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Two New Species of *Broiliellus* (Amphibians) from the Permian of Texas

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INTRODUCTION

The genus *Broiliellus* has been based entirely on the genotype, *Broiliellus texensis*, which was described (Williston, 1914, pp. 49-56) from two well-preserved specimens from Mitchell Creek of the Clyde Formation, Permian, of Texas. Langston (1953, p. 380) gave the genus considerable temporal dimensions by suggesting that *Aspido-saurus novomexicanus* (Case and Williston, 1913, pp. 7-9) from the early Permian Abo Formation of New Mexico was in reality a species of *Broiliellus*.

Undescribed specimens, some from the Arroyo Formation, others from a horizon that is probably earlier than the Clyde add information to the nature of the genus.

Acknowledgements.—This paper is one of several to result from a study of dissorophid amphibians initiated at the suggestion of E. C. Olson. I am grateful to him for his advice during all phases of this study. The illustrations were made by Mrs. Jane Hubby. Funds for the illustrations were provided by the University of Illinois Research Board.

Abbreviations.—Any abbreviations are explained in the figure captions except for the names of the museums from which the specimens were obtained. Thus, FMNH means Field Museum of Natural History and UT means the University of Texas.

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HISTORY OF THE STUDY OF BROILIELLUS

A family of amphibians with dorsal dermal armor, the Dissorophidae, has been recognized since the early 20th century (Boulenger, 1902, p. 383). However, the first study of reasonably comprehensive nature dates from the description of *Broiliellus* by Williston. In 1914 (p. 56) he constructed the following diagnosis of the genus: "Shields much broader than the vertebrae, not imbricated and not V-shaped; free from slender neural spines; skull spinose." This diagnosis was intended to separate *Broiliellus* from *Aspidosaurus* and *Alegeinosaurus* which were believed to be its closest relatives. Together these genera were placed in a new subfamily, the Aspidosaurinae, while the other known genera of dissorophids (*Dissorophus* and *Cacops*) were placed in another subfamily, the Dissorophinae.

These subfamilies were largely based on the number of armor segments for each vertebral segment. For each vertebral segment there were supposed to be two armored segments in the Dissorophinae and only one in the Aspidosaurinae.

DeMar (1966b) has shown that the number of armored segments per vertebral segment has no taxonomic value at the subfamily level, and that genera that are closely related have different numbers of armored segments per vertebral segment. *Broiliellus* is closely related to *Dissorophus*, whereas *Aspidosaurus*, *Cacops*, and *Alegeinosaurus* fall into another supergeneric group.

The earlier dissorophids, including some new ones, have been studied by Carroll (1964) and when this information is available a formal revision of *Broiliellus* will be possible. Until that time the two new species described here add to the known dimensions of the genus and give some evidence on the evolution of the genus.

Before the new species are described it should be pointed out that Romer (1947, p. 160) suggested that *Broiliellus* was in reality a synonym of *Tersomius* of the Belle Plains Formation. *Tersomius texensis*, the only described species, had originally been described by Case (1911, p. 51; 1946, p. 387) as a trimerorhachid, but Romer noted that the posterior part of the skull is broken and it actually should be interpreted as a dissorophid.

As Romer observed, the skull of *Tersomius* differs from that of *Broiliellus* in that it is very small, has open sutures, and does not have the exostoses and dermal pitting of *Broiliellus*. These are the characters of immature individuals, and thus, allowing for change of

form with growth, Romer concluded that the two genera were one. As he mentioned, the name *Tersomius* holds priority.

However, my own observations would seem to suggest that *Broiellus* is actually a valid genus. Specimen FMNH UC 41, from the Clyde Formation of the Permian of Texas, is a skull about 5 cm. in length (compared to about 3.5 cm. for that of *Tersomius*), and is in every way like the skull of *Broiellus texensis*. Thus, its skull roofing bones are firmly co-ossified, and it has a characteristic pattern of ridges and valleys on the skull roof. Since the size difference between this skull and that of *Tersomius* is not serious, they would appear to be from animals of comparable maturity. This would appear to support the concept that the two genera are distinct.

