig. 5) the sutural surface for the exoccipital basal process is triangular, with a

posteriorly pointed apex. Anterior to the sutural surface the vertical wall beneath the epipterygoid platform is quite damaged, and it cannot be determined if a conical recess for the basiptyergoid process of the basisphenoid, a feature usually present in labyrinthodonts, was excavated into the substance of the pterygoid. Anterior to



UCMP 42856

FIG. 7. *Batrachosuchus* sp. Composite illustration made from two right pterygoids, both numbered UCMP 42856. Medial view. $\times 1$.

this area only the posterior part of the basiptyergoid crest is retained and this, too, is very battered and chipped.

The broken base of the epiptyergoid is fused onto its platform but is too incomplete to give any indication of the original shape of the bone. The dimensions of the part preserved, however, suggest that the epiptyergoid was relatively much larger than in other labyrinthodont families.

In ventral view (fig. 4) the most notable feature is the course of the posterior edge of the corpus. It is straight but markedly diagonal to the midline of the original complete skull. It begins laterally at the angle between the corpus and the quadrate ramus and runs anteromedially to end just beneath the sutural surface for the exoccipital on the ascending ramus.

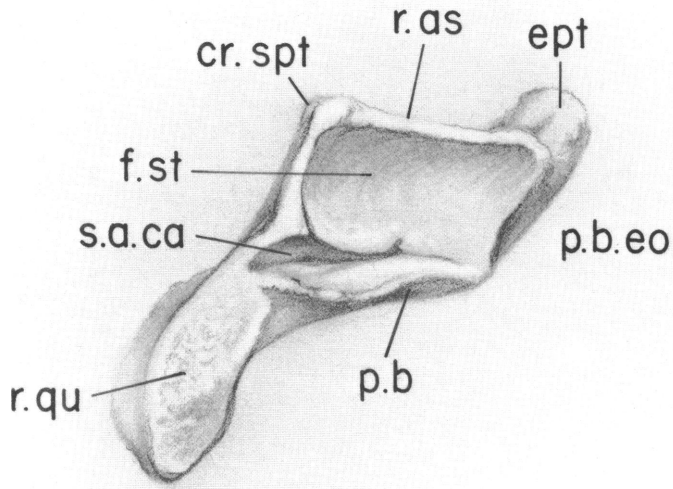
COMPARISONS

Hadrokkosaurus bradyi, UCMP 36247, (fig. 2) is mostly a complete left pterygoid from an individual approximately the same size as that represented by the Antarctic specimen which it also resembles in being somewhat battered and abraded. The quadrate and palatal rami are essentially complete but most of the upper part of the

ascending ramus, the portion forming a roof over the stapedial fossa, and a few pieces from the posterior edge of the corpus have broken away. The specimen includes, in addition to the pterygoid, the basal process of the exoccipital firmly fused to the sutural plate of the ascending ramus and a strip of the corpus of parasphenoid running along the medial edge from the basal process to the border of the interptyergoid vacuity.

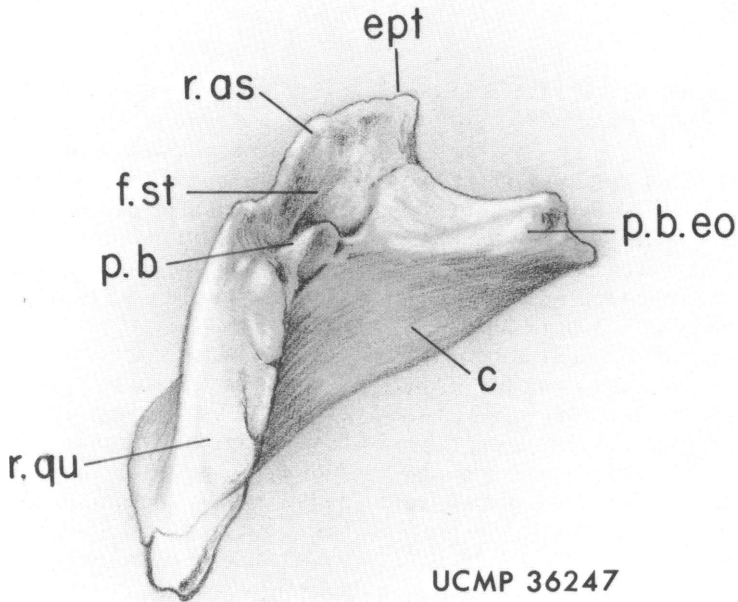
The general shapes of the corpus and the quadrate and palatal rami closely resemble those of AMNH 9346. A particular correspondence lies in the course of the posterior edge of the corpus. Although part of this is broken away on UCMP 36247 enough remains to show its shape and trend. As in AMNH 9346 the edge is a nearly straight line running anteromedially from the angular junction of the corpus with the quadrate ramus to the basal process of the exoccipital and, thereby, diagonal to the midline of the original complete skull.

Hadrokkosaurus bradyi also resembles *Austrobrachyops jenseni* in the possession of a proportionally large epiptyergoid bone. Although no part of this bone is included on the specimen, the supporting platform on the dorsal surface of the



AMNH 9346

FIG. 8. *Austrobrachyops jenseni*, new genus and species. AMNH 9346, type, left pterygoid, occipital view. X 1.



UCMP 36247

FIG. 9. *Hadrokkosaurus bradyi* (Welles). UCMP 36247, left pterygoid, occipital view. X 1.

anteromedial part of the ascending ramus defines the shape and size of its base.

Notable differences are present in the construction of the ascending ramus and associated features. Although this area on UCMP 36247 is

damaged and incomplete, enough remains to indicate the following contrasts to the Antarctic specimen:

1. The broken base of the ascending ramus suggests that the original complete structure was

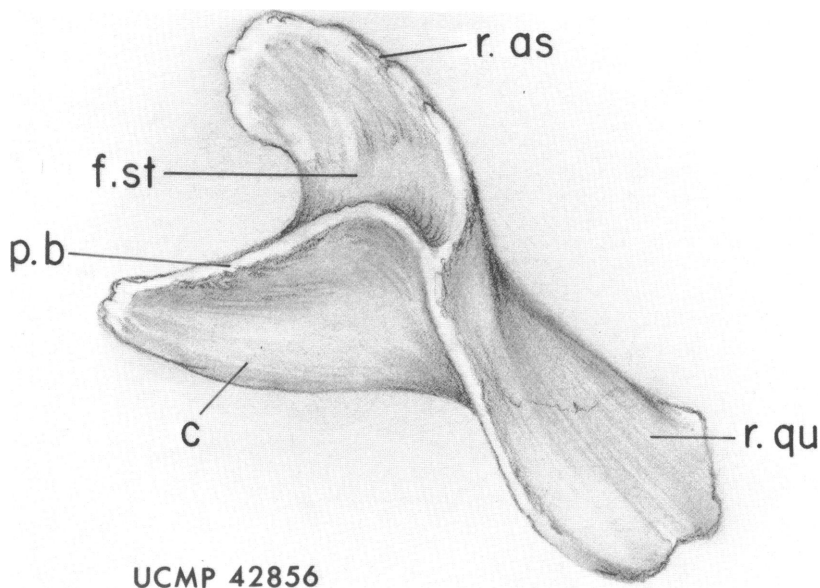


FIG. 10. *Batrachosuchus* sp. Composite illustration made from two right pterygoids, both numbered UCMP 42856. Occipital view. $\times 1$.

evenly curved throughout its extent rather than angular, and that, therefore, it formed a domed rather than flat roof for the stapedial fossa. This is confirmed on the holotype skull of *Hadrokkosaurus bradyi* (Welles and Estes 1969, fig. 27c, pl. 2c).

2. UCMP 36247 and the holotype skull carry no indication of a suprapterygoid crest on the dorsal surface of the ascending ramus.

3. The lateral edge of the stapedial fossa of UCMP 36247 is not incised by a sulcus for the internal carotid artery.

The basiptyergoid ridge on UCMP 36247 is complete and undamaged in contrast to that of AMNH 9346 and, therefore, should be noted briefly. It possesses a sharp crest that slopes down from the anterior corner of the epiptyergoid platform to the border of the interptyergoid vacuity. As in AMNH 9346, the bone surface slopes gently away from the lateral side of the crest and drops sharply down to the pterygoid-parasphenoid suture on the medial side. A very shallow depression seen on this medial wall of the crest is clearly the much reduced homologue of the conical recess for the basiptyergoid process of the basisphenoid found in other laby-

rinthodonts for which endocranial structures have been described.

The two right pterygoid fragments of *Batrachosuchus* sp., both numbered UCMP 42856, are far less complete than the pterygoids of *Austrobrachyops jenseni* and *Hadrokkosaurus bradyi*. The larger of the two includes most of the quadrate ramus, part of the corpus, the broken base of the ascending ramus, and a section of the parasphenoid corpus fused to its medial edge. The smaller specimen includes most of the ascending ramus and a small part of the corpus. Both are quite waterworn and very incomplete anteriorly. The areas anterior to and medial to the ascending ramus that contained the basiptyergoid ridge and the sutural surfaces for the exoccipital and epiptyergoid bones are not present on either. Figures 3, 7, and 10 show a composite, mostly taken from the larger specimen but with the upper part of the ascending ramus added from the smaller.

The main point of resemblance to *Austrobrachyops jenseni* is the presence of a suprapterygoid crest on the dorsal surface of the ascending ramus. The main point of difference is in the shape of the posterior edge of the ascending ramus, which is evenly curved as in *Hadrokkosaurus*.

