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A NEW PROCOLOPHONID AND A NEW TETRAPOD OF UNCERTAIN, POSSIBLY PROCOLOPHONIAN AFFINITIES FROM THE UPPER TRIASSIC OF VIRGINIA

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ABSTRACT—Two jaw fragments of small tetrapods from the Turkey Branch Formation of the Richmond basin (Newark Supergroup; Upper Triassic: lower to middle Carnian) of Virginia have highly distinctive dentitions. The robust, transversely broadened, and bicuspid teeth of *Gomphiosauridion baileyae*, gen. et sp. nov. support its placement in the Procolophonidae. The two cusps are linked by a pronounced transverse ridge, which divides the occlusal surface of the crown into two deep fossettes. The cusps have strongly fluted enamel. The heterodont dentition of *Xenodiphyodon petraios*, gen. et sp. nov. comprises transversely broadened, tricuspid posterior teeth and transversely compressed anterior teeth with distinct apical ridges. The posterior teeth of *Xenodiphyodon* closely resemble those of the alleged trilophosaurid taxa *Tricuspisaurus thomasi* and *Variodens inopinatus* from Upper Triassic fissure-fillings in southwestern England and ?*Trilophosaurus jacobsi* from the Upper Triassic Chinle Formation of Arizona. The latter is clearly distinct from the archosauromorph *Trilophosaurus buettneri* and is made the type species of the new genus, *Chinleogomphius*. All four genera may prove referable to the Procolophonia.

INTRODUCTION

The Procolophonia are a group of mostly small primitive amniotes of uncertain affinities (Ivakhnenko, 1979; Carroll and Lindsay, 1985). Most recently, Reisz and Laurin (1991) considered them the sister-taxon of turtles. Procolophonians range in time from the Late Permian to the Late Triassic (Norian) and are known from every continent. The Triassic genera of the Procolophonidae typically have a distinctly heterodont marginal dentition, which is differentiated into anterior "incisiform" and more posterior "molariform" teeth. The molariforms have transversely broadened, bulbous, and usually bicuspid crowns. A definite occlusal pattern was established between upper and lower teeth (Colbert, 1946; Gow, 1977b).

Among the numerous skeletal remains of mostly small tetrapods collected from the Turkey Branch Formation (Upper Triassic: lower to middle Carnian) of the Richmond basin (Newark Supergroup) of Virginia (Sues and Olsen, 1990), there are two tooth-bearing jaw fragments that we consider distinct enough from any other known tetrapod to be described as new taxa. One is definitely referable to the Procolophonidae; the affinities of the other form are uncertain but it may be related to the Procolophonia.

The first definite procolophonid reported from the Upper Triassic of North America was *Hypsognathus fenneri* Gilmore, 1928 from the Passaic Formation (Norian) of the Newark basin in New Jersey (Gilmore, 1928; Colbert, 1946). The holotype (USNM 11643) consists of a natural mold in sandstone of the mandible and much of the postcranial skeleton anterior to the pelvic region, exposed in ventral view. Subsequently, several skulls as well as skulls with partial skeletons referable to this taxon have been recorded from the Passaic Formation of New Jersey, the New Haven Arkose of Connecticut, and the upper portion of the Wolfville Formation of Nova Scotia, all of which are considered Norian in age (Colbert, 1946; Baird, 1986; Olsen, 1988). Colbert (1960) described a second alleged procolophonid, *Sphodrosaurus pennsylvanicus*, from the Hammer Creek Formation of Pennsylvania. As first suggested by Baird (1986) and confirmed by subsequent preparation of the holotype and only known specimen, this taxon is not referable to the Procolophonidae. Various features, including the distinctly sigmoidal curvature of the femur, indicate diapsid affinities instead (Sues et al., in press). Baird and Take (1959) and Baird (in Carroll et al., 1972) recorded the presence of three diversely specialized new taxa of Procolophonidae and of cf. *Leptopleuron* from the Upper Triassic (middle to upper Carnian) Wolfville Formation of Nova Scotia; a comprehensive description of this material is now in preparation by Baird and Sues.

The acronym MNA denotes the Museum of Northern Arizona, Flagstaff, and the acronym USNM the National Museum of Natural History (formerly United States National Museum), Washington, D.C.

SYSTEMATIC PALEONTOLOGY

AMNIOTA
PROCOLOPHONIA
PROCOLOPHONIDAE

Genus *GOMPHIOSAURIDION*, gen. nov.