In addition, there are certain other differences between the skulls of these two genera that are not readily explained by differential growth. The anterior margin of the otic notch of the skull of *Tersomius* is rounded, whereas that of *Broiellus*, including the smaller specimen, is a slanted, nearly straight shelf, facing dorsally and posteriorly. Moreover, the external nares of *Tersomius* are small and round, while those of *Broiellus*, even in the small specimen, are elongate and fairly large. Since openings in the skull tend to become proportionately smaller with age, not larger, all this data would seem to establish *Broiellus* and *Tersomius* as distinct genera.

SYSTEMATICS

Class Amphibia

Order Rhachitomi

Family Dissorophidae Boulenger, 1902

Genus *Broiellus* Williston, 1914

Broiellus arroyoensis, new species

Holotype.—FMNH UR 431, from the Arroyo Formation at East Coffee Creek, Lower Permian, Baylor County, Texas. This specimen is from Olson's *Broiellus* pocket (DeMar, 1966a). It consists of the anterior two-thirds of a skull, including the entire skull roof to a point just posterior to the orbits, and the complete upper and lower jaws to the articulation on the right side.

Referred Material.—Five specimens from the same locality as the holotype. FMNH UR 808, a sacral rib and five articulated vertebrae; FMNH UR 809, part of the anterior portion of the skull and the sphenethmoid; FMNH UR 810, a nearly complete armor cara-

pace; FMNH UR 811, the posterior part of the skull and braincase; FMNH UR 812, part of the shoulder girdle and carapace.

Diagnosis.—The skull is, from a dorsal aspect, roughly triangular with nearly straight maxillary margins, and with a sharply rounded snout. The skull is low, but somewhat deeper than that of *Broiliellus texensis*, and rises gradually from the snout posteriorly. The skull roof sculpture is sharp and has higher relief than that of any other *Broiliellus* species.

Description and Discussion.—The skull of *Broiliellus arroyoensis* is represented by three previously undescribed specimens from the *Broiliellus* pocket. Only one of these specimens, FMNH UR 431, is relatively complete and that specimen does not have a preserved braincase.

The skull roof is best represented on FMNH UR 431. This specimen shows that the skull is about 9.6 cm. long, and is in the shape of an isosceles triangle from a dorsal aspect. The triangle has as its base the posterior part of the skull (8 cm.) and, as its equal sides, the maxillary-jugal-quadratojugal margin (9.5 cm.). The only strong interruption to the resemblance to an isosceles triangle is the fact that the snout is rounded, though more sharply than in the other species of *Broiliellus*.

The external nares are very much like those of *Broiliellus texensis* and are large, marginal, and anterior. They are directed more laterally than vertically or anteriorly. The orbits are directed laterally and dorsally, and are in the shape of an irregular oval that is elongated parallel to the lateral margin of the skull. Unlike the situation in *Broiliellus texensis*, the anterior margin is almost flat.

It is impossible to describe the otic notch accurately, as the material is incomplete. As seen in specimen FMNH UR 811, from Olson's *Broiliellus* pocket, it is deep and has the ventrally directed half-moon-shaped flange on the dorsal margin (DeMar, 1966a) that is characteristic of the dissorophid otic notch.

The sutures between the skull roofing bones cannot be made out, but they must be like those of *Broiliellus texensis* (Romer, 1947, p. 160). Also they are no doubt like those of *Broiliellus olsoni* (illustrated in Figure 2).

The teeth of *Broiliellus arroyoensis* are well preserved on FMNH UR 431, except for those on the premaxillary bones. The marginal teeth are all slender and pointed. The most anterior teeth are about 3 mm. long and are slightly curved internally and posteriorly. Toward