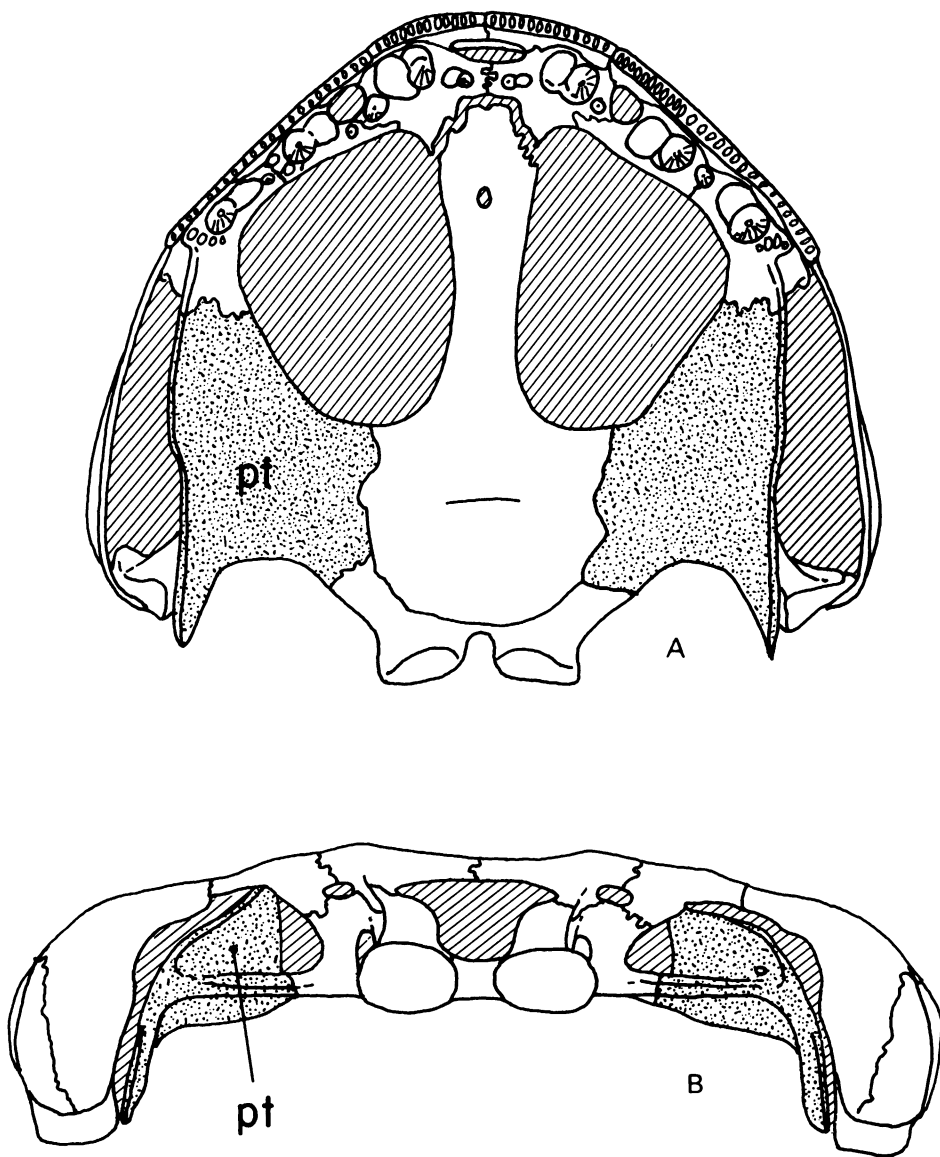


FIG. 11. *Hadrokkosaurus bradyi* (Welles). (A) Palatal view and (B) occipital view of skull, to show position and relationships of the pterygoid bones. Not to scale.

saurus bradyi rather than angular. *Batrachosuchus* sp., therefore, has a domed rather than flat roof over the stapedial fossa. Also, in concurrence with *H. bradyi* and in contrast to *Austrobrachyops jenseni*, the lateral edge of the fossa is not incised by a sulcus for the internal carotid artery.

The posterior border of the corpus distinguishes *Batrachosuchus* sp. from the Arizona and Antarctic species. This border, complete on the larger specimen, was normal to the midline of the original complete skull rather than oblique.

Restorations of the occipital surfaces of *Brachyops laticeps* (Welles and Estes, 1969, fig.

15c), *Brachyops allos* (Howie, 1971, fig. 2a), and *Bothriceps australis* (Welles and Estes, 1969, fig. 16c) show arched ascending rami forming domed rather than flat roofs over the stapedial fossae. These species, therefore, resemble *Batrachosuchus* sp. and *Hadrokkosaurus bradyi* in this respect rather than *A. jenseni*. The occipital surface of the holotype of *Blinasaurus henwoodi* (Cosgriff, 1969, fig. 5b) is too incomplete to allow an accurate interpretation of the contained portions of the pterygoid bones. The pterygoid construction is not known for the remaining brachyopid species cited at the beginning of this section.

General Morphology of the Brachyopid Lower Jaw

Direct comparisons have been made between AMNH 9301, the articular fragment of the left lower jaw ramus of *Austrobrachyops jenseni* (fig. 12) from Graphite Peak and five articular fragments from lower jaws of *Batrachosuchus* sp. found at the Bethal Farm locality that produced the pterygoid bones. Four of these are from right rami and the other, the most poorly preserved, from a left ramus. All are numbered UCM 42856. Figure 7 is a composite of the two more complete right rami, drawn in mirror image for easier comparison with the Graphite Peak specimen that is from a left ramus.

Comparisons have also been made with descriptions and illustrations of the following brachyopids: *Batrachosuchus* (Watson, 1956, pp. 336-337, fig. 9); *Blinasaurus henwoodi* (Cosgriff, 1969, pp. 74, 77, figs. 7-10); *Boreosaurus thorslundi* (Nilsson, 1943, pp. 34-41, figs. 21-25, pl. 9); and *Hadrokkosaurus bradyi* (Welles, 1947, pp. 246-254, figs. 3-6; Welles and Estes, 1969, pp. 41-43, fig. 20).

As discussed by Cosgriff (1969), a feature of the lower jaw that is diagnostic of the family as a whole is the position of the posterior meckelian foramen and angular-prearticular suture on the ventral surface or very low on the lingual surface. Additional unusual features in the family that are characteristic of most of the species for which lower jaw material is known but either not universal or unknown for all species, include the following:

1. The entire jaw ramus is usually bowed upward in labial and lingual view. It is strongly so in *Blinasaurus henwoodi* and *Boreosaurus thorslundi* and slightly so in *Hadrokkosaurus bradyi*. None of the known jaw material of *Batrachosuchus* is complete enough to ascertain if this overall shape is characteristic of the genus.

2. The retroarticular process is quite elongate in the species of *Batrachosuchus*, in *Blinasaurus henwoodi*, and especially so in *Hadrokkosaurus bradyi*. This process is broken off just behind the articular facet on the sole specimen of *Boreosaurus thorslundi* but was probably equal in relative dimensions to those of *Batrachosuchus* and *Blinasaurus*.

3. The labial wall of the adductor fossa is evenly convex upward and much higher than the lingual wall in *Blinasaurus henwoodi*. The jaw fragments of *Batrachosuchus* sp. from Bethal Farm and the fragment referred to *Batrachosuchus* by Watson (1956, fig. 9) are all broken off just anterior to the articular facet but enough remains on all of them to indicate that the labial wall of the adductor fossa was similar to that of *Blinasaurus henwoodi*. The jaw of *Boreosaurus thorslundi* is an internal mold of the meckelian space but enough remains in the area of the adductor fossa to clearly suggest a high labial wall and low lingual wall. This feature is present in *Hadrokkosaurus bradyi* but in a far less pronounced fashion—the labial wall of the fossa is only slightly convex and is only slightly higher than the lingual wall.

Particular Features of *Austrobrachyops jenseni*, AMNH 9301

Portions retained on AMNH 9301 include the labial portion of the articular facet, most of the retroarticular process, and the posterior part of the labial wall of the adductor fossa. The articular bone forms the floor of the articular facet. The surangular bone contributes the upper part of the sculptured labial surface including the labial wall of the adductor fossa and also the dorsal surface of the retroarticular process. The angular bone forms the sculptured lower part of the labial surface. All the smooth lingual surface retained on the specimen is formed by the prearticular bone.

The surface sculpture on the surangular and angular bones is very coarse and consists, for the most part, of elongate pits separated from each other by round-crested ridges. These pits are very irregular both in size and in shape. They range from 1 mm. to 4 mm. in least diameter.

The oral groove of the lateral line system runs longitudinally across the surangular bone, beginning on the retroarticular process and, crossing just below the articular facet, enters onto the labial wall of the adductor fossa. It ends at the broken anterior edge of the specimen and undoubtedly crossed the entire length of the original complete lower jaw. It is shallow and about 5 mm. in width through most of its length. The mandibular groove crosses the ventral portion of the angular bone just above the lower edge of the specimen. It is narrower than the oral groove, only about 2 mm. in width.

