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Small tetrapods from the Upper Triassic of the Richmond basin (Newark Supergroup), Virginia

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Introduction

During the Triassic period, profound changes took place in the composition of continental biotas (Cox, 1967; Benton, 1986; Olsen and Sues, 1986). Late Permian communities of continental tetrapods were dominated by nonmammalian synapsids. During the Triassic, these assemblages gave way to communities that were dominated by archosaurian reptiles, especially dinosaurs, but also included other important elements of later continental biotas, such as lepidosaurs, mammaliaform synapsids, and turtles. Despite the obvious importance of this faunal transition, the pattern of change among Triassic continental tetrapods has yet to be fully documented. Much of the currently available fossil record has been recovered from stratigraphically poorly constrained strata of Middle and Late Triassic age in the southern continents, especially in Argentina, Brazil, and Tanzania (Romer, 1966; Cox, 1973). These assemblages appear to differ from the classic Late Triassic tetrapod assemblages from Europe and the American Southwest in their taxonomic composition, which is puzzling in view of the fact that the Triassic was the only period in tetrapod history during which a single landmass existed for the entire length of the period (Cox, 1973; Parrish, Parrish, and Ziegler, 1986).

The early Mesozoic Newark Supergroup comprises the remnants of the sedimentary and igneous fill of an extensive series of partially fault-bounded basins that formed in continental crust along the eastern margin of North America in response to extensional forces during the initial phase of the breakup of Laurasia (Olsen, Schlische, and Gore, 1989). Its sedimentary rocks, ranging in age from the Middle Triassic to Early Jurassic, have traditionally been regarded as virtually devoid of tetrapod bones, although tracks and trackways representing a considerable variety of tetrapods

are locally very abundant. Starting in the 1950s, renewed collecting efforts, first by Donald Baird (formerly of Princeton University) and subsequently by Paul Olsen and his associates, have resulted in the discovery of several stratigraphically well constrained tetrapod-bearing localities in strata of the Newark Supergroup (Olsen, 1988; Olsen et al., 1989).

We report here on an early Late Triassic tetrapod assemblage from the Tomahawk Creek Member of the Turkey Branch Formation in the Richmond basin of east-central Virginia. It is quite unlike any other known from North America and raises a number of important questions regarding early Mesozoic biogeography and faunal change. A brief report on the Tomahawk assemblage has already been published (Sues and Olsen, 1990). This chapter presents a preliminary review of the small tetrapods and discusses the general significance of the Tomahawk tetrapod assemblage.

Geological setting

The Richmond basin (Figure 8.1) is located in east-central Virginia close to the eastern edge of the Piedmont, some 19 km west of Richmond. It is surrounded by igneous and metamorphic rocks of the Piedmont Province and is bounded on the western side by a series of normal faults. As exposed today, the basin is 53 km long and about 15 km wide at its widest point, covering an area of only 273 km² (Cornet and Olsen, 1990). Its small size, compared with many other basins of the Newark Supergroup, however, is deceptive, because close similarities in facies development suggest that it was once continuous with the Taylorsville basin, which lies just 11 km to the north (Ressetar and Taylor, 1988; Cornet and Olsen, 1990). A large portion of the latter basin underlies the Atlantic Coastal Plain to the northeast, where it is probably