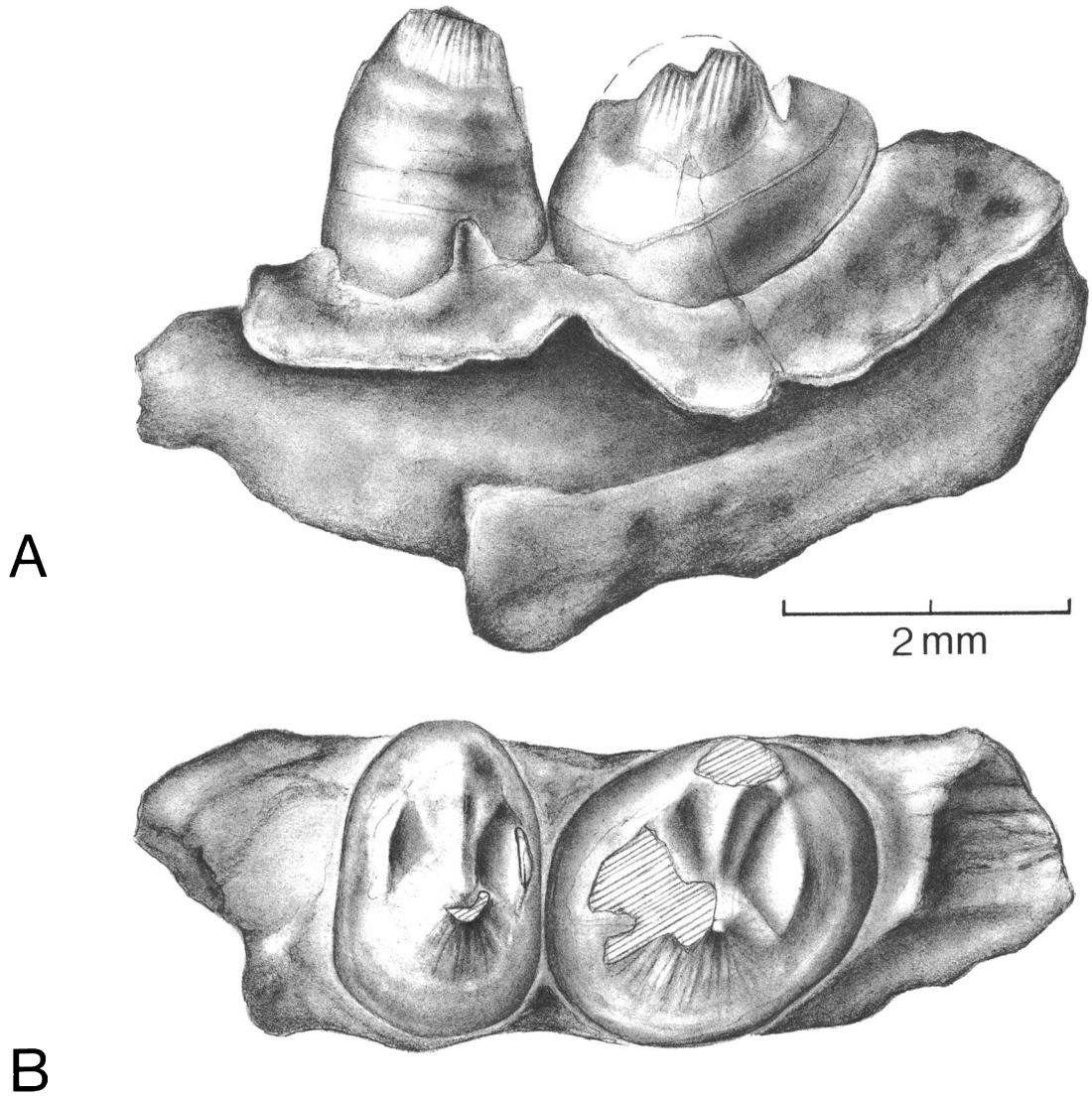

FIGURE 1. *Gomphiosauridion baileyae,* gen. et sp. nov. USNM 448630 (holotype). Fragment of right maxilla in **A**, lingual and **B**, occlusal view. Hatching indicates areas of breakage.

Type Species—*Gomphiosauridion baileyae,* sp. nov.

Diagnosis—Transversely broadened maxillary teeth with two cusps linked by a pronounced transverse ridge, which separates deep anterior and posterior fossettes. Cusps with strongly fluted enamel.

Etymology—Greek *gomphios,* cheek tooth, and Greek *sauridion,* little lizard or reptile.