The high labial wall of the adductor fossa and the elongate retroarticular process identify AMNH 9301 as a brachyopid. The construction of both of these features is particularly close to

conditions seen on the jaws from Bethal Farm referred to *Batrachosuchus*. The dorsal edge of the labial wall of the fossa curves sharply up from the anterolateral corner of the articular facet. Although no part of the lingual wall of the fossa is retained, the inner portions of the articular facet are set low and indicate that the lingual wall of the fossa must have been much lower than the labial wall. Although the posterior portion of the retroarticular process is missing on AMNH 9301, the original outline of this structure can easily be reconstructed by projecting the curvature of the retained portions of the lower edge of the jaw posterodorsally to the point where it intersects the projected straight dorsal edge of the jaw. When this is done, it can be seen that the entire retroarticular process as measured along its dorsal surface was about three times the anteroposterior length of the articular facet. This is close to the proportionate size of the retroarticular process on the most complete right jaw fragment of *Batrachosuchus* from Bethal Farm.

Comparison of AMNH 9301 with *Batrachosuchus* and *Blinasaurus*

Among the brachyopids for which lower jaw material is known, meaningful comparisons are possible with ?*Batrachosuchus* (Watson, 1956, fig. 9), *Blinasaurus henwoodi* (Cosgriff, 1969, figs. 7-10); *Hadrokkosaurus bradyi* (Welles, 1947, figs. 3-6; Welles and Estes, 1969, fig. 20), and the jaw fragments of *Batrachosuchus* sp. from Bethal Farm, but not with *Boreosaurus thorslundii* (Nilsson, 1943, figs. 21-25, pl. 9). The sole specimen of the latter is an internal cast of the meckelian space of the lower jaw, incomplete and lacking most of the labial wall of the adductor fossa.

Closest relationships lie with ?*Batrachosuchus* (Watson, 1956, fig. 9), *Batrachosuchus*, and *Blinasaurus henwoodi*. In each of these, as in AMNH 9301, the labial wall of the adductor fossa is considerably higher than the lingual wall and the retroarticular process, as measured along its dorsal surface, is approximately three times the anteroposterior length of the articular facet.

Surface sculpture and lateral line grooves of the labial surface serve to distinguish AMNH 9301 from the various jaw fragments referred to *Batrachosuchus*. The sculpture on the Antarctic

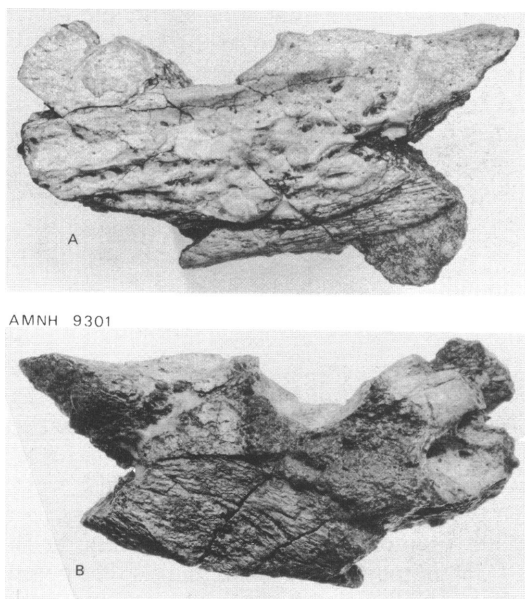


FIG. 12. *Austrobrachyops jenseni*, new genus and species. AMNH 9301, referred specimen, portion of left mandibular ramus. A. Labial view. B. Lingual view. Both $\times 1$.

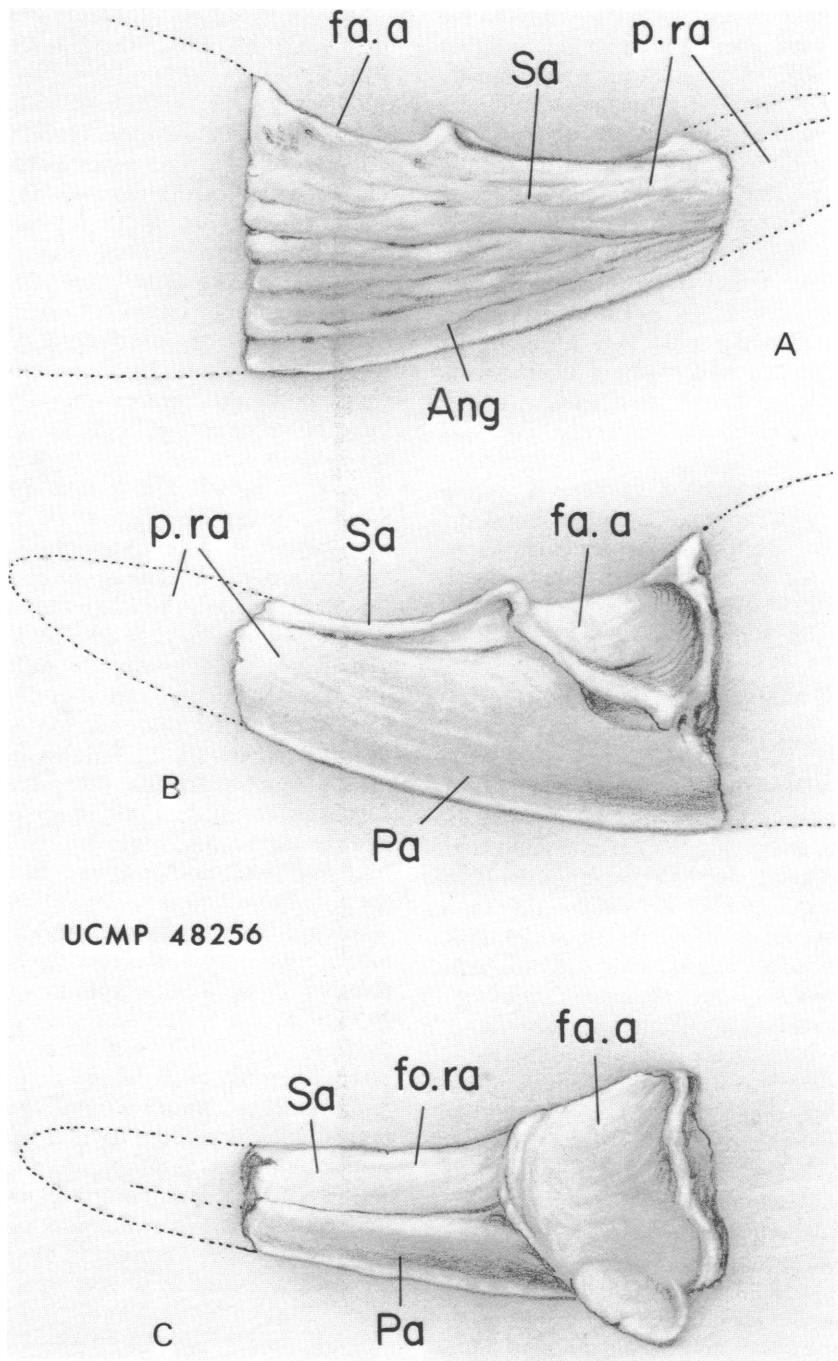


FIG. 13. *Batrachosuchus* sp. Composite illustration of two right lower jaw articular fragments, both numbered UCMP 48256. Reversed to appear as a left articular fragment. A. Labial view. B. Lingual view. C. Dorsal view. All X 1.

specimen consists of elongate pits, whereas in the South African specimens it is composed of rather regular ridges and grooves that run longitudinally across the labial surface. The oral and mandibular grooves, well marked on the Antarctic specimen, are lacking on those from South Africa. Sculpture and lateral line grooves are not well preserved on any of the lower jaws of *Blinasaurus henwoodi* and, hence, the affinities of this species in these respects cannot be determined.

The lower jaws of *Hadrokkosaurus bradyi* contrast with those of the other forms in the height of the labial wall of the adductor fossa and in the relative length of the retroarticular process. In *Hadrokkosaurus bradyi* the labial wall of the fossa is only slightly higher than the lingual wall, but the retroarticular process is proportionally very long, approximately six times the anteroposterior length of the articular facet. Additionally, surface sculpture is poorly developed on the labial surface and there are no traces of the lateral line grooves.

SUPERFAMILY RHINESUCHOIDEA

FAMILY LYDEKKERINIDAE

Watson (1919, p. 66) founded the family for *Lydekkerina (Bothriceps) huxleyi* (Lydekker, 1889, p. 476), and in his 1919 account and later (1951) established it as a component of the large rhinesuchoid-capitosauroid division of the Temnospondyli that ranged from the Upper Permian through the Upper Triassic. He demonstrated that the lydekkerinids are, in general, evolutionary intermediates between the Permian rhinesuchoids and the Triassic capitosauroids. However, as they are also a Triassic group, they are too late in time to be ancestral to the latter. The features of evolutionary intermediacy, confined to the braincase and adjacent bony elements of the palatal and occipital surfaces of the skull, are reviewed, partly reinterpreted, and incorporated into a new diagnosis of the family given in an account by the junior author (In press) of the Lower Triassic Temnospondyli of Tasmania. As the braincase, palatal, and occipital areas of the skull are not known for the new lydekkerinid from the Fremouw Formation, herein described, these important diagnostic characters of the family will not be considered in this account.