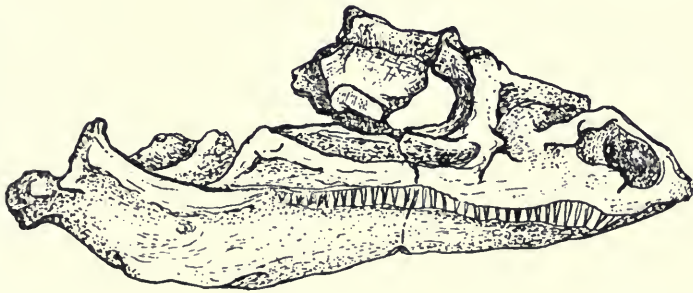
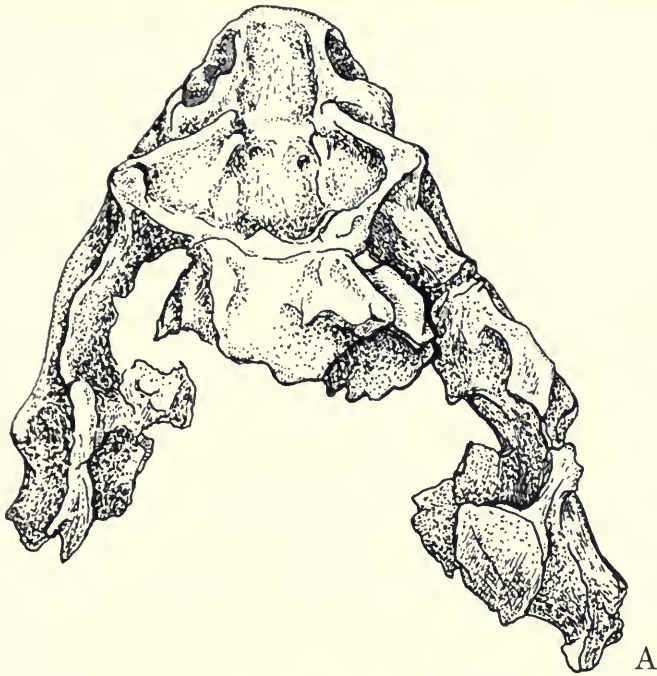


FIG. 1. A, dorsal view of the skull of *Broiliellus arroyoensis*, n. sp., FMNH UR 431; B, lateral view of the same specimen. Both figures $\times 1$.

the back of the tooth row the teeth gradually decrease in size so that the most posterior maxillary teeth are 1 mm. in length. There are about 45 teeth on each side.

The exostoses, or tubercles, ridges and depressions of the skull roof of *Broiliellus arroyoensis* reach the known extreme size for any dissorophid and, as a consequence, are exceptionally well defined.

Most of them may be discerned by examining Figure 1. In addition, FMNH specimen UR 811 possesses a very large tubercle on each postparietal, a moderately large tubercle on the posteriormost portion of each tabular, and a ridge of variable proportions along the dorsal margin of the otic notch. All of the tubercular development, except for the greater size and relief, is very much like the situation in other species of *Broiliellus*, and in *Dissorophus*.

The palate of *Broiliellus arroyoensis* is not well preserved on any specimen, but can best be seen on FMNH specimens UR 431 and UR 811. No palatal teeth are preserved, but they were almost certainly present since they have been described for *Broiliellus novomexicanus* (Langston, 1953, p. 381) and for other members of the family. The vacuities are large and the palate is firmly fused to the braincase.

The braincase is not well preserved in the holotype, except for a part of the cultriform process and sphenethmoid region, but FMNH specimen UR 811, from Olson's *Broiliellus* pocket, has a fairly well-exposed braincase from the pituitary fossa posteriorly. Specimen UR 809, from the same locality, has parts of the sphenethmoid region and the cultriform process.

The braincase is well ossified, except for parts of the pro-otic, and is very much like that of other rhachitomes, such as *Eryops* (Sawin, 1941, pp. 431-44), and *Trematops* (Olson, 1941, p. 165). Thus, only brief comments are necessary. The parasphenoid is standard in appearance with somewhat enlarged posteriorly directed flanges for ventral neck musculature. The fenestra ovalis is poorly preserved, but is apparently round, and occurs just posterior and dorsal to the parasphenoid flanges, as in *Eryops*. The pro-otic incisure appears just anterior to the parasphenoid flange, on the lateral surface of the braincase.

Twin foramina for the carotid arteries are present just posterior to the cultriform process and pass dorsally into the pituitary fossa. The braincase is immovably fused to the palate by the firmly ossified basipterygoid processes. Anteriorly the cultriform process of the parasphenoid is a slender rod ventral to the well-ossified sphenethmoid. The sphenethmoid does not expand anteriorly, as it does in *Eryops* (Sawin, 1941, pl. 3), but is approximately the same width throughout, a condition that is universal in the dissorophids and trematopsids.

Specimen FMNH UR 808, which was found in association with specimens of *Broiliellus arroyoensis*, *Trematops* sp., and *Longiscitula houghae*, consists of a partial vertebral column and attached sacral

rib. On the basis of size it would appear to be most reasonably assigned to *Broiliellus arroyoensis*, though this is not certain. It is described here because its form can be compared significantly with the form of the sacral rib in other dissorophids.