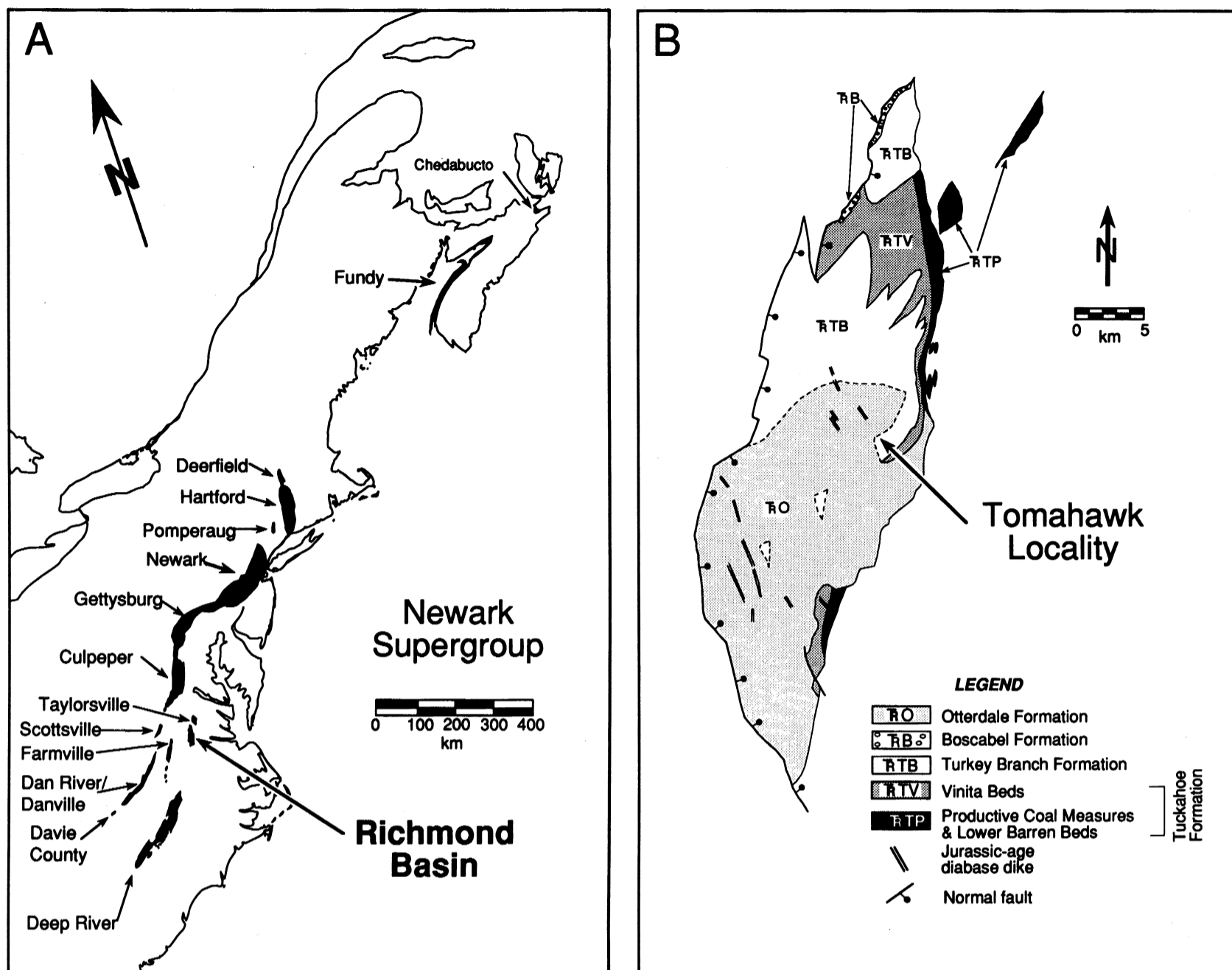


Figure 8.1. (A) Distribution of the principal rift basins of the Newark Supergroup in eastern North America. (B) Geological map of the Richmond basin. (Modified from Olsen et al., 1989.)

continuous with the recently discovered Queen Anne basin of the Delmarva Peninsula in Maryland (Hansen, 1988) and possibly a basin in southern New Jersey (Sheridan, Olsson, and Miller, 1991). The resulting structure would represent one of the largest rifts of the Newark Supergroup, one with a very distinctive stratigraphic sequence and sedimentary fill.

The Richmond basin occupies the southwestern side of an elongated rift valley region and may preserve only a portion of the original rift valley south of the Taylorsville and Queen Anne basins. Despite a long history of intermittent study of the geological structure of the basin, dating back to the pioneering work of Lyell (1847), it is still rather poorly understood because suitable exposures and outcrops are scarce. Extensive drilling for oil and gas and seismic-reflection work in the 1980s have clarified some aspects of the stratigraphic sequence and structure of the basin (Cornet, 1989; Cornet and Olsen, 1990). The Richmond basin contains some of the stratigraphically oldest sedimentary rocks of the Newark Supergroup currently

recognized south of Nova Scotia (Olsen et al., 1989). Based on palynological data, the ages of its strata may range from late Ladinian to early Carnian (Ediger, 1986) or, more likely, from early to middle Carnian (Cornet, 1989; Cornet, in Olsen et al., 1989). A few dikes of Jurassic diabase intrude both the rocks in the Richmond basin and the surrounding Piedmont. The Carnian sedimentary sequence rests unconformably upon igneous and metamorphic basement. The Richmond and Taylorsville basins contain gray and black sedimentary rocks of lacustrine to paludal origin, rather than the red and brown playa and fluvial sedimentary rocks characteristic of other Newark Supergroup basins (Olsen et al., 1989). The Richmond basin contains relatively extensive coals and highly bioturbated shallow-water lacustrine and fluvial sequences, which suggest persistently humid conditions (Cornet and Olsen, 1990). Cornet and Olsen divide the main basin sequence into three formations (from oldest to youngest): Tuckahoe Formation, Turkey Branch Formation, and Otterdale Sandstone.