Romer (1947, pp. 315-317) provided a formal taxonomic hierarchy that corresponds largely with Watson's (1919) concepts on the evolutionary relationships between the various large divisions of the Temnospondyli. Included in Romer's classification are the Superfamilies Rhinesuchoidea and Capitosauroidea with the Family Lydekkerinidae listed under the former. He provided diagnoses for each of these taxa and, in the case of the Lydekkerinidae, the cited characters include some of Watson's features of evolutionary intermediacy in the construction of the basal region of the skull. The only strictly definitive character in this diagnosis that can be used in referring the new Antarctic form to the Lydekkerinidae is one also cited in Watson's original diagnosis: "orbits . . . in the middle of the (skull) length." Subsequent accounts of *L. huxleyi*, descriptions of species later added to the family, and the analysis of the new species from Antarctica have verified this character as a definitive feature of the family. In all lydekkerinid species, as noted in the following discussion, the preorbital portion of the skull roof constitutes only half or less of the total skull roof midline length. In other families of the Rhinesuchoidea, as in all of the Capitosauroidea, the preorbital portion constitutes more than half of the total skull roof midline length and, consequently, the orbits are relatively much farther to the rear than they are in the Lydekkerinidae.

Comparisons of the new Antarctic form with previously described members of the family have revealed an additional definitive character: the grooves of the lateral line system on the skull roof are very weakly developed, being entirely absent in some areas where they are normally found in other temnospondyls and much interrupted and obscured by the ridges and pits of the surface sculpture in places where they are present. However, as noted in the following comparative section, there is no consistency among members of the family in regard to the areas in which the weakly developed grooves are present.

Contents of the Family

Prior to the discovery of the new species in the Fremouw Formation, the known distribution of the Lydekkerinidae was limited to the Lower Triassic *Lystrosaurus* Zone of the Beaufort series

of South Africa and to the Lower Triassic Knocklofty Formation of Tasmania. The species from the *Lystrosaurus* Zone include *Lydekkerina huxleyi*, *Limnoiketes paludinans* (Parrington, 1948, pp. 435-440, figs. 5, 6), and an unnamed form (Watson, 1951, p. 43, fig. 15). A new form from Tasmania, generically and specifically distinct from these African representatives of the family, has been described by the junior author (In press).

Lydekkerina huxleyi is a common species in the *Lystrosaurus* Zone. The holotype, BMNH¹ R5707, a small skull in the British Museum (Natural History), was described and figured by Lydekker (1889, p. 476; 1890, pp. 172-173, fig. 41) as *Bothriceps huxleyi*. Watson (1919, p. 12) removed it from this brachyopid genus and provided the new generic name. A considerable quantity of referred cranial and postcranial material, collected over the years from the *Lystrosaurus* Zone, is housed in South African, European, and American museums and much of it has been extensively described by Watson (1912, p. 585; 1919, pp. 12-18), Broom (1915, p. 366; 1930, pp. 5-7), Broili and Schroeder (1937, pp. 39-55), and Parrington (1948, pp. 426-430). The specimen available to the authors for comparative study that is referred to in following passages consists of a particularly fine skull, lower jaws, and dermal shoulder girdle, with some parts of the skeleton.

Limnoiketes paludinans (Parrington, 1948, pp. 435-440, figs. 5, 6), known from a single complete skull, is separated from *Lydekkerina huxleyi* by its relatively larger orbits and interpterygoid vacuities, broader temporal region, and deeper occiput. It is further distinguished by the irregularity of its lateral skull margin, which is convex in the snout region, concave in the region lateral to the orbit, and convex again in the temporal region. In *Lydekkerina huxleyi*, by contrast, the lateral skull margin is strongly and evenly convex throughout. Parrington considered *Limnoiketes paludinans* possibly to be a young individual of a species that attained a larger adult size than that attained by *Lydekkerina huxleyi*, as comparatively large orbits and deep occiputs tend to be juvenile characters in species populations of other members of the Temnospondyli.

¹ BMNH, British Museum (Natural History), London.

The new Tasmanian lydekkerinid, known from a complete skull, several incomplete skulls, lower jaw material, and postcranial elements, resembles both *Lydekkerina huxleyi* and *Limnoiketes paludinans*—the preorbital portion of the skull roof is short, constituting less than half of the skull roof midline length, the grooves of the lateral line system are very weakly developed, and the tabular horns are pointed. It is distinct from both of the South African forms in three particulars of the skull roof: the lateral skull margin is straight from snout tip to posterolateral corner; the snout region is exceptionally narrow; and the lacrimal bone has a border on the external naris rather than being separated from the external naris by a short maxillary-nasal suture. Further features of the palatal and occipital surfaces also distinguish the Tasmanian species from those of the *Lystrosaurus* Zone but these are not pertinent to the present discussion.

Four additional species, each known only from a single skull, have been referred to the family. Three of these, "*Lydekkerina*" *dutoiti*, placed by Romer in a separate genus *Broomulus* (Romer, 1947, p. 202), *Lydekkerina putterilli*, and *Putterillia platyceps* are from the *Lystrosaurus* Zone and were described briefly by Broom (1930, pp. 7-10). Romer (1947, pp. 202-203) pointed out that *Broomulus dutoiti* is possibly a synonym of *Putterillia platyceps*. Parrington (1948, p. 438) has shown that the skull of *L. putterilli* may be a young individual of the rhinesuchid genus *Uranocentrodon*. The fourth species is *Deltacephalus whitei* (Swinton, 1956, pp. 60-64) from the Lower Triassic Sakamena beds of Madagascar. The holotype skulls of all four are quite small and incompletely preserved. They are much shorter and rounder than typical lydekkerinid skulls and have as their only point of resemblance the central positions of the orbits on the skull roofs. Because we lack further information either to support or deny their retention in the family they should be listed as *incertae sedis* among the contents of the Temnospondyli.

CRYOBATRACHUS, NEW GENUS

Etymology. Cryo, from Greek kryos = cold; batrachus, from Greek batrachos = frog.

Diagnosis. A lydekkerinid in which the greatest

skull width across the quadratojugals is approximately three-fourths the midline length of the skull. The otic notch is crescentic, terminating anteromedially in a sharply pointed border and extending as far forward as the anterior border of the tabulars. The skull breadth in the region of the orbits is approximately equal to the breadth at the quadratojugals. The interorbital breadth is narrow, as is the tip of the snout. In both cases the transverse measurement between the orbits and between the nares is approximately one-sixth the skull length along the median line. The lateral skull margins are markedly convex.

Type. Cryobatrachus kitchingi, new species.

***Cryobatrachus kitchingi*, new species**

Etymology. Named in honor of Dr. James W. Kitching, who discovered the type specimen.

Holotype. AMNH 9503, a skull, in the rock, lacking the palate and braincase, of which the ventral surface is visible. Kitching Ridge, Shackleton Glacier.

Paratype. AMNH 9556, impression of a portion of a skull roof. Mount Kenyon, McGregor Glacier.

Referred Specimens. The following fossils, all from Coalsack Bluff, are here listed as referred specimens, rather than as paratypes. They probably belong to the genus and species here being described, but the point cannot be proved. At least they represent a small lydekkerinid, of a size corresponding to the type of *Cryobatrachus kitchingi*.

AMNH 9331, a very fine right clavicle, nearly complete

AMNH 9339, a fragment of a mandibular ramus with four teeth, of a very small individual

AMNH 9340, a small portion of a skull roof

AMNH 9342, a large portion of a right clavicle

AMNH 9343, a part of a left clavicle

AMNH 9344, fragment of an interclavicle

The following specimens from Coalsack Bluff also are referred to the genus and species now under consideration. They are included here with less certainty than the specimens previously listed. It can be stated, however, that they are small labyrinthodont amphibians, comparable in size to *Cryobatrachus*.

AMNH 9332, right radius

AMNH 9341, intercentrum

AMNH 9345, left ilium

AMNH 9347, articular portion of mandible

AMNH 9348, articular portion of a left mandibular ramus

AMNH 9382, tibia

AMNH 9383, left exoccipital

AMNH 9384, fragment of a clavicle

AMNH 9385, left exoccipital

AMNH 9386, centrum of atlas

AMNH 9387, articular

AMNH 9388, interclavicle

In addition the following specimens are referred to *Cryobatrachus*.

AMNH 9537, scattered fragments of skull and jaws, in a red matrix from Kitching Ridge, Shackleton Glacier

AMNH 9540, a small skull, crushed, broken and distorted, also from Kitching Ridge

AMNH 9541, portion of a maxilla of a small skull from Halfmoon Bluff, Shackleton Glacier

Horizon. Lower portion of the Fremouw Formation, Lower Triassic.

Locality. Kitching Ridge, Transantarctic Mountains, immediately east of Shackleton Glacier, about opposite its confluence with Logie Glacier, for the type. *Thrinaxodon* Col, on the southwest flank of Mount Kenyon, about 25 km. or 15 miles due east of the type locality, for the paratype. Approximately at latitude 85° 13' S., longitude 177° 0' W., for the type; latitude 85° 13' S., longitude 174° 30' W., for the paratype. Coalsack Bluff, Transantarctic Mountains, approximately at latitude 84° 15' S., longitude 162° 20' E., for the referred specimens. Antarctica.

Diagnosis. Same as for genus.