GOMPHIOSAURIDION BAILEYAE, sp. nov.
(Fig. 1)

Etymology—Named for Elizabeth Bailey Sues who found the holotype and many other important tetrapod specimens at the Tomahawk locality.

Holotype—USNM 448630, fragment of a right maxilla with two teeth (Fig. 1). Collected by E. B. Sues on March 11, 1990.

Horizon and Locality—Tomahawk Member, Turkey Branch Formation, Newark Supergroup. Age: Late Triassic (early to middle Carnian). USNM locality 39981 (Tomahawk Locality), 0.16 km (0.1 miles) E of the eastern branch of Little Tomahawk Creek along the northeastern side of Old Hundred Road (VA 652), near Midlothian, Chesterfield County, Virginia. Lat. 77°40′15″N, long. 37°27′45″W; Hallsboro 7.5 Minute Quadrangle.

Diagnosis—Type and only known species of the genus as diagnosed above.

Description—The holotype is a fragment of a right maxilla with two slightly damaged but generally well-preserved teeth and a small piece of the base of a third tooth. Although both teeth are of equal maximum width (2.7 mm), one tooth is more rounded in occlusal view than the other and, by comparison to the maxillary

teeth of *Hypsognathus* (Colbert, 1946:fig. 15) and of *Tichvinskia* from the Lower Triassic of Russia (Ivakhnenko, 1979:fig. 3b), is interpreted as the more anteriorly placed tooth.

The teeth have robust, transversely broadened, bicuspid crowns. It is difficult to ascertain the nature of tooth implantation; it appears to be ankylothecodont. The maximum width of the tooth crown is at its base, from which it narrows uniformly toward the apices of the cusps, resulting in sloping sides of the crown. The two cusps are linked by a transverse ridge, which is rather sharp on the more posterior tooth but is weakly developed on the more anterior tooth. Anterior and posterior to this ridge, there is a deep pocket or fossette, which is bounded by a sharp cingular ridge on the side opposite to the transverse ridge. The cusps have strongly fluted enamel. The teeth are tightly apposed.

The transversely broadened tooth crowns with two apical cusps linked by a transverse ridge support placement of *Gomphiosauridion* in the Procolophonidae (Huene, 1912; Gow, 1977a, b; Ivakhnenko, 1979; Carroll and Lindsay, 1985), but it differs from other members of this group in the presence of two deep fossettes, rather than one. The prominent fluting of the enamel on the cusps is an additional diagnostic feature for *Gomphiosauridion*. *Thelegnathus* from the Lower or Middle Triassic of South Africa also exhibits fluted enamel on the more posterior "molariform" teeth (Gow, 1977a; Spencer, pers. comm.).

?PROCOLOPHONIA

Genus *XENODIPHYODON*, gen. nov.

Type Species—*Xenodiphyodon petraios*, sp. nov.

Diagnosis—Tooth-bearing ramus of dentary deep dorsoventrally but narrow transversely. Lower dentition distinctly heterodont, with anteroposteriorly aligned, transversely compressed anterior teeth and transversely broadened, tricuspid posterior teeth.

Etymology—Greek *xenos*, strange, Greek *diphyes*, double, twofold, and Greek *odous* (specifically the Ionian variant *odon*), tooth, in allusion to the presence of two distinct tooth types.

XENODIPHYODON PETRAIOS, sp. nov.
(Fig. 2)

Etymology—Greek *petraios*, of or belonging to a rock, from Greek *petra*, rock, also the etymological root for the first name of the discoverer of the holotype, Peter A. Kroehler.

Holotype—USNM 448631, incomplete right dentary with nine teeth (Fig. 2). Collected by P. A. Kroehler on July 7, 1991.

Horizon and Locality—Tomahawk Member, Turkey Branch Formation, Newark Supergroup. Age: Late Triassic (early to middle Carnian). USNM locality 39981 (Tomahawk Locality), 0.16 km (0.1 miles) E of the eastern branch of Little Tomahawk Creek along the northeastern side of Old Hundred Road (VA 652), near Midlothian, Chesterfield County, Virginia. Lat. 77°40′15″N, long. 37°27′45″W; Hallsboro 7.5 Minute Quadrangle.

Diagnosis—Type and only known species of the genus as diagnosed above.

