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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 pelynomorphs 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 Forma-

tion 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.

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 Cummock 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

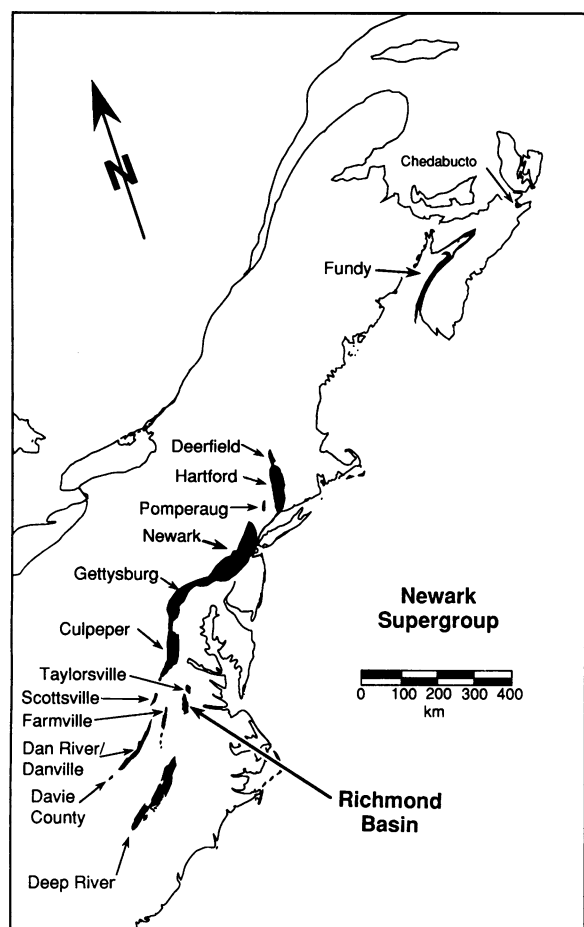


Fig. 1. Distribution of the major rift basins of the Newark Supergroup in eastern North America [modified from (3)].

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).

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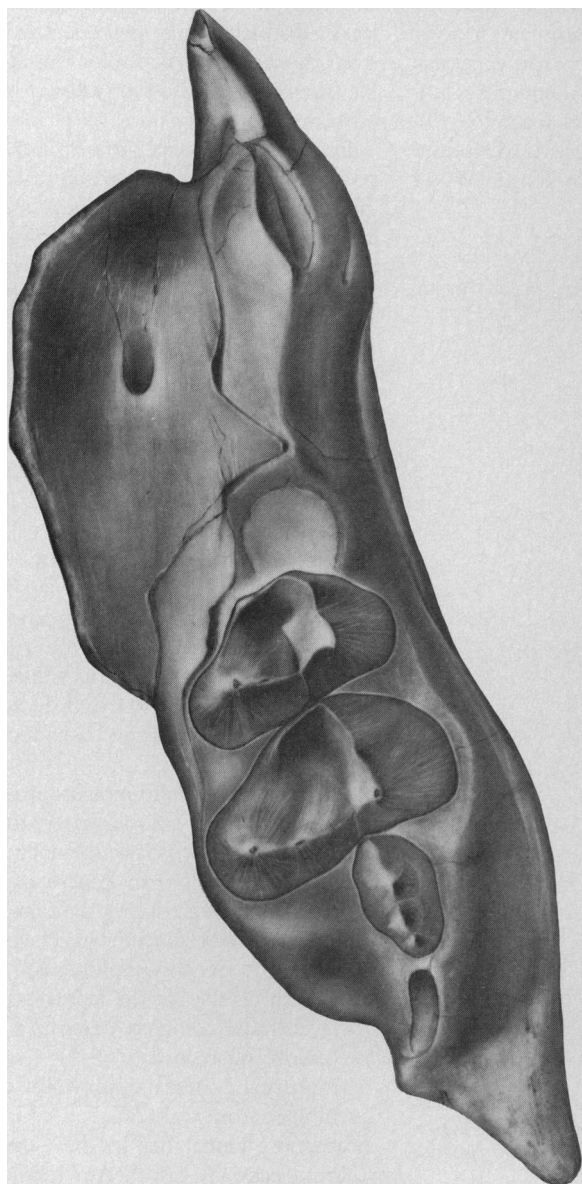


Fig. 2. *Boreogomphodon jeffersoni*, new genus and species. USNM 437632, holotype. Left maxilla with postcanine dentition in occlusal view. Scale equals 5 mm. Anterior end is toward top of the figure.