DESCRIPTION AND DISCUSSION

AMNH 9503. The type specimen is slightly crushed, but distortion of the fossil is so minor that the specimen fairly approximates its original shape. As noted in the listing of the materials, the type consists of a skull in the rock, with the inner surface of the skull roof exposed, which, of course introduces complications into the study of the fossil. It would be much better to have the dorsal surface available. However, the specimen is so delicate that it would be ill-advised to attempt to expose the top of the skull, for such a procedure would be risky, and would involve, among other things, the expenditure of an untold

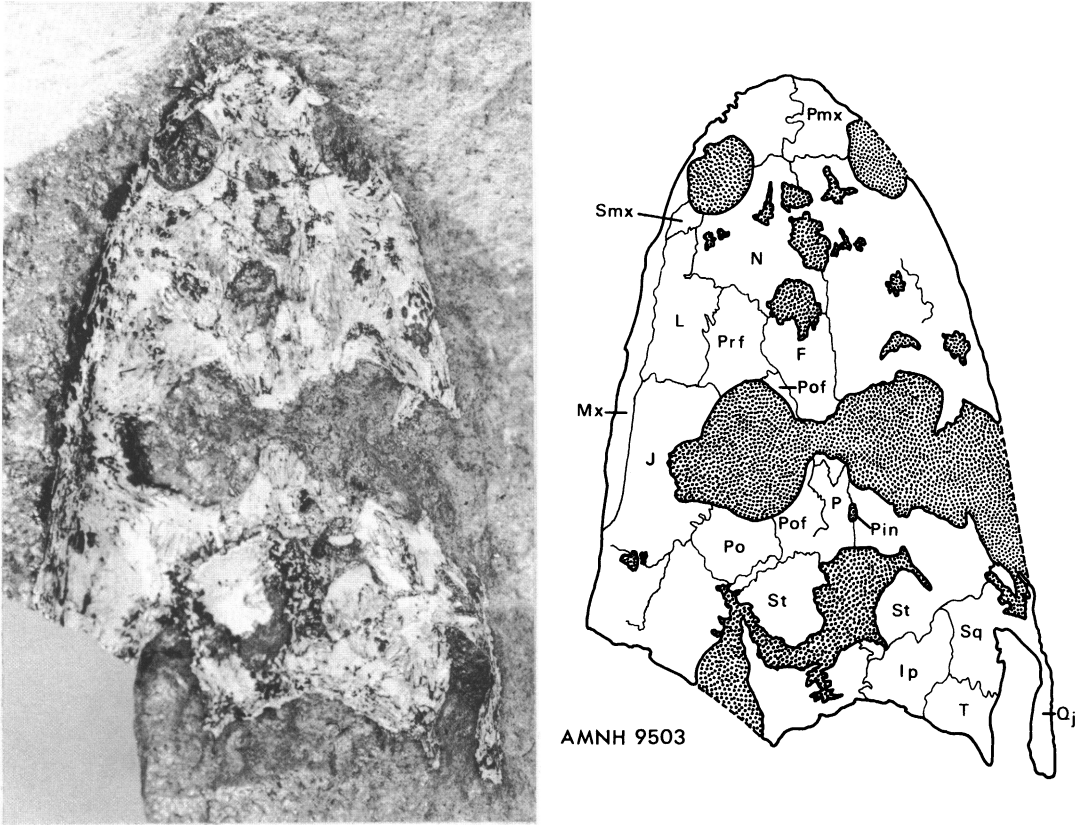


FIG. 14. *Cryobatrachus kitchingi*, new genus and species. AMNH 9503, type, skull. On left, photograph of ventral surface of skull roof. On right, interpretation of photograph, showing bones of skull, so far as they could be determined. $\times 2$.

amount of time and effort. Therefore the fossil necessarily has been studied from the underside. Fortunately, certain diagnostic features have to do with proportions, which can be determined from the skull as it is exposed within the rock. Moreover, it has been possible to interpret with some degree of satisfaction the pattern of skull bones (fig. 14) which, so far as can be determined, is typical for temnospondyls.

The skull is small, about $4\frac{1}{2}$ cm. in length, which may or may not be of taxonomic importance. A typical *Lydekkerina* skull is significantly larger, 7 to 8 cm. in length and, as Parrington (1948) pointed out, the holotype skull of *Limnoiketes paludinatus* may represent a young individual of a taxon whose members attained a very large adult size. A recently collected ptery-

goid bone of the Tasmanian lydekkerinid is derived from a skull that was 30 to 40 cm. in midline length.

The elongate oval shape of the skull roof, broadly rounded snout, and deeply incised otic notches identify the new form as a member of the rhinesuchoid-capitosauroid division of the temnospondyli. The position of the hinge line of the quadrate condyles relative to the hinge line of the exoccipital condyles further serves to limit consideration of its taxonomic affinities to the Triassic Lydekkerinidae and Capitosauridae. As Watson (1919) perceived, typical rhinesuchids have quadrate condyles that lie on a line distinctly posterior to the level of the exoccipital condyles, whereas in capitosaurids the quadrate condyles are either on the same hinge line as the

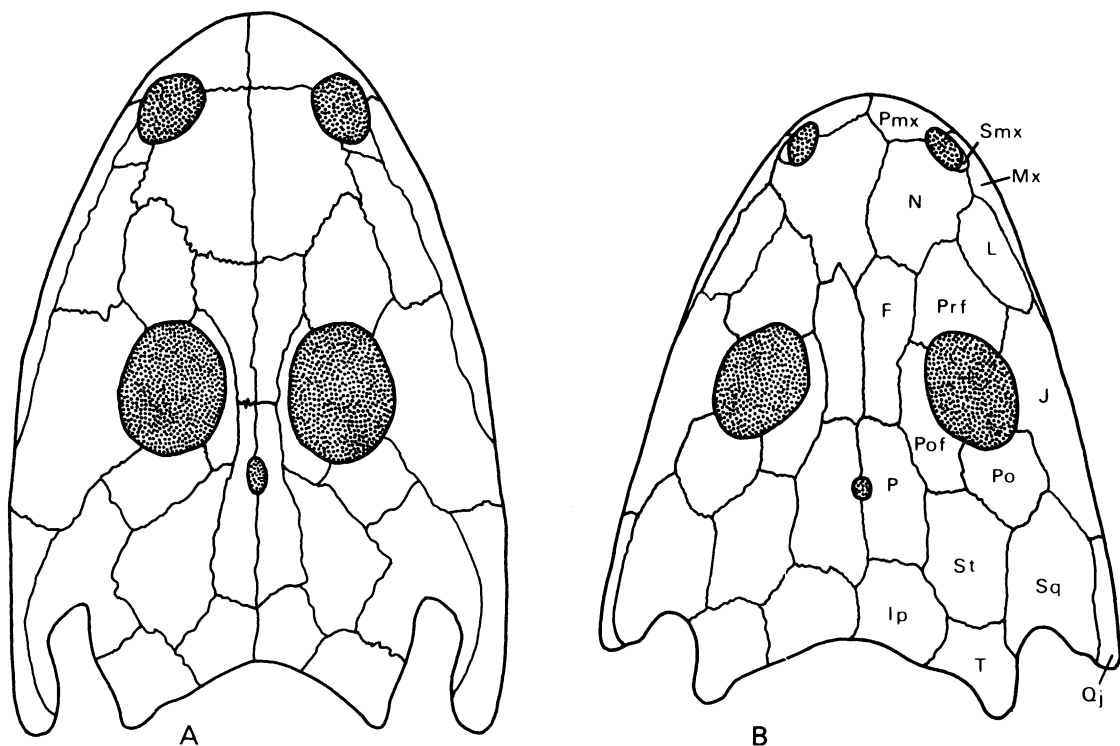


FIG. 15. A. *Cryobatrachus kitchingi*, new genus and species. Interpretation of dorsal view of skull, based upon AMNH 9503, type. $\times 2$. B. *Lydekkerina huxleyi* (Lydekker), dorsal view of skull, after Parrington. $\times 1$.

exoccipital condyles or lie slightly anterior to them. The relative positions of the two sets of condyles can also be observed on the skull roof, as the quadratojugal bones at the posterolateral corners directly overlie the quadrate condyles and the tabular bones at the midline rear of the skull lie only slightly anterior to the exoccipital condyles. The new Antarctic form resembles capitosaurids rather than rhinesuchids, as the tips of quadratojugal and tabular bones lie on the same transverse line. The other lydekkerinid species also concur with capitosaurids in that all of them have the tips of the quadratojugal bones either level with or anterior to the tips of the tabular bones.

The prime feature of AMNH 9503 that identified *Cryobatrachus kitchingi* as a member of the Lydekkerinidae is the short preorbital portion of the skull roof. In this specimen as in all specimens of the other species of the family the

length from the snout tip to a line across the anterior margins of the orbits is less than half of the total midline length of the skull roof. As computed from the measurements listed in table 1 the index of preorbital length to total midline length is 43.7 in AMNH 9503 and 47.0 in the specimen of *Lydekkerina huxleyi*, AMNH 9799. The range for this index computed from published illustrations of *Lydekkerina huxleyi* is from 43.0 in Lydekker (1890, fig. 41) to 50.0 in Broili and Schroeder (1937, fig. 1). It is 42.0 in *Limnoiketes paludinatus* (Parrington, 1948, fig. 5) and 48.0 in the new species from Tasmania. In all rhinesuchids and capitosaurids, on the other hand, this index exceeds 50.0. The range in the Rhinesuchidae extends from 52.0 in *Muchocephalus muchos* (Watson, 1962, fig. 5) to 67.0 in *Rhinesuchoides tenuiceps* (Olson and Broom, 1937, fig. 1). Among capitosaurids, the entire range is encompassed by the range of 57.0-68.0

in the species population of *Parotosaurus peabodyi* (Welles and Cosgriff, 1965, table II).

In regard to other proportions of the skull roof, the width across the orbit centers and the width across the quadratojugal bones are nearly equal (see table 1) and each is approximately three-fourths of the skull roof midline length. The lateral margins are evenly rounded from the tip of the snout to the posterolateral corners of the cheek region. The posterior border between the tips of the tabular horns is evenly concave. The tabular horns are narrow and quite pointed.