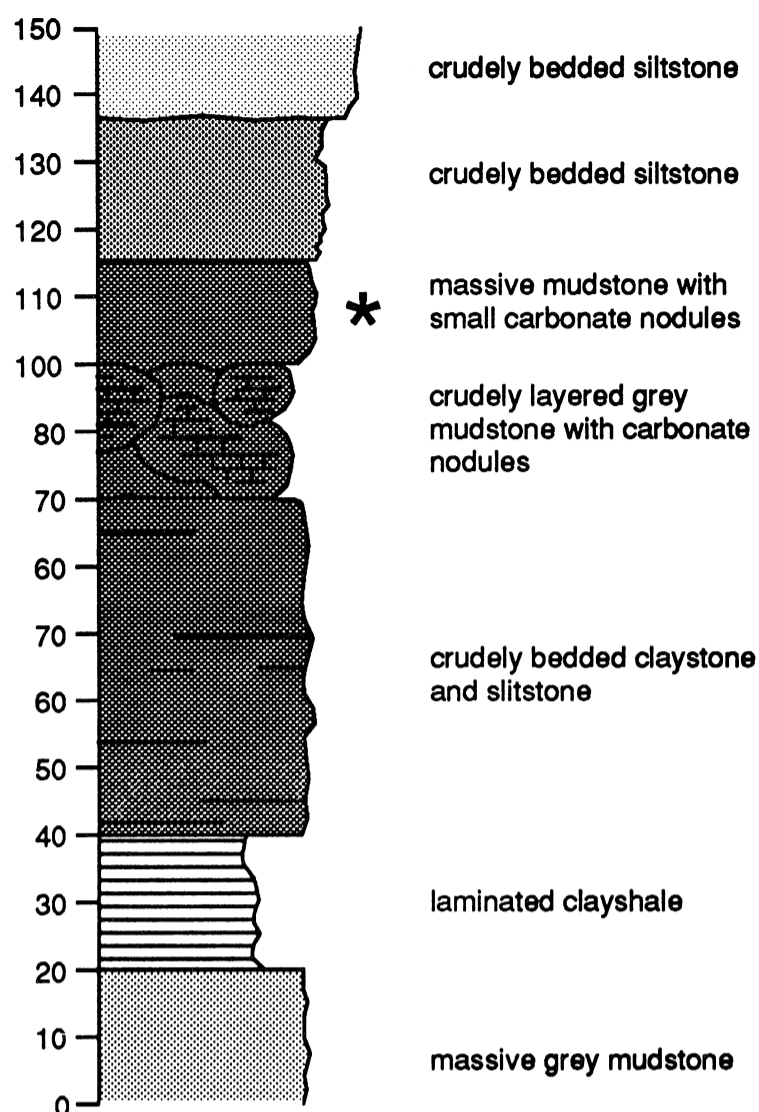


Figure 8.2. Stratigraphic section of the Turkey Branch Formation at the Tomahawk Locality and in its immediate surroundings. Asterisk denotes tetrapod-bearing mudstone horizon.

Grammer (1818) first reported the occurrence of fossil fishes in pits and mine shafts in the famous Coal Measures of the Richmond basin. In 1845, Charles Lyell visited the Blackheath mines, situated south of the James River and northeast of the town of Midlothian in Chesterfield County, and obtained a specimen of the distinctive redfieldiid 'holostean' *Dictyopyge macrura*, which he subsequently illustrated in his description of the coal field in the Richmond basin (Lyell, 1847). *Dictyopyge* is endemic to the Richmond, Taylorsville, and smaller associated basins and occurs in large numbers throughout much of the stratigraphic sequence (Schaeffer and McDonald, 1978). The fish specimens generally are incomplete and disarticulated and commonly are associated with conchostracans, ostracods, plant remains, coprolites, and occasional gastropods and reptilian teeth.

Olsen discovered the vertebrate-bearing Tomahawk Locality in July 1981, during geological reconnaissance in the Richmond basin. The first geological map of the Richmond basin by Shaler and Woodworth (1899) shows a dip symbol at this location, indicating that an outcrop already existed there at the time of their survey. The site (USNM locality 39981) is located along the northeastern bank of the old course of Old

Hundred Road (VA 652), 0.1 mile (0.16 km) east of the eastern branch of Tomahawk Creek, near Midlothian, Chesterfield County. We refer to the site as the Tomahawk Locality because of its proximity to Little Tomahawk Creek on the old Tomahawk Plantation. The tetrapod bones occur in a 15–20-cm-thick stratum of massive calcareous mudstone, together with small (1–10 mm) carbonate nodules, poorly preserved root traces, and countless fish scales and bones (Figure 8.2). At least two irregular layers of fissile, more silty mudstone extend within the massive mudstone and contain vast quantities of fish scales and bones along with isolated tetrapod bones and teeth. The fossiliferous strata form part of the middle Tomahawk Creek Member of the Turkey Branch Formation (B. Cornet, pers. commun.), an extensive sequence of sedimentary rocks of shallow-water lacustrine origin. The poorly exposed stratigraphic sequence in the area of the excavation consists of laminated dark gray claystone with conchostracans, that grades upward into massive mudstone and nodular limestone. The Turkey Branch Formation is unconformably overlain by the coarse-grained sandstones of the possibly late Carnian Otterdale Formation, which appears to represent a braided-stream deposit and thus far has yielded only petrified wood.

Most tetrapod remains occur as dissociated bones (or fragments of bones) and teeth. For this reason, we have generally adopted a conservative approach in taxonomic identification of the material now at hand. In a few instances, skulls and partial skeletons are disarticulated, but the component elements still remain in close association. The superbly preserved bones and teeth show relatively few signs of crushing and distortion.

Most of the associated fish material can be assigned to the ubiquitous *Dictyopyge*. A few isolated teeth document the presence of small hybodont sharks referable to *Lissodus* (A. K. Johansson, pers. commun.). The only invertebrates preserved in the tetrapod-bearing mudstone are as yet unidentified gastropods, which are documented by shell fragments and rare complete specimens in steinkern preservation. Macroscopic plant remains comprise a single poorly preserved fern pinnule (B. Cornet, pers. commun.), poorly preserved root traces, and carbonized wood scraps.

Field collection and preparation

The locality was initially quarried by means of hand tools. As the area of excavation was expanded, a backhoe was used on several occasions to remove several meters of overlying clay and weathered rock, but care was taken not to uncover the actual fossiliferous horizon during that phase of site preparation.

The bones and teeth can be readily separated from the enclosing mudstone matrix using needles ground from rods of tungsten carbide and mounted in pin

vices. The fossils usually are stained black and display even minute structural details. Many teeth have light gray or bluish enamel and black dentine. Most of the small bones and teeth are penetrated by minute fractures, and often they rapidly disintegrate as the enclosing mudstone dries. Application of cyanoacrylate glues was used to retard disintegration during collecting; the adhesives can be removed with acetone or by careful peeling with a needle during preparation in the laboratory.

Bulk samples of fossiliferous mudstone were disintegrated in hot water or treated using kerosene and water. The resulting residue was screened, dried, and manually sorted under a dissecting microscope. This procedure yielded numerous skeletal remains of a variety of small tetrapods, as well as abundant scales referable to *Dictyopyge*.

