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Triassic Vertebrates of Gondwanan Aspect from the Richmond Basin of Virginia

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A new locality of early Late Triassic age in the Richmond basin of east-central Virginia has yielded abundant remains of a diversified assemblage of small to medium-sized tetrapods that closely resembles Southern Hemisphere (Gondwanan) assemblages in the predominance of certain synapsids. Associated palynomorphs indicate an early middle Carnian age for the fossiliferous strata. The discovery suggests that previously recognized differences between tetrapod assemblages of early Late Triassic age from Gondwana and Laurasia at least in part reflect differences in stratigraphic age, rather than geographic separation.

DURING THE TRIASSIC, SYNAPSID-dominated assemblages of terrestrial vertebrates, persisting from the late Paleozoic, gave way to the archosaur-dominated assemblages that came to characterize the Age of Reptiles. Despite the importance of this profound change in the structure of continental ecosystems, many details of the faunal succession during the early Mesozoic remain unresolved. The transition from the Middle to the Late Triassic is particularly poorly understood. Recent claims of a mass-extinction event among tetrapods at the Carnian-Norian boundary in the Late Triassic (*1*) probably reflect, at least to some extent, an apparent temporal discontinuity between the geographically disjunct Middle Triassic synapsid-dominated assemblages of Gondwana and the classic archosaur-dominated communities from the Upper Triassic of Laurasia. Discovery of tetrapods of early Late Triassic age in strata of the Newark Supergroup in Virginia sheds new light on this longstanding problem.

The Richmond basin (Fig. 1), located in east-central Virginia, about 19 km west of Richmond, is a half-graben that is surrounded by igneous and metamorphic rocks of the Piedmont Province. It is part of a system of rift-basins along the eastern margin of North America that formed during a 45-million-year episode of crustal thinning and stretching preceding the Jurassic breakup of Pangaea. The strata deposited in these rift-basins are collectively referred to as the Newark Supergroup (*2*). The Richmond basin and the neighboring Taylorsville basin contain the oldest sedimentary rocks of the Newark Supergroup currently known south of Nova Scotia (*2, 3*). The Richmond basin is also one of the geologically most poorly understood basins of the Newark Supergroup because exposures of strata are scarce and the region is characterized by deep and intense weathering. The Richmond and the adjacent Taylorsville basins differ from other basins of the Newark Supergroup in the predominance of gray and black lacustrine to paludal sedimentary rocks, rather than red and brown playa and fluvial sedimentary rocks (*2, 3*).

Tetrapod material was collected from what was originally a small roadside exposure near Midlothian, Chesterfield County, Virginia. In view of its close geographic proximity to Little Tomahawk Creek, the site will henceforth be referred to as the Tomahawk locality. Most of the tetrapod bones and teeth occur in a massive calcareous gray mudstone with root traces, abundant coalified plant debris, and numerous small calcareous nodules. The mudstone is

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part of the Tomahawk Creek Member of the Turkey Branch Formation (*3*) and is overlain by a thinly bedded siltstone, which contains countless scattered scales and bones of the holostean fish *Dictyopyge* and rare archosaurian teeth. The tetrapod bones are excellently preserved but almost always dissociated. Exceptions include several partial skulls and part of a skeleton of eucynodont synapsids, an associated but disarticulated skeleton of a small reptile, and associated osteoderms and bones of an armored archosaurian reptile.

On the basis of palynological evidence, age estimates for the sedimentary rocks in the Richmond basin range from either late Ladinian to early Carnian (*4*) or early to middle Carnian (*5*). The uncertainty stems from a lack of abundant palynoflorules from the respective European type sections, rather than from absence of palynological data from the Richmond basin, which contains many productive levels. On balance, an early middle Carnian age for the fossiliferous strata appears most likely.

The most common identifiable faunal element is a new traversodont eucynodont (*6*). In the structure of its upper postcanine teeth, this synapsid most closely resembles *Luangwa* from the Anisian Ntawere Formation of Zambia and *Traversodon* from the Carnian Santa Maria Formation of Brazil (*7*). It is, however, sufficiently different from all previously described traversodont eucynodonts in a number of dental features to warrant taxonomic recognition as a new genus and species, *Boreogomphodon jeffersoni* that is characterized by lower postcanine teeth with three, rather than two, transversely oriented mesial cusps and upper postcanine teeth with a single mesial buccal accessory cusp and a large mesial basin (*8*) (Fig. 2). Among known traversodont eucynodonts, lower postcanine teeth of *Boreogomphodon* share the presence of three mesial cusps only with an isolated, as yet indeterminate, lower postcanine tooth from the middle Wolfville Formation of Nova Scotia (*6*). This tooth, however, particularly differs from those of *Boreogomphodon* in the considerable mesiodistal compression of the crown and in the absence of a raised distal rim on the heel.