The otic notch is distinctive, i.e., deeply incised into the skull table, crescentic in shape, and pointed anteriorly. In accordance with the general narrowness of the skull, the orbits in the type specimen are oval, with the longer dimensions directed anteroposteriorly, and with the anteromedial borders bluntly rounded. The parietal foramen is somewhat elongated. The nares are oval,

with their long axes parallel to the lateral borders of the skull.

The interorbital breadth in *Cryobatrachus kitchingi* is narrow, i.e., slightly less than the diameter of the orbit and about one-sixth of the skull roof midline length. The separation between the nares is by about the same factor as that between the orbits.

AMNH 9556. This fragmentary specimen consists of an impression in rock of the right posterolateral portion of a skull roof and includes the posteromedial border of the right orbit and most of the outlines of the right otic notch. The notch and the adjacent tabular horn closely correspond with these features on the type specimen and insure its referral to the species. Even in its incomplete state it does supplement the type in that it reveals the character of the dorsal surface of the skull.

A latex mold made from the rock impression,

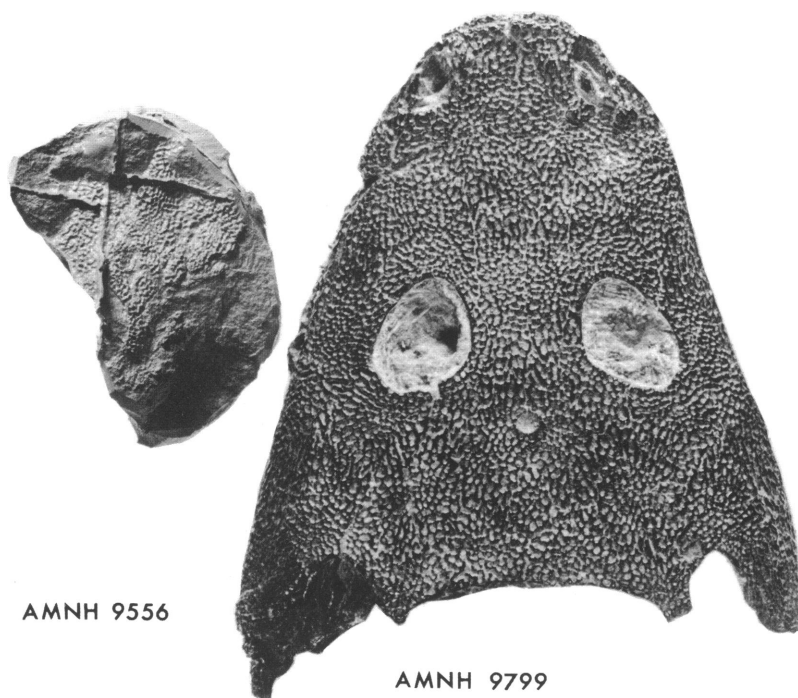


FIG. 16. Left, AMNH 9556, *Cryobatrachus kitchingi*, new genus and species, latex cast from natural mold in rock showing fragment of skull roof with characteristic sculpturing. Right, AMNH 9799, *Lydekkerina huxleyi*, skull, dorsal view. Both $\times 1$.

shows that the sculpture of the skull roof resembles that of *Lydekkerina huxleyi* in that the individual bones are pitted over their entire surfaces without the grooving that is seen in many other labyrinthodont amphibians. The pits are round to oval in outline and average about 0.5 mm. in diameter.

Another lydekkerinid feature present on this specimen is the rudimentary and incomplete state of the system of lateral line grooves. The only portion of this system apparent on the latex peel is a section of the right supraorbital groove that runs just medial to the orbit and is invaded in places by the pitting of the surrounding sur-

face area. The peel includes portions of the skull roof in which sections of the infraorbital, temporal, and jugal grooves are normally present in other temnospondyl families but there are no traces of these to be seen. The lateral line system of the specimen of *Lydekkerina huxleyi*, AMNH 9799, is also lightly impressed on the skull roof, discontinuous and, where present, usually invaded by pitting. Portions of all the major grooves—supraorbital, infraorbital, temporal, and jugal—are visible but they do not form the clearly incised and continuous system found in other groups such as the capitosaurids. Parrington's (1948, fig. 5) illustration of the skull roof of

TABLE 1
SKULL MEASUREMENTS (IN MILLIMETERS) OF *Cryobatrachus kitchingi*
COMPARED WITH *Lydekkerina huxleyi*

	<i>Cryobatrachus kitchingi</i> AMNH 9503 (Holotype)	<i>Lydekkerina huxleyi</i> AMNH 9799
Midline length	43.7	75.6
Snout, tip to line across anterior margins of orbits	20.7	36.3
Snout, tip to line across anterior margin of nares	3.5	4.4
Line across anterior margins of orbits to line across posterior margins of nares	12.1	24.2
Line across posterior margins of orbits to front edge of parietal foramen	2.0	3.6
Line across posterior margins of orbits to back of skull at midline	11.9	25.5
Greatest width across quadratojugals	31.5	74.8
Width across orbit centers	30.5	54.4
Width, one-fifth of distance back from tip of snout	19.8	34.4
Width across centers of nares	15.1	27.4
Least distance between orbit and otic notch	L. 8.2 R. 8.0	L. 23.1 R. 22.2
Orbit, length	L. 11.3 R. 9.9	L. 16.2 R. 16.2
Orbit, width	L. — R. 6.7	L. 12.2 R. 11.6
Nares, length	L. 5.8 R. 5.6	L. 8.5 R. 8.5
Nares, width	L. 3.0 R. 3.2	L. 5.3 R. —
Interorbital width	7.0	14.4
Orbit from lateral edge of skull	L. — R. 6.8	L. 12.1 R. 10.4
Interotic width	20.0	40.7
Internarial width	7.2	16.6
Distance of parietal foramen in front of otic notches	5.7	16.6

Limnoiketes paludinatus indicates discontinuous infraorbital and jugal grooves but shows no traces of the supraorbital and temporal grooves. Small portions of all the grooves can be made out on the holotype skull of the new Tasmanian lydekkerinid but, again, these are of short extent and partly obscured by sculpture pattern.

DIAGNOSTIC CHARACTERS OF *CRYOBATRACHUS KITCHINGI*

The most distinctive feature of the holotype of the new Antarctic species noted in comparisons with other lydekkerinids is the relative narrowness of the skull. The index greatest breadth across the quadratojugal bones at the posterolateral skull corners: skull roof midline length is 0.72 as computed from measurements listed in table 1. The same index for the reference specimen of *Lydekkerina huxleyi* (AMNH 9799) is 0.99 and it ranges from 0.89 (Broili and Schroeder, 1937, fig. 1) to 1.00 (Lydekker, 1890, fig. 41) among published illustrations of skulls of this species. This index is 0.99 in *Limnoiketes paludinatus* (Parrington, 1948, fig. 5) and 0.97 in the holotype of the Tasmanian lydekkerinid. In *Cryobatrachus kitchingi* the index of breadth across orbit centers to skull roof midline length is 0.70, only slightly less than the greatest breadth index. In the other lydekkerinids the skull roof narrows rapidly anterior to the posterolateral corners so that the orbit center breadth is considerably less than the greatest breadth.

A second quantitative character that distinguishes the new form from related species is the close spacing of the orbits on the skull roof. In the holotype of *Cryobatrachus kitchingi* the index of least interorbital width to skull roof midline length is 0.16, whereas in the reference skull of *L. huxleyi* it is 0.19. The range for this index among published illustrations is from 0.17 in Broili and Schroeder (1937, fig. 1) to 0.19 in Broom (1915, fig. 3). It is 0.17 in *Limnoiketes paludinatus* and 0.19 in the Tasmanian lydekkerinid.

The narrow, crescentic otic notch with bluntly pointed anterior margin of *Cryobatrachus kitchingi* separates this species from the other species of the family, all of which have wide

notches that are U-shaped in outline with broadly rounded anterior margins.

The oval parietal foramen, anteroposteriorly elongate, of *Cryobatrachus kitchingi* may be a taxonomic character. This foramen is circular in the other lydekkerinids as it is in most temnospondyls.

One feature of the skull roof may indicate a closer relationship of *Cryobatrachus kitchingi* to the African species than to the Tasmanian form. As in *Lydekkerina huxleyi* and *Limnoiketes paludinatus* the anterior tip of the lacrimal bone seems to be separated from the posterior margin of the naris by a short maxillary-nasal or septomaxillary-nasal suture. In the Tasmanian form, however, the lacrimal has a broad border on the naris. Other than this one, possibly not significant, feature, nothing can be discerned among the material of *Cryobatrachus kitchingi* that might suggest special taxonomic affinities of the species within the family.

Referred Specimens

The skull fragment (AMNH 9340), the mandibular ramus section (AMNH 9339), the partial right clavicles (AMNH 9331 and 9342), the partial left clavicle (AMNH 9343), and the interclavicle fragment (AMNH 9344) are all referred with question to *Cryobatrachus kitchingi* because of their small size and the nature of the sculpture pattern preserved on their external surfaces. In the skull fragment (AMNH 9340) and mandibular ramus section (AMNH 9339) this pattern closely matches that of AMNH 9556 in that it consists entirely of small distinct pits, round to oval in outline averaging 0.5 mm. in diameter. In the case of the clavicles (AMNH 9331, 9342, 9343) similar pitting can be observed at the ossification centers on the posterolateral corners, but grooving covers most of the remainders of the ventral



FIG. 17. *Cryobatrachus kitchingi*, new genus and species. AMNH 9339, portion of mandibular ramus with four teeth. Labial view. $\times 3$.