Systematic paleontology

Synapsida

Cynodontia

“Traversodontidae”

Boreogomphodon jeffersoni Sues and Olsen, 1990

This small traversodont cynodont is by far the most abundant identifiable tetrapod taxon at the Tomahawk Locality. [We use only the informal term “traversodont” because the family Traversodontidae Huene, 1936 probably constitutes a paraphyletic grouping (Hopson, 1984).] It is represented by three excellently preserved partial skulls (including one with a natural endocast), scattered remains of a fragmentary skeleton, a number of isolated dentaries, maxillae, and premaxillae, and many isolated teeth. In addition, a few isolated cynodont limb-bones (humerus, femur) may prove referable to this taxon.

B. jeffersoni most closely resembles *Traversodon stahleckeri* Huene, 1936 from the Carnian Santa Maria Formation of southern Brazil and *Luangwa drysdalli* Brink, 1963 from the Anisian Ntawere Formation of Zambia (Kemp, 1980) in the structure of its upper postcanine teeth. The upper postcanines have buccolingually expanded crowns, with three principal cusps posteriorly and a large anterior basin (Figure 8.3). Only a single accessory cusp is developed anterior to the buccal principal cusp. A posterior cingulum is present. The enamel typically shows coarse vertical wrinkling. The lower postcanine teeth differ from those of *Luangwa*, *Traversodon*, and most other known traversodont taxa in the presence of three, rather than two, anterior cusps. This character state is shared only by *Arctotraversodon* from the Wolfville Formation (middle to upper Carnian) of Nova Scotia and an undescribed traver-

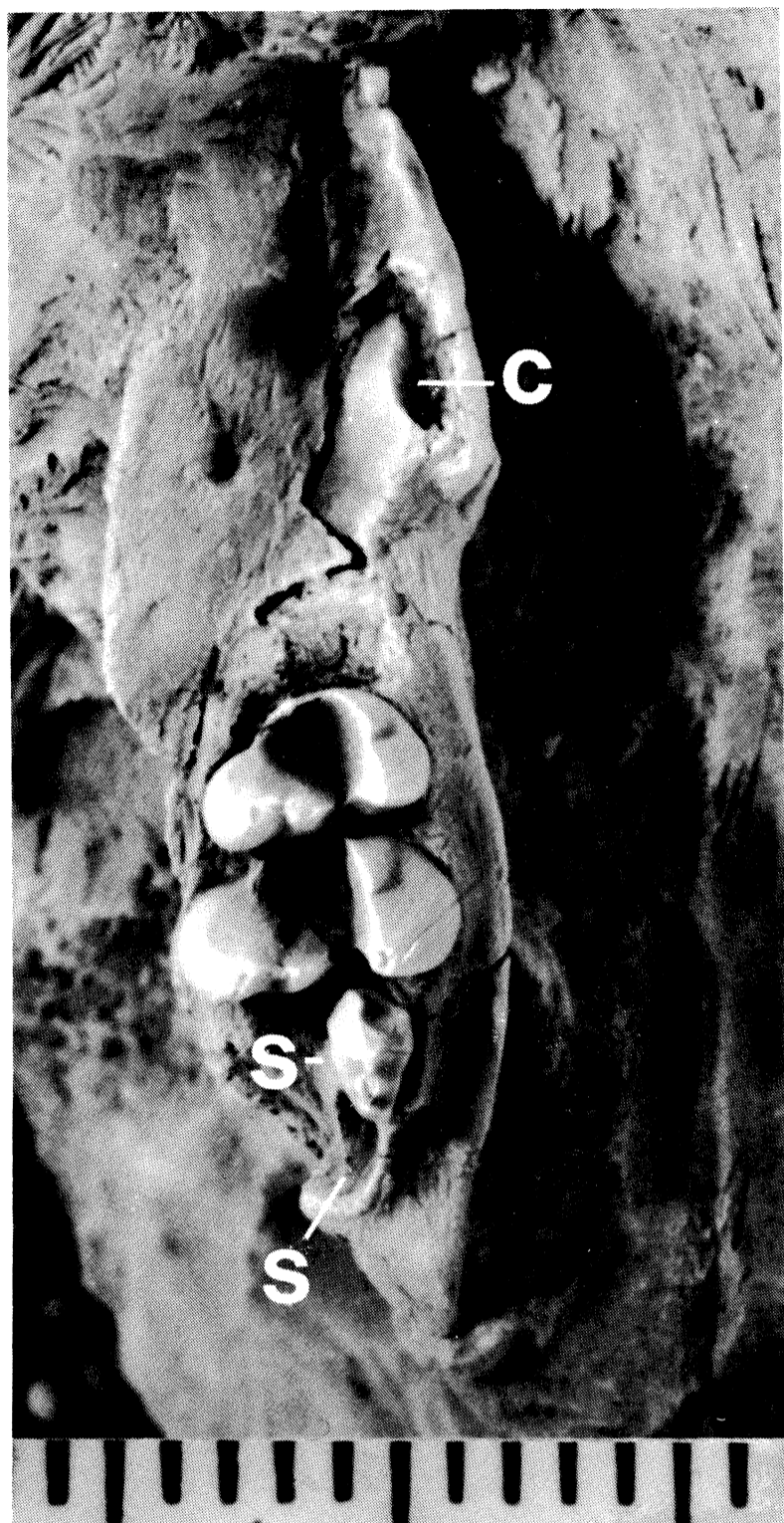


Figure 8.3. Left maxilla of *Boreogomphodon jeffersoni* Sues and Olsen, 1990, USNM 437632 (holotype), in occlusal view. Specimen coated with ammonium chloride. Divisions of scale bar each equal 1 mm. Abbreviations: c, canine alveolus; s, sectorial tooth and alveolus for sectorial tooth.

sodont from the Lettenkeuper (Ladinian) of southern Germany (Sues, Hopson, and Shubin, 1992).

