

A LATE TRIASSIC TRAVERSODONT CYNODONT FROM THE NEWARK SUPERGROUP OF NORTH CAROLINA

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ABSTRACT—A new traversodont cynodont, *Plinthogomphodon herpetairus*, is described on the basis of a partial snout from Late Triassic strata of the Newark Supergroup exposed in the Deep River basin (Durham sub-basin) of North Carolina. In the structure of its upper postcanine teeth, *Plinthogomphodon* most closely resembles *Boreogomphodon* from the Upper Triassic (Carnian) of Virginia and *Luangwa* from the Middle Triassic (Anisian) of Zambia. It differs from these taxa only in some features of these teeth.

INTRODUCTION

During the Middle to Late Triassic, one group of non-mammalian cynodonts, the Gomphodontia, was particularly abundant and diverse. Gomphodont cynodonts are primarily characterized by the possession of buccolingually expanded, molariform postcanine teeth that met in crown-to-crown occlusion (Crompton, 1972; Battail, 1991; Hopson, 1991). They are especially common in continental strata of Middle and Late Triassic age in Argentina and Brazil. Traditionally, most of these forms have been referred to the Traversodontidae Huene, 1936 (Bonaparte, 1963; Romer, 1967; Battail, 1991). The monophyly of this group is controversial (Hopson, 1985, 1991), and we only use the informal term "traversodont" in this paper.

Traversodont cynodonts were once thought to be exclusively Gondwanan in their geographic distribution, but they are now also known from Europe (Hahn et al., 1988; Godefroit and Battail, 1997) and North America. Hopson (1984) described the first taxon from the Late Triassic (Carnian) of North America, *Scalenodontoides plemmyridon*, on the basis of several dentary fragments from the Wolfville Formation of the Fundy basin of the Newark Supergroup in Nova Scotia. Subsequent recognition of distinctive postcanine teeth referable to this taxon led Sues et al. (1992) to propose a new genus *Arctotraversodon* for the reception of *S. plemmyridon*. A second traversodont from the Carnian of North America, *Boreogomphodon jeffersoni*, was reported by Sues and Olsen (1990) and is now represented by a large sample of skeletal remains and teeth from the Turkey Branch Formation (sensu Cornet and Olsen, 1990) of the Richmond basin of the Newark Supergroup in Virginia.

In this paper, we describe a new traversodont cynodont from Late Triassic strata in the Deep River basin of the Newark Supergroup in Durham County, North Carolina. The specimen was found as "float" in close association with as yet undescribed skeletons of a rauisuchian and a sphenosuchian archosaur.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA

CYNODONTIA

"TRAVERSODONTIDAE"

PLINTHOGOMPHODON, gen. nov.

Type-Species—*Plinthogomphodon herpetairus*, sp. nov. (by monotypy).

Etymology—Greek *plinthos*, brick, *gomphios*, molar, and *odous* (variant *odon*), tooth, in allusion to the common use of

the local mudstones for the production of bricks and the molariform postcanine teeth.

Diagnosis—Upper postcanine teeth with moderately large anterobuccal cusp and smaller cusp anterior to the latter. Posterobuccal cusp absent. (This diagnosis should be considered preliminary in view of the limited nature of the holotype and the as yet uncertain polarity of various dental character-states.)

PLINTHOGOMPHODON HERPETAIRUS, sp. nov.

(Figs. 1, 2)

Etymology—Greek *herpeton*, creeping animal, reptile, and *hetairos*, companion, "companion of reptiles," in reference to its close association with the skeletal remains of archosaurian reptiles.

Holotype—Collections of the Department of Geology, University of North Carolina, Chapel Hill (UNC), no. 15576, partial snout preserved in two pieces (Fig. 1). Collected by B. Coffey in 1994.

Type Horizon and Locality—Muddy sandstone of Lithofacies Association II sensu Hoffman and Gallagher (1989). Durham sub-basin of Deep River basin, Newark Supergroup. Latitude 35°52'09"N and longitude 78°53'67"W. Genlee, Durham County, North Carolina. At the request of the landowner, detailed locality information is only available to qualified investigators. Age: Late Triassic (late Carnian or early Norian; see discussion below).

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

DESCRIPTION

The holotype of *Plinthogomphodon herpetairus* comprises the tooth-bearing portions of both sides of the snout (Fig. 1). The two fragments can no longer be joined along the midline because much of the intervening bone was lost prior to discovery. The right fragment includes much of the premaxilla and septomaxilla situated behind the external naris. The crowns of all functional teeth have been largely obliterated. An unerupted, nearly complete molariform postcanine is preserved within the last alveolus of the left maxilla and was exposed during preparation. The last alveolus of the right maxilla also contains an erupting molariform, but its lingual portion is still obscured by a tricuspid sectorial tooth. Most of the dorsal roof of the snout has been destroyed by erosion. The overall proportions of the snout and the presence of a sectorial tooth (sensu Crompton,