FIG. 18. *Cryobatrachus kitchingi*, new genus and species. AMNH 9331, right clavicle. AMNH 9342, portion of right clavicle. AMNH 9344, portion of interclavicle. All ventral views. $\times 1$.

surfaces. This grooving is delicate and regular in texture and, as grooved sculpture is typical of the clavicles of even very small individuals of other temnospondyl species, it cannot be regarded as a significant feature. The sculpture on the interclavicle fragment (AMNH 9344) is also dominated by grooves, and these resemble those of the clavicles in size and texture.

In all probability, these various referred specimens are derived from small lydekkerinids, but it cannot be definitely established that they represent individuals of *Cryobatrachus kitchingi*.

TEMNOSPONDYLI INCERTAE SEDIS

Specimen. AMNH 9330, an isolated left tabular bone, nearly complete but missing a small piece from the posterior edge of its dorsal surface and a small piece from the lower surface of the paraoccipital bar.

Horizon. Lower part of the Fremouw Formation, Lower Triassic.

Locality. Coalsack Bluff, Transantarctic Mountains, latitude $84^{\circ} 15' S$, longitude $162^{\circ} 20' E$.

DESCRIPTION AND DISCUSSION

All features of possible taxonomic significance are observed on the dorsal surface (fig. 20). Most of this surface is comprised of the projecting horn portion that, in the complete skull, formed

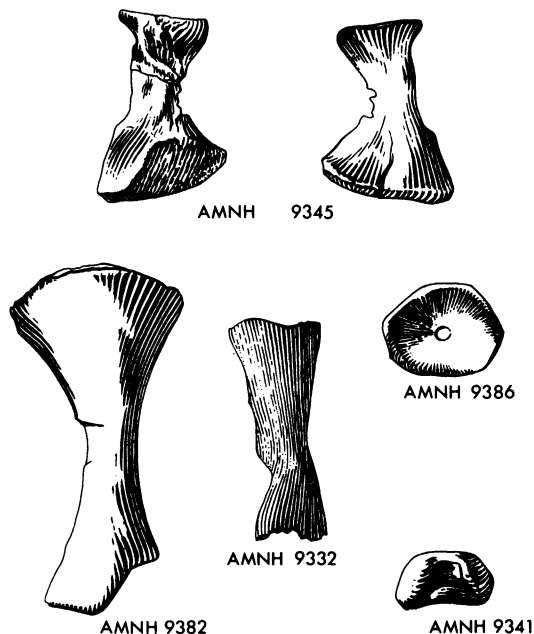
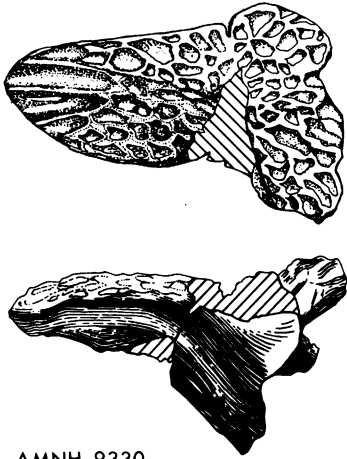


FIG. 19. *Cryobatrachus kitchingi*, new genus and species. AMNH 9345, left ilium; external and internal views. AMNH 9382, right tibia, anterior view. AMNH 9332, right radius, anterior view; AMNH 9386, centrum of axis; AMNH 9341, intercentrum. All $\times 1$, except 9341, which is $\times 1\frac{1}{3}$.

the posterior border of the otic notch. The horn is comparatively broad and ends posterolaterally in a bluntly pointed tip. The anterior and posterior edges of the horn are roughly parallel to each other. The sculpture is quite coarse, consisting of irregularly shaped pits over most of the surface but with three elongate grooves extending inward from the tip of the horn.

These features exclude the specimen from both the Brachyopidae and the Lydekkerinidae. Brachyopids possess shallow otic embayments rather than notches on the posterior edge of the skull roof and entirely lack tabular horns. Lydekkerinids, including *Cryobatrachus kitchingi*, as already described, have narrow, rather sharply pointed tabular horns and fine-textured, evenly pitted surface sculpture.

Although AMNH 9330 establishes the presence of a third temnospondyl in the vertebrate fauna of the Fremouw Formation, it cannot be allocated to even a family with certainty. Com-



AMNH 9330

FIG. 20. Temnospondyl. AMNH 9330, left tabular, dorsal and posterior views. $\times 1$.

parisons with Triassic temnospondyl skulls in the literature and with a few replicas on hand seems to limit consideration to three families—the Benthosuchidae, Capitosauridae, and Trematosauridae. *Benthosuchus sushkini* (Bystrov and Efremov, 1940, figs. 21, 22, 62, 63, 65) of the Benthosuchidae has tabular bones whose dorsal surfaces closely correspond in outline with AMNH 9330. The anterior and posterior edges of the horn are roughly parallel to each other and the tip is bluntly pointed. The sculpture consists principally of pits, and some of the specimens suggest grooving at the tip. The pits, however, are more regular both in size and in outline. Among the Capitosauridae, all species of the genus *Parotosaurus* have tabular bones that are somewhat similar in outline to the present specimen but those of *Parotosaurus nasutus* (Schroeder, 1913, pl. 16, Welles and Cosgriff, 1965, fig. 20) are particularly close. The pits of the sculpture pattern, although more regular in size and outline than those of AMNH 9330, are less so than those of *Benthosuchus sushkini*. Among the genera of the family Trematosauridae, although there is considerable variation in the shape of the tabular horns, those of *Trematosaurus brauni* (Wagner, 1935, figs. 10, 21; Säve-Söderbergh, 1935, fig. 11) and *Trematosuchus sobeyi* (Haughton, 1915, pl. VIII) resemble to a limited extent the tabular horns of *Benthosuchus sushkini*, *Parotosaurus*

nasutus, and AMNH 9330. In both of these trematosaurus the tip of the horn is bluntly pointed and the pits of the surface sculpture are large and irregular. However, in both, the anterior and posterior edges converge somewhat toward the tip rather than being parallel, giving the horn a slightly triangular shape.

All considered, the bone probably derives from a Capitosauroid temnospondyl, either a benthosuchid or a capitosaurid. It is to be hoped that future collecting will secure skeletal material of this form that can be more exactly identified.

LITERATURE CITED

- Barrett, Peter J., Ralph J. Baillie, and Edwin H. Colbert
1968. Triassic amphibian from Antarctica. *Science*, vol. 161, no. 3840, pp. 460-462.
- Broili, Ferdinand, and Henry C. Schroeder
1937. Beobachtungen an Wirbeltieren der Karrooformation. XXVI. Ueber *Lydekkerina* Broom. Sitzber.-Ber. Bayerischen Akad. Wiss., Munich, 1937, pp. 39-57.
- Broom, Robert
1903. On a new stegocephalian (*Batrachosuchus browni*) from the Karroo beds of Aliwal North, South Africa. *Geol. Mag.*, ser. 4, vol. 10, pp. 499-501.
1915. The Triassic stegocephalians, *Brachyops*, *Bothriceps*, and *Lydekkerina*, gen. nov. *Proc. Zool. Soc. London*, 1915, pp. 363-368.
1930. Notes on some labyrinthodonts in the Transvaal Museum. *Ann. Transvaal Mus.*, vol. 14, pp. 1-10.
1950. A new small labyrinthodont from the Karroo beds of South Africa. *Ann. Transvaal Mus.*, vol. 21, pt. 3, pp. 251-252.
- Bystrov, A. P., and J. A. Efremov
1940. *Benthosuchus sushkini* Efr.—Labyrinthodont is Eotriasa rek Sharzhengi. (*Benthosuchus sushkini* Efr.—A labyrinthodont from the Eotriassic of Sharzhenga River). *Trav. Inst. Paleont. Acad. Sci. U.R.S.S.*, vol. 10, pp. 1-152.
- Case, Ermin Cowles
1946. A census of the determinable genera of the Stegocephalia. *Trans. Amer. Phil. Soc.*, new ser., vol. 35, pt. 4, pp. 325-420.

Colbert, Edwin H.

- 1970. The fossil tetrapods of Coalsack Bluff. *Antarctic Jour.*, vol. 5, no. 3, pp. 57-61.
- 1971a. Tetrapods and continents. *Quart. Rev. Biol.*, vol. 46, no. 3, pp. 250-268.
- 1971b. Triassic tetrapods from McGregor Glacier. *Antarctic Jour.*, vol. 6, no. 5, pp. 188-189.
- 1971c. Antarctic fossil vertebrates and Gondwanaland. Research in the Antarctic. Amer. Assoc. Adv. Sci., Special Publ., pp. 685-701.
- 1972. Antarctic Gondwana tetrapods. Second Gondwana Symp., South Africa, 1970, pp. 659-664.
- 1974. *Lystrosaurus* from Antarctica. *Amer. Mus. Novitates*, no. 2535, 44 pp.

Cosgriff, John W.