The buccal surface of the maxilla bears a pronounced longitudinal ridge that overhangs the tooth row buccally. The dentary has a large posterior mental foramen. These features, in conjunction with the inset lower and upper rows of postcanine teeth, provide suggestive evidence for a flexible cheek and a buccal oral vestibule, as inferred for other traversodont cynodonts (Hopson, 1984).

Most of the jaws referable to *Boreogomphodon* found to date represent juvenile individuals. This assessment is based on the small overall size of the specimens, the

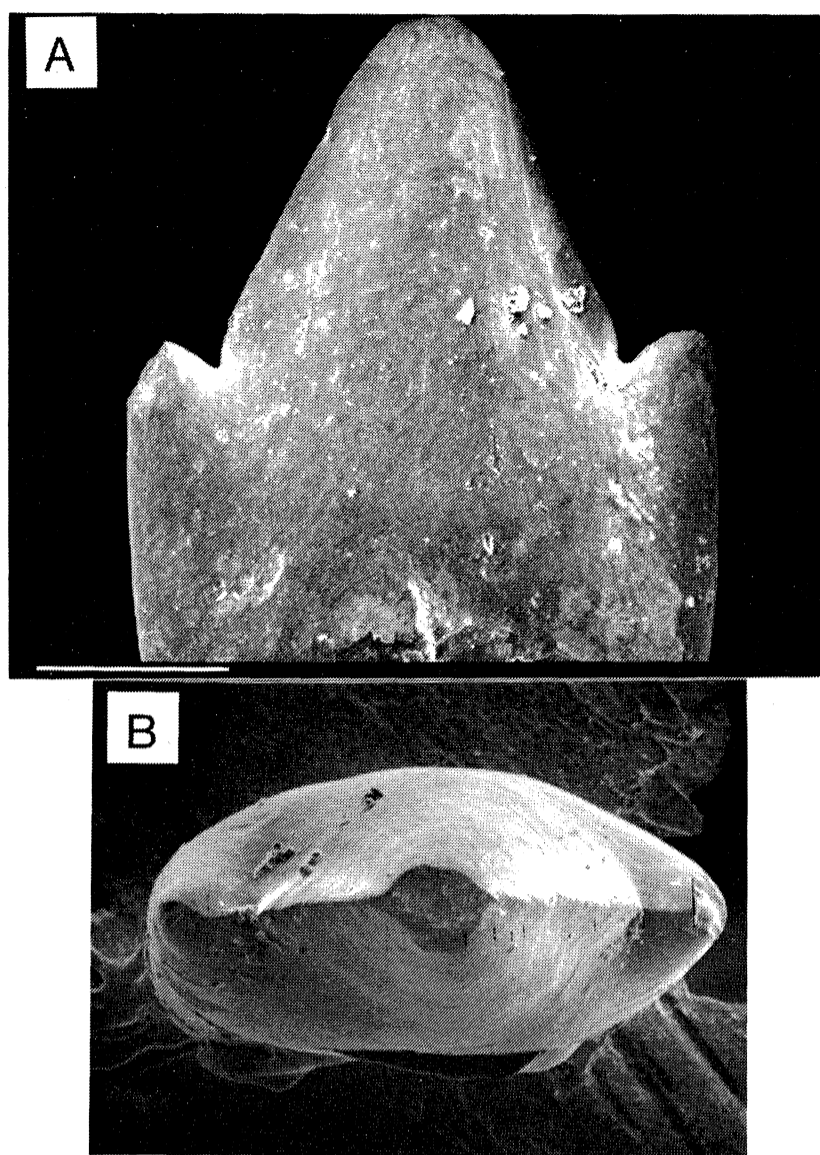


Figure 8.4. Isolated postcanine tooth of *Microconodon tenuirostris* Osborn, 1886, USNM 448600, in buccal (A) and occlusal (B) views. Scale bar equals 400 μ m.

low number (four or five) of postcanine teeth, the proportional shortness of the snout, and the proportional depth of the dentary (Hopson, 1984). It is further borne out by the presence of multicuspoid "sectorial" teeth in the two posterior alveoli of several maxillae (Figure 8.3). Such teeth have previously been recorded only in juvenile specimens of other gomphodont cynodonts, such as *Diademodon* (Hopson, 1971) and *Massetognathus* (J. A. Hopson, pers. commun.).

Cynodontia incertae sedis

Microconodon tenuirostris Osborn, 1886

Three dentaries and several isolated postcanine teeth document the presence of this very mammal-like cynodont, which previously was known only from a right dentary from the upper Carnian Cumnock Formation of North Carolina (Osborn, 1886; Simpson, 1926). The teeth are also very similar to the isolated teeth of *Pseudotriconodon* from the middle Norian Steinmergel-Gruppe of Luxembourg (Hahn, Lepage, and Wouters, 1984; Sigogneau-Russell and Hahn, Chapter 10).

The postcanine teeth typically bear three pointed

cusps that are anteroposteriorly aligned behind one another (Figure 8.4). The tall principal cusp is anteroposteriorly long and has sharp anterior and posterior cutting edges. It is symmetrically flanked by much smaller cusps anteriorly and posteriorly, Cingula are absent. The root of an isolated upper(?) postcanine tooth shows a pronounced anteroposterior constriction. The dentary has a long, low tooth-bearing ramus and lacks a distinct angular process. Its robust symphyseal region holds alveoli for one canine and three slightly procumbent incisors. In the smallest known dentary from the Tomahawk Locality, the postcanine dentition comprises simple anterior and more posterior tricuspid teeth; furthermore, no diastema is present. In the largest dentary found to date, the anterior postcanines have been lost, and a prominent diastema separates the canine and the exclusively tricuspid postcanines.