Description—The tooth-bearing ramus of the dentary is deep dorsoventrally but very narrow transversely, slightly increasing in width posteriorly. Its anterior and posterior ends are broken off. The labial surface is distinctly convex dorsoventrally, especially more posteriorly. The dentary fragment holds nine teeth, the first of which is represented only by its base. A shallow sulcus extends anteroposteriorly lingual to the tooth row. Judging from inspection of the broken ends of the jaw fragment, implantation of the teeth appears to be ankylothecodont, although this remains to be verified by dissection of additional material. The anterior six teeth have anteroposteriorly aligned, transversely strongly compressed crowns with distinct apical ridges. The first tooth was apparently long anteroposteriorly. The lingual surfaces of the anterior crowns are flattened and obliquely inclined (although these features may have been accentuated by wear). The crown of the sixth tooth is less compressed transversely in occlusal view than those of the preceding teeth. The posterior three teeth have transversely broadened crowns, which increase in labiolingual width from the first to the last (1.0 and 1.4 mm, respectively). Two shallow grooves extend anteroposteriorly and divide the occlusal surface of each posterior tooth into three cusps, the central one of which is the largest (especially on the first tricuspid tooth). The apices of all cusps appear to be worn.

Discussion—*Xenodiphyodon* is so decidedly distinct that even its placement in a major group of tetrapods is difficult at present, but it appears to be most similar to certain genera of Procolophonidae in the structure of its dentition. Its anterior teeth resemble the anteroposteriorly aligned posterior teeth in the dentary and maxilla of a new procolophonid from the Upper Triassic Wolfville Formation of Nova Scotia, first reported by Baird and Take (1959) and currently under study by Baird and Sues. Somewhat similar teeth also occur in *Colognathus* Case, 1928 from the Upper Triassic Dockum Group of Texas, a poorly known form that has been considered a procolophonid by some authors (e.g., Murry, 1986) if it is, in fact, a tetrapod.

The tricuspid posterior teeth of *Xenodiphyodon* closely resemble those of *Trilophosaurus buettneri* Case, 1928 from the Upper Triassic Dockum Group of Texas and *Tricuspisaurus thomasi* Robinson, 1957 from the Upper Triassic fissure-fillings of Ruthin Quarry near Cowbridge, Glamorgan (England). Although placement of *Trilophosaurus buettneri* in the Archosauromorpha is well corroborated by numerous cranial and postcranial synapomorphies (Gauthier, 1984), the trilophosaurid affinities of other taxa such as *Tricuspisaurus* are questionable. Reviewing both Robinson's original material and more recently collected referred specimens, Fraser (1986) argued that *Tricuspisaurus* is a procolophonid. Some of the transversely broadened