Most of the new traversodont specimens represent juvenile individuals, as indicated by the small size, the low number (four or five) of postcanine teeth, the proportional shortness of the snout (*6, 9*), and the retention of multicuspid sectorial teeth (*9, 10*). Along with the fragmentary traversodont material from the Wolfville Formation of Nova Scotia, *Boreogomphodon* documents the presence of this Gondwanan group of eucynodonts in North America.

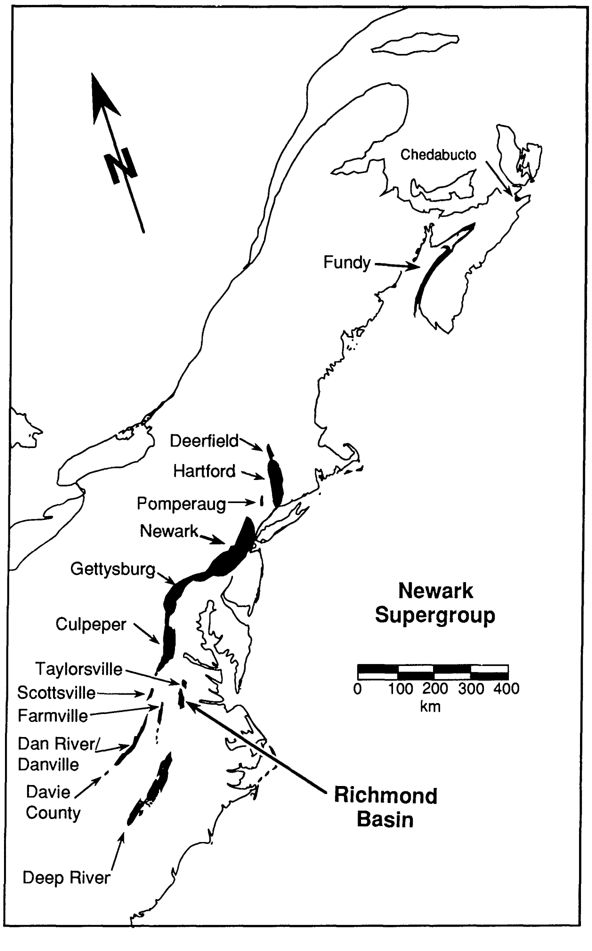

Fig. 1. Distribution of the major rift basins of the Newark Supergroup in eastern North America [modified from (*3*)].

A second eucynodont is represented by two dentaries with teeth and several isolated postcanine teeth. The postcanine teeth closely resemble those of *Microconodon* from the lower Cumnock Formation (middle Carnian) of North Carolina (*11*) and *Pseudotriconodon* and several other taxa that are represented mostly by isolated teeth from the Upper Triassic (Norian) of western Europe (*12*). Placed in the Mammalia by its original describers (*11*), *Microconodon* has most recently been interpreted as a possible representative of the Chiniquodontidae, which are otherwise known from the Middle to Upper Triassic of Argentina and Brazil (*13*). The postcanine teeth of the new eucynodont each bear three mesiodistally aligned cusps, the central one of which is the tallest, and are devoid of cingula. The roots of isolated teeth show a distinct figure-eight shape in transverse section. The dentary lacks a distinct angular process. The material from the Tomahawk locality closely resembles the holotype and only known specimen of *Microconodon tenuirostris*.

Parts of the dorsal armor and various postcranial bones appear to represent a single specimen of an unusual new archosaurian reptile. Two longitudinal rows of distinctive osteoderms formed a narrow carapace. Although they resemble osteoderms of *Doswellia* from the correlative Falling Creek Member of the Doswell Foundation in the adjacent Taylorsville basin (*14*) in the crocodile-like pattern of ornamentation, they differ most notably in the possession of prominent lateral spines. Numerous isolated teeth indicate the presence of several other archosaurian taxa including phytosaurs.

Isolated maxillae and dentaries indicate the presence of several taxa of lepidosauromorph diapsids, including a sphenodontian similar to *Diphydontosaurus* (*15*). A distinctive new reptile of uncertain affinities is at present only known from a left dentary with a distinctly heterodont and acrodont dentition.