To date, we have found no differences to justify taxonomic distinction between the material from the Tomahawk Locality and the holotype of *Microconodon tenuirostris* Osborn, 1886 (Academy of Natural Sciences, Philadelphia, no. 10248). The phylogenetic relationships of *Microconodon* are beyond the scope of this chapter and will be discussed elsewhere.

Diapsida

Archosauria

Crurotarsi

To date, only phytosaurs (*Parasuchia*) and a new suchian archosaur with diagnostic dorsal dermal armor, *Euscolosuchus olseni* Sues, 1992, have been confidently identified.

Although phytosaurs are rather large reptiles, their isolated tooth crowns, representing a wide spectrum of sizes, are very common in both the quarried and screen-washed material and hence merit inclusion in this review. Long, slender, and conical tooth crowns, with a round cross-section and smooth cutting edges, probably represent teeth from the anterior end of the snout, whereas the more robust and labiolingually compressed crowns with finely serrated cutting edges presumably are from the posterior regions of the jaws, much as in other phytosaurs. Many of the presumed anterior teeth occasionally show very pronounced vertical fluting of the enamel and closely resemble certain isolated phytosaurian tooth crowns from the Upper Triassic of Pennsylvania illustrated by Huene (1921). The material is of little diagnostic value. Traditionally, the mostly very fragmentary skeletal remains of phytosaurs from the Upper Triassic of eastern North America have all been referred to *Rutiodon* Emmons, 1856, but in most cases the available evidence neither supports nor contradicts this assumption.

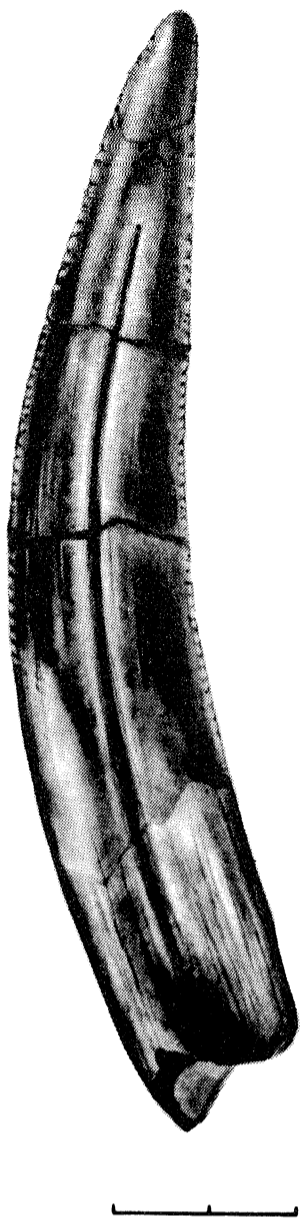


Figure 8.5. *Uatchitodon kroehleri* Sues, 1991, USNM 448624, nearly complete tooth in side view. Scale bar equals 1 mm.

?Archosauriformes incertae sedis

Uatchitodon kroehleri Sues, 1991

This taxon, of uncertain, possibly archosauriform, affinities, is known only from its highly distinctive teeth, which represent the earliest instance of a presumed oral venom-delivery system in reptiles recorded to date (Sues, 1991). The labiolingually strongly compressed, recurved, bladelike tooth crowns bear deeply infolded, enamel-lined median grooves on both their labial and lingual surfaces (Figure 8.5). Judging from the close structural similarity to the venom grooves on the teeth of extant poisonous snakes and lizards of the genus *Heloderma*, it seems likely that these features functioned in venom conduction. The grooves become narrow and shallow toward the tip of the tooth and disappear before reaching it. The anterior and posterior cutting edges of the crowns are serrated on all but two of the teeth recovered to date, with typically six or seven denticles per millimeter (Figure 8.6A). Inspection at higher magnification shows that the sharp cutting edge of each individual denticle is denticulated as well (Figure 8.6B). The tooth crowns of *Uatchitodon kroehleri* have an average height of about 10 mm, but

several fragments indicate the presence of larger teeth. The root indicates thecodont tooth implantation.

Diapsida

Lepidosauria

A new sphenodontian lepidosaur is represented by isolated maxillae with teeth (Figure 8.7A,B). The acrodont teeth have bluntly conical crowns that bear prominent radial ridges on the enamel. An enlarged anterior tooth is followed by three or four smaller teeth. The sphenodontian from the Tomahawk Locality appears to provide the stratigraphically oldest record of this group known to date.

A number of lizardlike jaws and jaw fragments show pleurodont tooth implantation (Figure 8.7C). The teeth are columnar and slightly recurved. Lingually, they are separated from the subdental ridge by a sulcus. These specimens may indicate the presence of an unidentified lepidosaur. Although of great interest as a potential early Late Triassic record of Squamata (see Rieppel, Chapter 2), the currently available material is too fragmentary to permit definite taxonomic identification.

Parareptilia sensu Gauthier et al., 1988

Procolophonia

Two distinctive new taxa are each documented by a jaw fragment with diagnostic teeth. One is clearly referable to the Procolophonidae, and the other may be related to certain advanced taxa of that group. This material has been described and compared in detail elsewhere (Sues and Olsen, 1993).