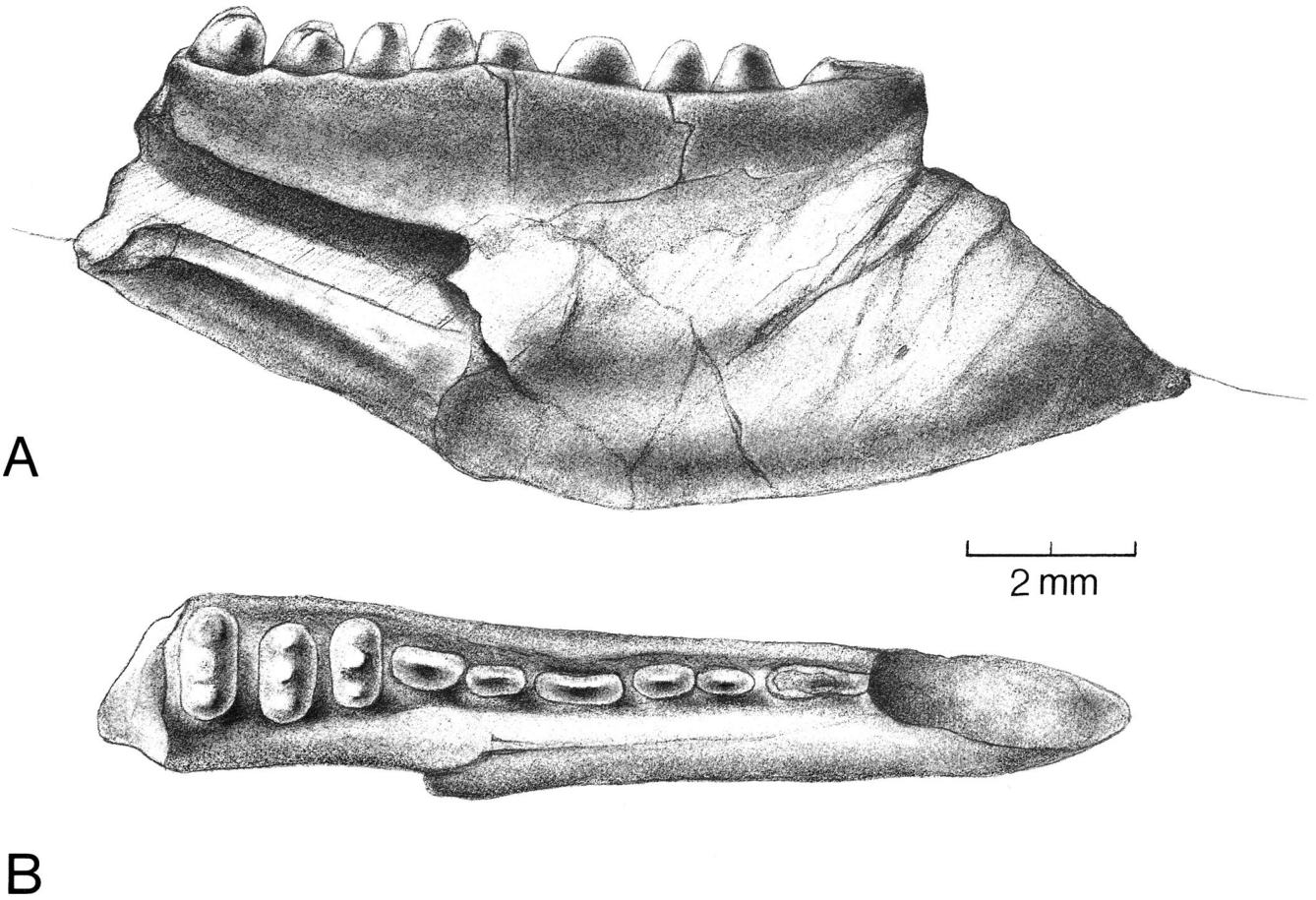

FIGURE 2. *Xenodiphyodon petraios,* gen. et sp. nov. USNM 448631 (holotype). Fragment of right dentary in **A**, right lateral and **B**, occlusal view.

teeth of this form have three blunt cusps of equal size whereas others, in the same tooth row, have a sharp apical or occlusal ridge instead of cusps (Robinson, 1957:pl. 6, fig. 4). A distinctive new procolophonid from the Upper Triassic Wolfville Formation of Nova Scotia has transversely aligned posterior teeth that have a cuspidate cutting edge when unworn (Baird in Carroll et al., 1972; Baird and Sues, unpubl. data). In another alleged trilophosaurid, *Variodens inopinatus* Robinson, 1957 from the Upper Triassic fissure–fillings of Emborough Quarry near Wells, Somerset (England), the more posterior teeth each bear three cusps, the median one of which is the largest (Robinson, 1957: pl. 5).

The dentary and maxillary tooth rows of ?*Trilophosaurus jacobsi* Murry, 1987 from the Petrified Forest Member of the Chinle Formation (Upper Triassic) of the *Placerias* Quarry near St. Johns, Arizona, are quite similar to those of the aforementioned taxa, especially *Variodens* (Murry, 1987:775). They comprise peg-like anterior and tricuspid posterior teeth (Murry, 1987: figs. 1, 2). The latter are diagonally oriented relative to the long axis of the jaw and have well-developed transverse crests ("cingula") linking the individual cusps. The large central cusp is displaced toward the labial margin of the tooth crown. Murry (1987:774) noted that these features, along with the absence of an edentulous anterior "beak," clearly set ?*T. jacobsi* apart from *Trilophosaurus buettneri.* Based on dental similarities, this taxon instead appears to be more closely related to *Tricuspisaurus* and *Variodens.* Therefore we propose a new generic name for ?*T. jacobsi, Chinleogomphius.* Murry (1987:774) has enumerated the diagnostic characters of *C. jacobsi,* which is the type and only known species of this genus. The holotype is MNA V3192, a fragment of a right dentary with five tooth positions, the last of which has a well-preserved tooth (Murry, 1987:fig. 1).

Xenodiphyodon most closely resembles *Tricuspisaurus* in the overall structure of its dentition but differs from the latter in the anteroposterior alignment of the non-cuspidate anterior teeth and in the presence of a large central cusp (shared by *Variodens*) and the absence of cingula on the transversely broadened, tricuspid posterior teeth. These three taxa, along with *Chinleogomphius,* may represent a group of procolo-

phonids with tricuspid teeth (Fraser, 1986), but more complete cranial material is needed to test this hypothesis of relationships.

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