The specimen, FMNH UR 808, consists of five articulated vertebrae, the most anterior of which probably articulated with the somewhat displaced sacral rib as it is significantly larger than its neighbors. The sacral rib has an enlarged articular head with an oval face for the transverse process and the intercentrum. The lateral face of the transverse process is correspondingly enlarged for the reception of this sacral articulation.

The sacral rib narrows distally to a neck, oval in cross-section, and then expands into a blade-like rib with unfinished bone at the extremities for articulation with the ilium. No direct observation of the nature of the articulation can be made, but it appears that the rib must have extended directly from the vertebra to the ilium without the downward flexed distal portion that exists in *Dissorophus*. Moreover, the rib is structurally similar to those of rhachitomes in general. This rib certainly more nearly resembles that of *Dissorophus* than those of *Cacops*.

The armor of this species has been described in another paper (DeMar, 1966b), so here it is only necessary to point out that it is identical in every observed detail to that of *Broiliellus texensis*. Fortunately, it has been possible to examine the ventral surface of the armor and to ascertain that each segment has a ventrally directed flange that must have fit between the neural spines. This is like the situation in the internal series (DeMar, 1966b) of *Dissorophus*.

Broiliellus olsoni new species

Holotype.—UT 3189-8, consisting of two-thirds of a skull, including the almost complete anterior portion, and part of the posterior portion on one side, from the Thaxton Ranch locality, Wichita Group (probably the lower part), Lower Permian, Clay County, Texas.

Referred Material.—UT 3189-8, consisting of a ventral posterior lateral part of a skull, including part of the maxillary, posterior part of the lower jaw, and the ventral part of the otic notch, from the same locality as the holotype.

Diagnosis.—The skull is roughly triangular. From a dorsal aspect it has a broadly rounded snout, and a curved maxillary margin. The skull is broad, with the postorbital part of the skull relatively shorter

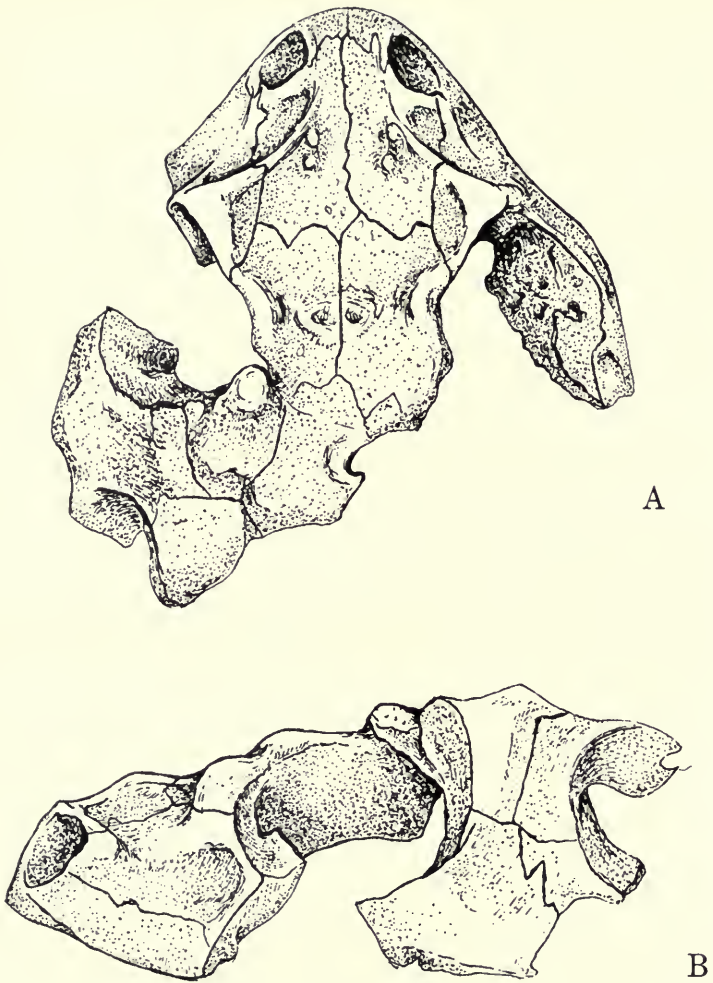


FIG. 2. A, dorsal view of the skull of *Broiliellus olsoni*, n. sp., UT 3189-8. $\times 1$. B, lateral view of the skull of *Broiliellus olsoni*, n. sp., UT 3189-8. $\times 1$.

than in other species. External nares are large and nearly circular. The skull is relatively high and with nearly the same depth from a point just posterior to the nares to the posterior margin. In connection with this form and depth, the anterior and lateral margins of the skull are sharply rounded downward. The anterior margin of the otic notch is steeper than in the other species.