To date, there are no remains attributable to temnospondyl amphibians, particularly Metoposauridae, which were widely distributed throughout North America, Europe, Morocco, and India during the Late Triassic (*16*). A tiny jaw fragment suggests the possible presence of "lissamphibians," on the basis of the nature of the tooth bases (*17*); however, more complete material is needed to confirm this record.

The eucynodont synapsids in the tetrapod assemblage from the Tomahawk locality indicate close faunal ties to the Gondwanan realm, specifically South America (*18*) and southern Africa (*7*). With the possible exception of the phytosaurs, the new assemblage shows no particularly close similarity to the classic assemblages from the Upper Triassic of the western United States (*19*).

Romer (*20*) distinguished three successive major types (A, B, and C) among Triassic tetrapod assemblages worldwide. A-type assemblages are best known from the Lower Triassic of South Africa and are characterized by the predominance of synapsids and paucity of archosaurs. B-type faunas, known especially from the Middle Triassic of Argentina, Brazil, and Tanzania, show a considerable diversity of traversodont eucynodonts and, in most (but not all) instances, rhynchosaurian reptiles. Virtually all of these occurrences are poorly constrained stratigraphically because of the lack of palynofloras and radiometric dates (*21*). The C-type assemblages from the Upper Triassic [many of which are actually Early Jurassic in age (*21*)] are dominated by a considerable variety of archosaurian reptiles, especially dinosaurs. In the general abundance of gomphodont eucynodonts, the Tomahawk tetrapod assemblage closely resembles Gondwanan B-type faunas and clearly differs from the C-type assemblages from the Upper Triassic of North America and Europe. This evidence strongly suggests that previously recognized differences between Carnian tetrapod assemblages from Gondwana and Laurasia reflect, at least in part, differences in stratigraphic age, rather than geographic separation.

The middle part of the Pekin Formation and the Cumnock Formation in the Deep River basin of North Carolina, which are slightly younger than the fossiliferous strata from the Richmond basin (*2, 3*), have produced typical C-type tetrapod assemblages that are dominated by phytosaurs and suchian archosaurs (*2, 22*). Synapsids are rare in these faunas. This difference suggests that a turnover among terrestrial tetrapods occurred during the Carnian, rather than an extinction event at the Carnian-Norian boundary (*1*).