- 1965. A new genus of Temnospondyli from the Triassic of Western Australia. *Roy. Soc. Western Australia*, vol. 48, pt. 3, pp. 65-90.
- 1967. Triassic labyrinthodonts from New South Wales. *Jour. Australian and New Zealand Assoc. Adv. Sci.*, 39th Congr., 1967, Melbourne, Section C, Abstr., pp. k4-k5.
- 1969. *Blinasaurus*, a brachyopid genus from Western Australia and New South Wales. *Roy. Soc. Western Australia*, vol. 52, pt. 3, pp. 65-88.

[In press.] The Lower Triassic Temnospondyli of Tasmania. *Geol. Soc. Amer.*, Special Paper, 149.

Elliot, David H., Edwin H. Colbert, William J.

- Breed, James A. Jensen, and Jon S. Powell
- 1970. Triassic tetrapods from Antarctica: evidence for continental drift. *Science*, vol. 169, no. 3951, pp. 1197-1201.

Elliot, David H., James W. Collinson, and Jon S. Powell

- 1972. Stratigraphy of Triassic tetrapod-bearing beds of Antarctica. In Adie, Raymond J. (ed.), *Antarctic geology and geophysics*. International Union of Geological Sciences, ser. B, no. 1, Universitetsforlaget, Oslo, pp. 387-392.

Haughton, Sidney H.

- 1915. Investigations in South African fossil reptiles and Amphibia. 1. On a new species of *Trematosaurus* (*T. sobeyi*). *Ann. South African Mus.*, vol. 12, pp. 47-51.
- 1925. Descriptive catalogue of the Amphibia of the Karroo system. *Ibid.*, vol. 22, pp. 227-261.

Howie, Ann

- 1971. A brachyopid labyrinthodont from the lower Trias of Queensland. *Proc. Linn. Soc. New South Wales*, vol. 96, pt. 4, pp. 268-277.
- 1972. On a Queensland labyrinthodont. In Joysey, K. A., and T. S. Kemp (eds.), *Studies in vertebrate evolution*. Edinburgh, Oliver and Boyd, pp. 51-64.

Huxley, Thomas H.

- 1859. On some amphibian and reptilian remains from South Africa and Australia. *Quart. Jour. Geol. Soc. London*, vol. 15, pp. 642-649.

Kitching, James W.

- 1968. On the *Lystrosaurus* Zone and its fauna with special reference to some immature Lystrosauridae. *Palaeont. Africana*, vol. 11, pp. 61-76.
- 1970. A short review of the Beaufort zoning in South Africa. Second Gondwana Symp., South Africa, 1970, *Proc. Papers*, pp. 309-312.

Kitching, James W., James W. Collinson, David H. Elliot, and Edwin H. Colbert

- 1972. *Lystrosaurus* Zone (Triassic) fauna from Antarctica. *Science*, vol. 175, no. 4021, pp. 524-526.

Lehman, Jean-Pierre

- 1955. Les Stégocéphales du Nord-Ouest de Madagascar. *Compt. Rendus Acad. Sci. Paris*, vol. 241, pp. 82-84.
- 1961. Les Stégocéphales du Trias de Madagascar. *Ann. Paléont.*, vol. 47, pp. 111-152.
- 1966. Nouveaux Stégocéphales de Madagascar. *Ibid.*, vol. 52, pp. 117-139.
- 1971. Nouveaux Vertébrés Fossiles du Trias de la série de Zarzaitine. *Ibid.*, vol. 57, pp. 71-93.

Lydekker, Richard

- 1889. Note on the occurrence of a species of *Bothriceps* in the Karroo system of South Africa. *Ann. Mag. Nat. Hist.*, ser. 6, vol. 4, pp. 475-476.
- 1890. Catalogue of the fossil Reptilia and Amphibia in the British Museum. Part IV. Containing the orders Anomodontia, Ecaudata, Caudata, and Labyrinthodontia; and supplement. London, xiii+295 pp., 66 figs.

Nilsson, Tage

- 1942. *Sassenisaurus*, a new genus of Eotriassic stegocephalian from Spitzbergen. *Bull. Geol. Inst. Univ. Upsala*, vol. 30, pp. 91-102.

1943. On the morphology of the lower jaw of Stegocephalia with special reference to Eotriassic stegocephalians from Spitsbergen. I. Descriptive part. K. Svenska Vetenskapskad. Handl., ser. 3, vol. 20, no. 9, pp. 1-46.
1944. On the morphology of the lower jaw of Stegocephalia with special reference to Eotriassic stegocephalians from Spitzbergen. II. General part. *Ibid.*, vol. 21, no. 1, pp. 1-70.
- Olson, Everett C.
1957. Catalogue of localities of Permian and Triassic vertebrates of the territories of the U.S.S.R. *Jour. Geol.*, vol. 65, pp. 196-226.
- Olson, Everett C., and Robert Broom
1937. New genera and species of tetrapods from the Karroo beds of South Africa. *Jour. Paleont.*, vol. 11, pp. 613-619.
- Owen, Richard
1855. Description of the cranium of a labyrinthodont reptile, *Brachyops laticeps*, from Mangali, central India. *Quart. Jour. Geol. Soc. London*, vol. 11, pp. 37-39.
- Parrington, Francis Rex
1948. Labyrinthodonts from South Africa. *Proc. Zool. Soc.*, vol. 118, pt. 2, pp. 426-445.
- Piveteau, Jean (ed.)
1955. *Traité de Paléontologie*, vol. 5. Paris, Masson et Cie., 1113 pp.
- Romer, Alfred Sherwood
1947. Review of the Labyrinthodontia. *Bull. Mus. Comp. Zool.*, vol. 99, no. 1, pp. 1-368.
1966. *Vertebrate paleontology*. Third edition. Chicago, The University of Chicago Press, 468 pp.
- Rozhdestvensky, A. K., and L. P. Tatarinov
1964. Amphibians, reptiles and birds. In Orlov, J. A. (ed.), *Paleontology*. Moscow, Acad. Sci. U.S.S.R., pp. 1-722. (In Russian).
- Säve-Söderbergh, Gunnar
1935. On the dermal bones of the head in labyrinthodont stegocephalians and certain primitive Reptilia with special reference to Eotriassic stegocephalians from East Greenland, Meddel, Grønland, vol. 98, pt. 3, pp. 1-211.
1936. On the morphology of Triassic stegocephalians from Spitzbergen, and the interpretation of the endocranium in the Labyrinthodontia. K. Svenska Vetenskapskad. Handl., ser. 3, vol. 16, pp. 1-181.
- Schroeder, Henry C.
1913. Ein Stegocephalen-Schädel von Helgoland. *Jahrb. Preussische Geol. Landesanst.*, vol. 33, pt. 2, pp. 232-264, pls. 15-21.
- Shishkin, M. A.
1966. [A brachyopid labyrinthodont from the Triassic of the Russian platform.] *Int. Geol. Rev.*, vol. 9, no. 3, pp. 310-322.
- Stephens, William J.
1887. On some additional labyrinthodont fossils from the Hawksbury sandstone of New South Wales. *Proc. Linnean Soc. New South Wales*, ser. 2, vol. 1, pp. 1175-1195.
- Swinton, William Elgin
1956. A neorhachitome amphibian from Madagascar. *Ann. Mag. Nat. Hist.*, ser. 12, vol. 9, pp. 60-64.
- von Huene, Friedrich
1956. *Palaeontologie und Phylogenie der Niederen Tetrapoden*. Jena, VEB Gustav Fischer Verlag, 716 pp.
- Wagner, Heinrich
1935. Das individuelle Wachstum von *Trematosaurus brauni* und der Nachweis von *Mastodonsaurus* in berner Buntsandstein. Halle, Eduard Kling, 70 pp.
- Watson, David M. S.
1912. On some reptilian lower jaws. *Ann. Mag. Nat. Hist.*, ser. 8, vol. 10, pp. 575-587.
1919. The structure, evolution and origin of the Amphibia. The "orders" Rachitomi and Stereospondyli. *Phil. Trans. Roy. Soc. London*, ser. B, vol. 209, pp. 1-73.
1951. *Paleontology and modern biology*. New Haven, Yale Univ. Press, 216 pp.
1956. The brachyopid labyrinthodonts. *Bull. British Mus. (Nat. Hist.)*, London, Geol., vol. 2, no. 8, pp. 315-392.
1962. The evolution of the labyrinthodonts. *Phil. Trans. Roy. Soc. London*, ser. B., Biol. Sci., vol. 245, no. 723, pp. 219-265.
- Welles, Samuel P.
1947. Vertebrates from the upper Moenkopi Formation of northern Arizona. *Univ. California Publ., Bull. Dept. Geol. Sci.*, vol. 27, pp. 241-289.
1957. A new name for a brachyopid laby-

- rinthodont. Jour. Paleont., vol. 31, p. 982.
- Welles, Samuel P., and John Cosgriff
1965. A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi*, n.sp., from the Wupatki Member of the Moenkopi Formation of Northern Arizona. Univ. California Publ. Geol. Sci., vol. 54, pp. 1-148.
- Welles, Samuel P., and Richard Estes
1969. *Hadrokkosaurus bradyi* from the upper Moenkopi Formation of Arizona, with a review of the brachyopid labyrinthodonts. Univ. California Publ. Geol. Sci., vol. 84, pp. 1-56.
- Wilson, J. A.
1941. An interpretation of the skull of *Buettneria*, with special reference to the cartilages and soft parts. Contrib. Mus. Paleont. Univ. Michigan, vol. 6, pp. 71-111.
- Woodward, Arthur S.
1909. On a new labyrinthodont from oil shale at Airly, New South Wales. Rec. Geol. Surv. New South Wales, vol. 8, pp. 317-319.