Description and Discussion.—The only material currently representative of this new species is one partial skull, and another small fragment of a skull and lower jaw. The material is a part of a large collection of fragmentary *Seymouria*, miscellaneous reptiles, and fragments of amphibian skeletal material from Thaxton Ranch. More of this material may belong to *B. olsoni*, but this is impossible to determine. A careful search of all the material has revealed no armor.

At least two individuals are included in the available material, and since armor is easily preserved, it would appear that there is some possibility that this species is not armored. If this is ever demonstrated to be so, it would be best to elevate this species to a new genus.

The best preserved skull is UT 3189-8. This specimen shows that the skull is almost the same as *B. texensis* in size and in the form and sculpture of the dermal skull bones. In dorsal aspect the skull is shaped almost like an equilateral triangle, except that the lateral and anterior margins are broadly rounded. The posterior margin is not preserved. In lateral aspect, beginning anteriorly, the skull roof rises sharply at about a 45° angle to a point just posterior to the nares, where the skull rounds off and increases only slightly in depth to the posterior extremity. The skull is very deep, compared with the other species of *Broieliellus*.

In addition to the great depth of the skull, the postorbital length of the skull is relatively short compared with that of *Broieliellus texensis* or *B. arroyoensis*. This, incidentally, seems to be characteristic of a number of Early Permian and Late Pennsylvanian dissorophids, including *Amphibamus grandiceps* (Gregory, 1950, p. 844) and *Broieliellus novomexicanus* (Langston, 1953, p. 380).

The external nares are lateral and anterior, and are directed forward, upward and laterally about equally. The nares are nearly circular, unlike those of most other dissorophoids.

The orbits are large, nearly circular, and are directed upward and laterally. As has been mentioned, the skull is shorter, posteriorly, than in most dissorophids, consequently the orbits occupy a slightly more posterior position than usual.

The otic notch is incompletely preserved, making it impossible to know the exact nature of the tabular, and whether the tabular joins the quadrate, thus closing the otic notch behind. At present, the otic notch can be described thus: The dorsal margin is horizontal, and about 2-3 mm. posterior to the squamosal-postparietal contact it curves downward, and partly backward, so that the anterior mar-

gin slopes 60° posteriorly, to a point just dorsal to the jaw articulation, where it becomes sharply horizontal. The steep slope of the anterior ventral face of the otic notch is no doubt connected with the shortness and great depth of the skull table.

The margin of the otic notch is smooth, has essentially no surface irregularities, and is formed from the following bones: Tabular (not preserved), supratemporal, squamosal or quadrate. Dorsally, the supratemporal and a small part of the squamosal are inflected downward, with a vertical external surface, so that a half-moon-shaped obstruction decreases the size of the otic notch, as in other dissorophids. Anteriorly, the squamosal is inflected inward and backward from the margin of the otic notch in a broad shelf, which declines to the jaw articulation, as previously described.

The internal posterior projection of the quadrate is inflected upward, and is terminated by a rough, broken surface, indicating that the otic notch was either partly closed behind, as in *B. texensis*, or completely closed, as in *Dissorophus*. This detail, however, does not seem very important, as it may have varied according to the age of the animal at death.

The surface details of the skull have some importance for taxonomic purposes, as in other dissorophids. One is struck by the general similarity of the surface detail of the skull of this animal to that of *Dissorophus*, of course, and more particularly to those of the other species of *Broiliellus*. The major difference is that the topography is more subdued in *B. olsoni* than in either *B. texensis* or *B. arroyensis*. The surface sculpture is illustrated in Figure 2.

The sutures between the skull roofing bones are clear, and show those bones which one would expect. There is no intertemporal. The orbit intersects the jugal, lacrimal, prefrontal, frontal and post-frontal bones, as in other genera with large orbits. The squamosal is strongly indented by the otic notch. Details can be seen in the illustrations.