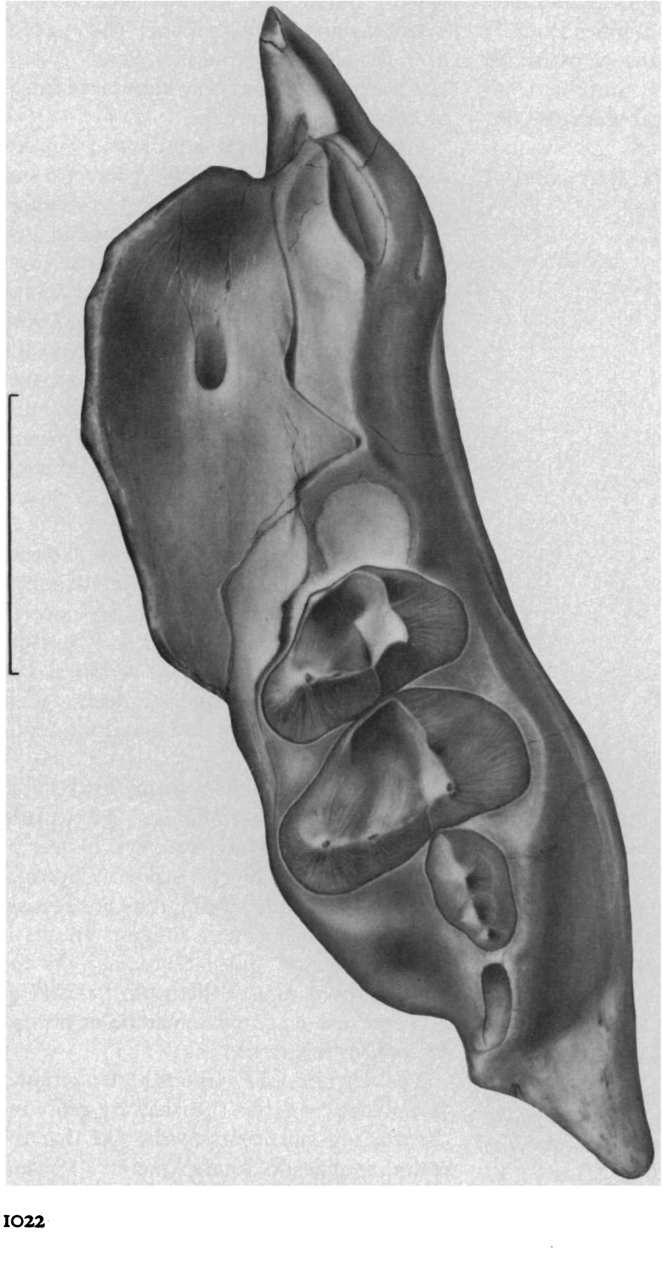

Fig. 2. *Boreogomphodon jeffersoni*, new genus and species. USNM 437632, holotype. Left maxilla with postcanine dentition in occlusal view. Scale equals 5 mm. Anterior end is toward top of the figure.

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Department of Transportation for permission to excavate the Tomahawk site. We thank E. B. Sues and P. A. Kroehler for expert help in the field. Field crews also included M. A. Parrish, K. A. Pitt, R. W. Schlische, and B. J. Small. W. W. Amaral prepared several specimens. M. A. Parrish drew Fig. 2. We thank J. R. Bolt and J. A. Hopson for their help in the identification of certain taxa.

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Alteration of α1 Na$^+$,K$^+$-ATPase ^{86}Rb$^+$ Influx by a Single Amino Acid Substitution

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The sodium- and potassium-dependent adenosine triphosphatase (Na$^+$,K$^+$-ATPase) maintains the transmembrane Na$^+$ gradient to which is coupled all active cellular transport systems. The R and S alleles of the gene encoding the Na$^+$,K$^+$-ATPase α1 subunit isoform were identified in Dahl salt-resistant (DR) and Dahl salt-sensitive (DS) rats, respectively. Characterization of the S allele–specific Na$^+$,K$^+$-ATPase α1 complementary DNA identified a leucine substitution of glutamine at position 276. This mutation alters the hydropathy profile of a region in proximity to T_3(Na), the trypsin-sensitive site that is only detected in the presence of Na$^+$. This mutation causes a decrease in the rubidium-86 influx of S allele–specific sodium pumps, thus marking a domain in the Na$^+$,K$^+$-ATPase α subunit important for K$^+$ transport, and supporting the hypothesis of a putative role of these pumps in hypertension.

THE SODIUM- AND POTASSIUM-DEPENDENT adenosine triphosphatase (Na$^+$,K$^+$-ATPase) maintains the Na$^+$ electrochemical gradient across the plasma membrane by actively transporting Na$^+$ and K$^+$ ions (*1–3*). Maintenance of this Na$^+$ gradient is critical to other vectorial transport systems of the cell (*4*). The Na$^+$,K$^+$-ATPase therefore plays a central role in general and specialized cellular functions such as regulation of cellular volume and pH; ion and solute uptake in the kidney, intestine, liver, and bone; nerve impulse; and muscle contraction, to name a few (*5*). Three α subunit isoforms (*6, 7*) and two β subunit isoforms of Na$^+$,K$^+$-ATPase (*8–10*) with varying αβ cognate pairing in different tissues (*10–12*) have been identified, providing a versatile mechanism for the observed functional diversity. DS rats are salt-sensitive, as shown by hypertension induced by high salt (8%) diets, in contrast to the relative salt resistance of DR rats, marked by normotension despite high salt (8%) diets (*13*). We therefore investigated the possibility of a genetic difference in Na$^+$,K$^+$-ATPase activity in these rats.

Restriction fragment length polymorphism (RFLP) analysis (Fig. 1A) of genomic DNA from DS and DR rats identified homozygosity for a Na$^+$,K$^+$-ATPase α1 allele (S allele) with a 2.5-kb Pst I restriction fragment in DS rats; this is in contrast to the R allele, which is shown by a 3.0-kb Pst I restriction fragment in DR rats. Heterozygosity was marked by the presence of both the 2.5- and 3.0-kb Pst I restriction fragments in equal amounts in two non-inbred rat strains tested: Sprague-Dawley, from which the Dahl rats were derived, and Wistar rats (*14*). This Pst I RFLP is specific for Na$^+$,K$^+$-ATPase α1 gene, as the hybridization patterns of α2 and α3 Pst I restriction digest genomic fragments were unequivocally different from those of α1 (Fig. 1B). Analysis of the nucleotide sequence of the 2.5-kb Pst I genomic fragment from the S allele confirmed specificity for and localization within the Na$^+$,K$^+$-ATPase α1 transcription unit (*14*).