Importance of the Tomahawk tetrapod assemblage

The preliminary faunal inventory presented here underscores the unusual importance of the Tomahawk tetrapod assemblage for the study of the early Mesozoic history of continental biotas. First, it represents a very diverse assemblage of continental vertebrates of early Late Triassic age from North America and contains a number of previously unknown taxa. Second, the Tomahawk tetrapod assemblage is unlike other known North American assemblages (from the Chinle and Dockum formations in the American Southwest and the rest of the Newark Supergroup) in the numerical predominance of traversodont cynodonts, which indicates close faunal ties to the Gondwanan realm (Argentina, Brazil, and Tanzania) (Romer, 1966; Cox, 1973). The slightly younger tetrapod assemblages from very similar strata of the Pekin and Cumnock formations of North Carolina (Olsen et al., 1989)

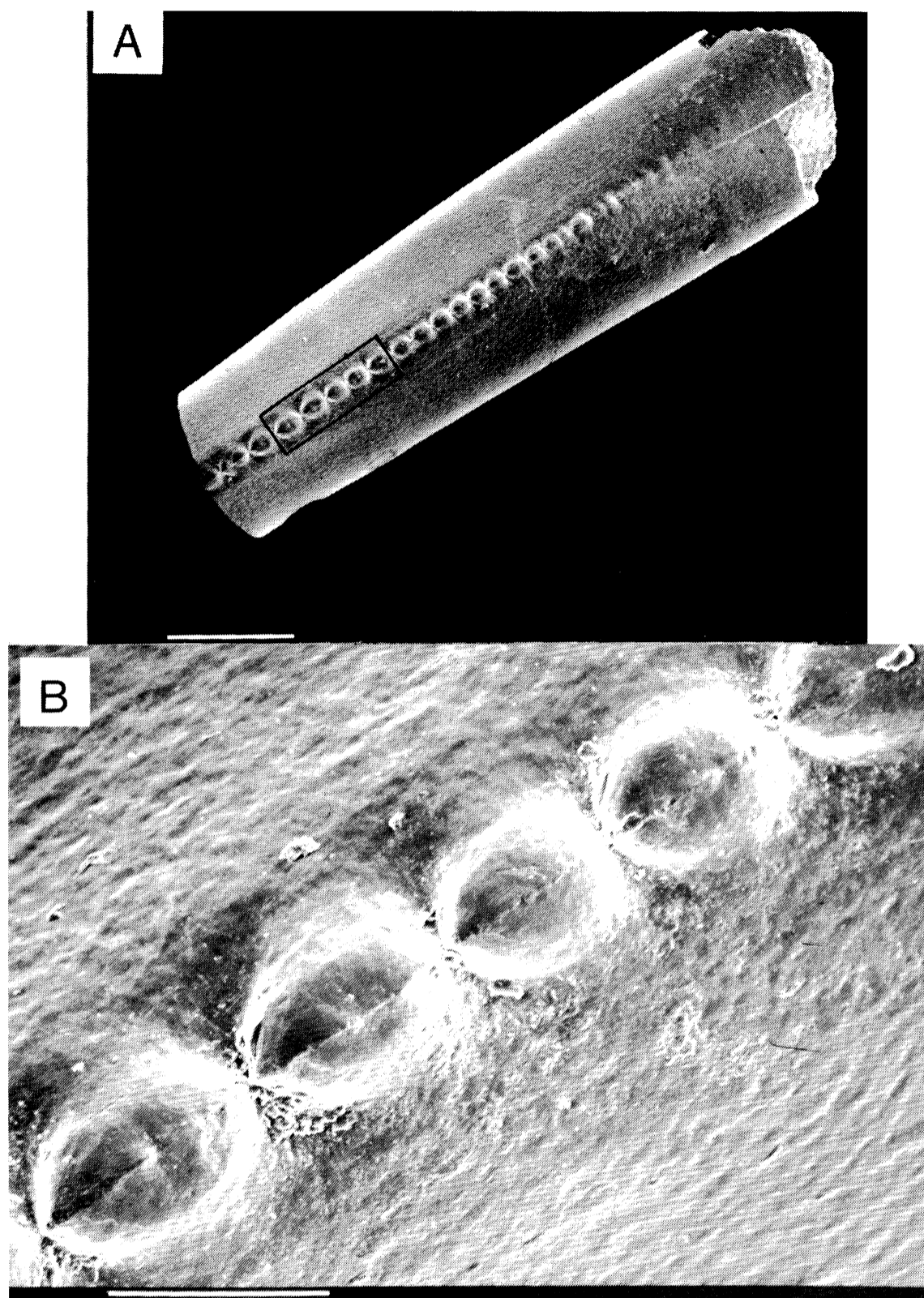


Figure 8.6. *Uatchitodon kroehleri* Sues, 1991. (A) Tooth fragment in posterior view, showing denticles along cutting edge (carina). Scale bar equals 1 mm. (B) Closeup of denticles delineated by rectangular box in A. Scale bar equals 200 μm .

include taxa known from the Chinle and Dockum formations of the American Southwest and demonstrate that the distinctive faunal composition of the Tomahawk assemblage probably is not related to differences in depositional environments. The Tomahawk tetrapod assemblage shares the presence of phytosaurs with other Laurasian assemblages, but it apparently lacks metoposaurid temnospondyl amphibians, which otherwise were widely distributed throughout Europe (Fraas, 1889), North America (Colbert and Imbrie, 1956; Hunt, 1989), Morocco (Dutuit, 1976), and India (Roy-Chowdhury, 1965) during the Late Triassic.