The marginal teeth are not well preserved on the holotype. The margins of the maxillary and premaxillary bones apparently have a single row of small, pointed teeth which are continuous, except on the extreme posterior part of the maxillary, where they are absent. There are approximately 47-48 teeth on either side of the upper jaw in this marginal series. They are fairly homogeneous in size, except for the most posterior teeth, which are slightly smaller.

The referred specimen, UT 3189-8, from Texas, has the only well-preserved teeth. These are about 2 mm. long and are pointed. They are apparently directed somewhat inward.

The palate is similar to that of other dissorophids. The palatal vacuities and the internal nares are large. The internal nares are marginally placed, and elongated parallel to the margin of the jaw. The bones of the palate are difficult to distinguish, although some sutures can be made out. There is nothing obviously irregular, except possibly that the cultriform process of the parasphenoid is firmly interdigitated to the vomers.

The braincase is preserved only in the sphenethmoid region. The sphenethmoid is well ossified, and passes throughout the known extent without variation in width, unlike *Eryops*, but similar to the situation in other known dissorophids. The cultriform process is firmly attached to the sphenethmoid.

DISCUSSION AND CONCLUSIONS

Two new species of *Broiliellus*, *B. olsoni* and *B. arroyoensis*, have been described. There is little question that these two species, together with *B. novomexicanus* and the genotype, *B. texensis*, form a closely knit group of species. However, there is also little doubt that these species are truly distinct. There are not enough specimens to evaluate variation properly, but all of the type specimens are of about the same size, so that it is unlikely that the relative maturity of the individuals can explain their differences. In addition, such growth stages as are known indicate that there is little differentiation of skull form with age.

Moreover, these species are all from different horizons. *B. olsoni* is from the Thaxton Ranch locality, which is, most probably, Lower Wichita, possibly the Admiral Formation, according to Romer (1958, p. 176). *B. texensis* is from the Clyde Formation, and *B. arroyoensis* is from the Arroyo Formation.

Broiliellus novomexicanus (Langston, 1953, p. 380) is certainly another species of *Broiliellus*, and is known only from the Lower Permian of New Mexico. This is approximately equivalent to the Moran and Admiral Formations in Texas (Langston, 1953, p. 411), which means that this species is about the same age as *B. olsoni*. This species cannot be reviewed here thoroughly, because of the difficulty of studying certain specimens. However, it can be said that

this species stands out from the other named species because of its early occurrence, its generally low skull, its narrow armor (DeMar, 1966b), and its short postorbital skull length.

Thus *Broiliellus* is one of the most diverse and long-lived of Permian amphibian species. We cannot be sure of the phylogeny, because of the scarcity of specimens, but we can recognize certain evolutionary trends. There is a gradual development in the armor from the early, lightly armored *B. novomexicanus*, or possible lightly armored *B. olsoni*, to the heavily armored *B. texensis* and *B. arroyoensis*. In addition, there appears to be a progressive development of greater relief and sharpness in the skull roof topography, and of more complete closure of the sutures between the skull roofing bones. All of these features can be interpreted together as causing a general increase in the strength of the skull.

In general, dissorophids of Arroyo age and later (*B. arroyoensis*, *Dissorophus multicinctus* and *Cacops aspidephorus*, especially) have firmly constructed skulls, and are well ossified with good articulations. This has been interpreted (DeMar, 1966a) as evidence that the dissorophids were becoming more completely adapted to terrestrial life. From this point of view, it would be preferable that the species of *Broiliellus* represent a single phyletic ramus.

On the other hand, there is the possibility (with continuous-permutations with the previous one) that the species of *Broiliellus* provide an all-too-dim look at the adaptive radiation of the genus. In this case, these four species would be related only by having a common ancestor. The terrestrial adaptations would be interpreted in the same way as before, but there would be no record of a gradual development toward a more terrestrial state.

Another paper will deal with the distribution and general adaptation of the dissorophids, but it can be pointed out here that none of these species is found associated with the common aquatic or semi-aquatic species of the Permian. Instead, they are found with reptiles or terrestrial-appearing amphibians. This would suggest that *Broiliellus* avoided aquatic environments, and lived in the more upland portions of the Permian depositional area.

Note: Since this paper was submitted in 1964, new material has been published by Carroll. Since the main purpose of the present paper is to describe new species of *Broiliellus*, this information is not discussed here.

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