To determine whether there were functional differences between S- and R-specific α1 Na$^+$ pumps, equal amounts of α1 mRNA from kidney polyadenylated [poly(A)$^+$] RNA [an abundant source of α1 mRNA (*11*) and protein (*15*)] from age-matched normotensive DS and DR rats were microinjected (75 to 100 ng per 50 nl) into *Xenopus* oocytes (*16–18*). Equality of nondegraded α1 mRNAs was ascertained by Northern blot analysis and densitometric quantitation of α1-specific hybridizing signal (Fig. 2A). After 3 days of incubation, ouabain-sensitive rubidium-86 ion (^{86}Rb$^+$) influx was assayed (*19*) in the presence of 20 μM monensin, 140 mM Na$^+$, and 5 mM Rb$^+$ with and without 1 mM ouabain. The oocytes microinjected with homozygous R (RR) RNA had greater ouabain-sensitive ^{86}Rb$^+$ influx as compared to the oocytes microinjected with homozygous S (SS) RNA (Fig. 2B). Results from three independent experiments were concordant, showing that the 20-min time point of incubation (20°C), SS-specific ^{86}Rb$^+$ influx was 25 to 45% of RR-specific ^{86}Rb$^+$ influx (Table 1). These results have been confirmed in another experimental system: ouabain-sensitive ^{86}Rb$^+$ influx measurements between age-matched normotensive DS and DR rat erythrocytes (*20*).

To determine whether the decreased ^{86}Rb$^+$ influx of the S-specific α1 Na$^+$ pump

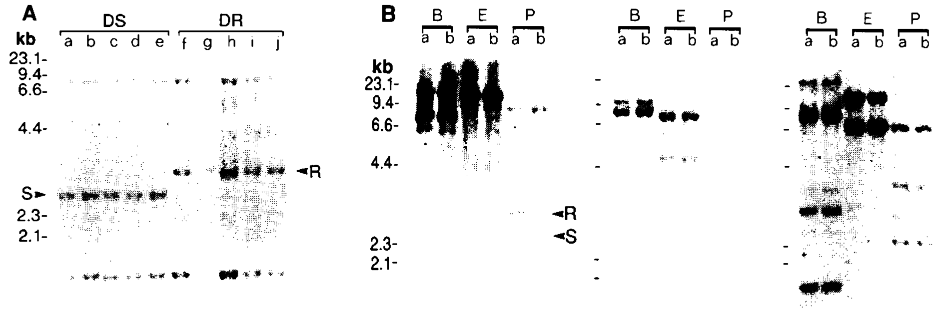

Fig. 1. RFLP analysis of Na$^+$,K$^+$-ATPase α1 gene in DS and DR rats and comparative Southern (DNA) blot analysis of Na$^+$,K$^+$-ATPase α1, α2, and α3 genes. (**A**) Southern blot analysis of Na$^+$,K$^+$-ATPase α1 Pst I restriction digest of genomic DNA from DS and DR rats detects a RFLP identifying the S allele marked by a 2.5-kb Pst I restriction fragment (S), and the R allele marked by a 3.0-kb Pst I restriction fragment (R). Five of 15 animals tested for each group, (a through e) DS and (f through j) DR, are shown. DNA molecular weight markers (in kilobases) are shown on the left. (**B**) A panel of three Southern blots showing distinct isoform-specific genomic restriction fragments for Na$^+$,K$^+$-ATPase α1, α2, and α3 genes. The Pst I RFLP (R) and (S) is detected only in the Na$^+$,K$^+$-ATPase α1 Southern blot. Restriction enzymes used: Bam HI (B), Eco RI (E), Pst I (P); genomic DNA obtained from DR (a), and DS (b) rats. The isoform-specific α subunit hybridization probes used were: α1, 1.8-kb Eco RI–Bam HI restriction fragment; α2, 3.0-kb Eco RI–Eco RI cDNA; α3, 3.0-kb partial Sac I–Eco RI restriction fragment (*12*). Southern blot analysis was performed as described (*7*) with three 15-min washes at 65°C, in 0.1× saline sodium citrate, 0.1% SDS.

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