The Tomahawk tetrapod assemblage is demonstrably slightly older than other well-documented Laurasian assemblages, and Sues and Olsen (1990) have previously suggested that the traditionally recognized differences between Carnian tetrapod assem-

blages from Laurasia and Gondwana reflect differences in stratigraphic age, rather than geographic separation. The apparent faunal provinciality might thus reflect poor stratigraphic sampling of the transition from the Middle to the Late Triassic in Laurasia. Floral provinciality during the early part of the Late Triassic, however, is well established, with Laurasian plant assemblages dominated by cycadophytes and conifers and Gondwanan macrofloras dominated by the seed-fern *Dicroidium* and palynofloras of the Ipswich-Onslow type (Cornet and Olsen, 1985). This floral provinciality does not correspond geographically and temporally in a simple way to the distribution of continental tetrapods. In India, typical Laurasian tetrapod assemblages with abundant phytosaurs and metoposaurs (Roy Chowdhury, 1965; Chatterjee and Roy-Chowdhury, 1974) occur in association with *Dicroidium*-dominated

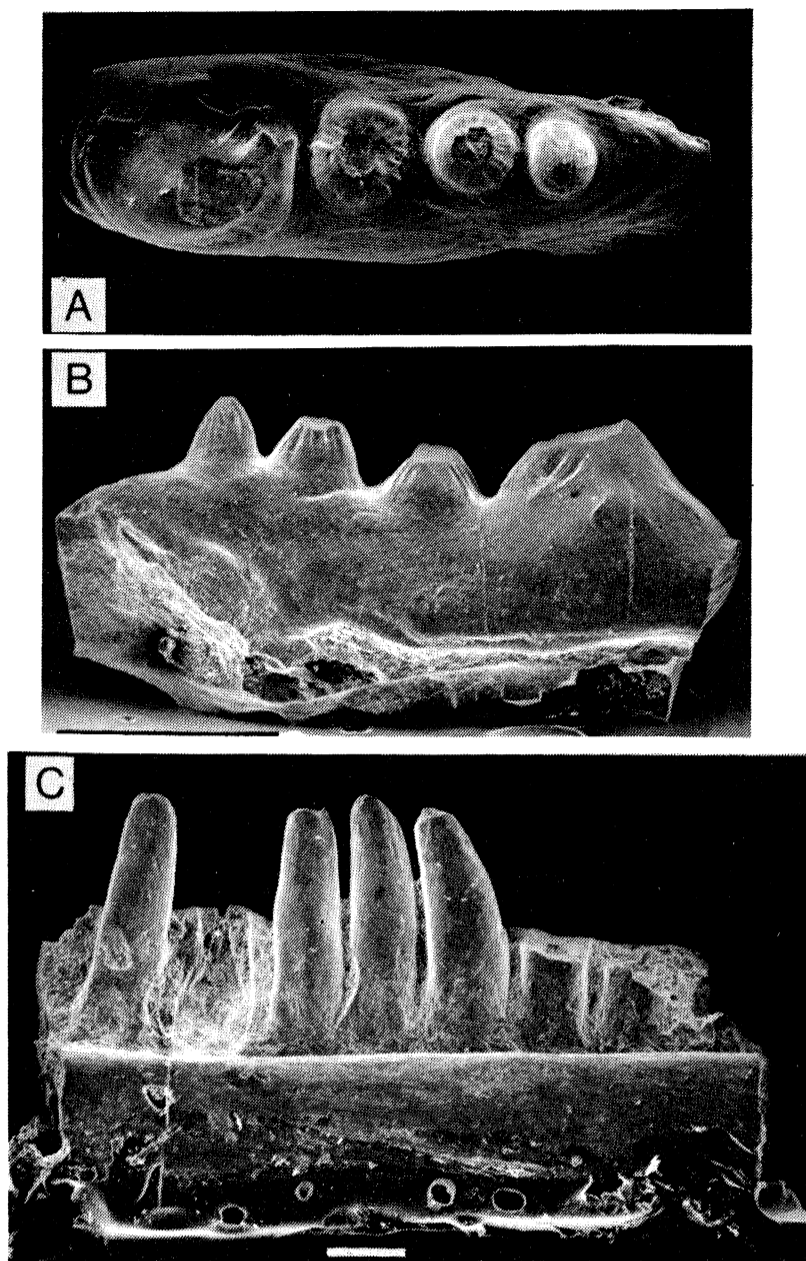


Figure 8.7. Maxilla fragment of undescribed sphenodontian in occlusal view (A) and side view (B). Scale bar equals 2 mm. (C) Dentary fragment of indeterminate lepidosaur in lingual view. Scale bar equals 400 μ m.

assemblages of plant macrofossils and with Ipswich-Onslow-type palynofloras (Kumaran and Maheswari, 1980). The tetrapod material from the Richmond basin described here is associated with diverse, typically Laurasian florules (Fontaine, 1883; Cornet and Olsen, 1990) although B. Cornet (pers. commun.) has recently identified two new plant taxa with Gondwanan affinities.

Romer (1966) informally distinguished three successive stages in the historical development of continental Triassic tetrapod assemblages worldwide. He did not attempt to fit these stages into a chronostratigraphic framework, but they broadly correlate with the Triassic standard sequence (Shubin and Sues, 1991). The Early Triassic A-type assemblages are composed predominantly of nonmammalian therapsids and are best known from the Beaufort Group (Karoo Supergroup) of South Africa. B-type assemblages are characterized by the abundance of traversodont cynodonts and, in most (but not all) cases, rhynchosaurian reptiles and are well documented from the Middle and Late Triassic of Argentina, Brazil, and

Tanzania. The Late Triassic (and Early Jurassic) (Olsen and Sues, 1986) C-type assemblages are dominated by a great diversity of archosaurian reptiles, especially dinosaurs. Together with tetrapod material (mostly still undescribed), including both rhynchosaurs and traversodont cynodonts, from the Wolfville Formation of Nova Scotia (Baird and Take, 1959; Baird, in Carroll et al., 1972; Baird and Olsen, 1983; Sues et al., 1992), the Tomahawk assemblage clearly establishes both the existence of B-type communities in the Northern Hemisphere and their persistence into the Late Triassic.

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