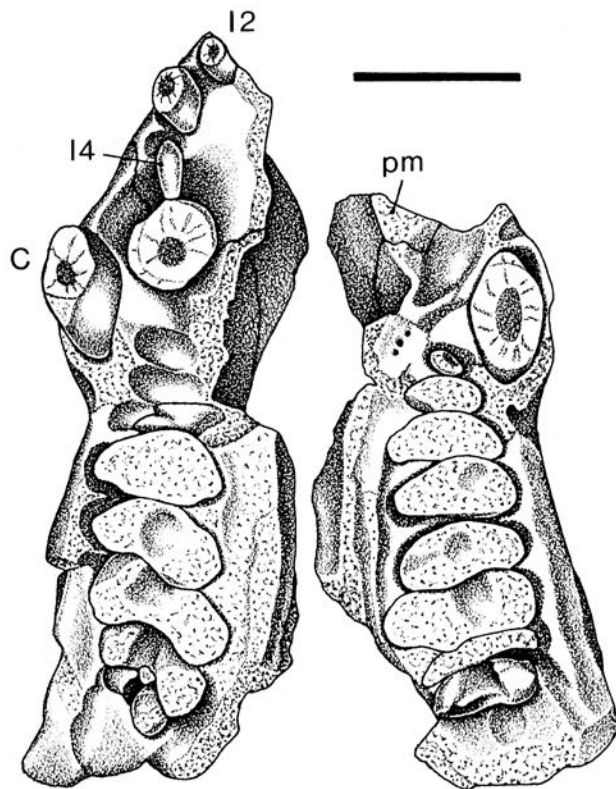


FIGURE 1. *Plinthogomphodon herpetairus*, UNC 15567 (holotype), both halves of partial snout in palatal view. Abbreviations: c, upper canine; 12–14, incisors 2–4; pm, premaxilla. Scale bar equals 1 cm.

1972) in the last maxillary alveolus indicate that the holotype of *Plinthogomphodon herpetairus* may represent an immature individual.

As in other traversodont cynodonts, the snout is robust and rather short. Its rostral portion is distinctly swollen in the region of the deeply implanted upper canines and set off from the remainder of the snout by a slight constriction behind the canines. The external surfaces of the premaxilla and maxilla are distinctly sculptured with pits, grooves, and foramina. Just above the alveolar margin in front of the canine, the anterolateral surface of the right maxilla is marked by four posterodorsally extending sulci that terminate in large foramina. On the external aspect of the maxilla, pronounced grooves extend anteroposteriorly above the postcanine teeth and terminate in large, rounded foramina. On the left side, three large neurovascular foramina are present above the second to fourth postcanines.

The incisors are not enlarged, and, based on the condition in related taxa, the complete premaxilla probably held four incisors. The stumps of the apparently slightly procumbent second and third incisors and the dislodged fourth incisor are preserved in the right premaxilla. The exposed cutting edge of the crown of the fourth incisor appears to lack serrations. The broken base of a single canine is present in each maxilla. The large upper canine is distinctly oval in transverse section and is deeply rooted in the bone. The base of the left upper canine has an anteroposterior diameter of 7.2 mm and a buccolingual diameter of 4.3 mm. The tip of the right lower canine is preserved in the deep paracanine fossa lingual and slightly anterior to the right upper canine. There is no apparent diastema between the canine and the small first postcanine tooth, which is transversely oval in cross-section. On the right side, there are two, pos-

sibly three longitudinally aligned buccal cusps and one more lingually placed cusp of a sectorial replacement tooth preserved within what appears to be the second postcanine alveolus. The two buccal cusps of this tooth are buccolingually compressed and bear distinct cutting edges.

Starting at the second postcanine position, the crowns of the tightly packed upper postcanine teeth are molariform and much wider buccolingually than long anteroposteriorly (mesiodistally). They progressively increase in buccolingual width toward the posterior end of the series. The crown of the erupting postcanine tooth in the last alveolus of the left maxilla (Fig. 2B, C) has a buccolingual width of 6.6 mm. It is well preserved, but several cracks have slightly displaced portions of the tooth crown relative to each other. A transverse row of three large cusps is situated between the center and posterior margin of the tooth crown. The central cusp is situated close to the lingual one. Together with the latter, it forms a tall transverse ridge, which has steep, nearly vertical anterior and posterior surfaces and is separated from the buccal cusp by a deep, V-shaped notch. The tall buccal cusp forms part of a prominent anteroposterior ridge along the buccal margin of the tooth crown. On the buccal margin of the crown, slightly anterior and buccal to the latter cusp, is the base of a broken accessory cusp. There is no trace of a buccal cingulum. A moderately large cusp is situated just anterior to the large buccal cusp on the anterior downward slope of the ridge and is only weakly separated from the latter. The buccal ridge descends anteriorly and turns lingually to enclose a deep basin that is bounded posteriorly by the transverse row of the three principal cusps and occupies about half the anteroposterior length of the crown. At its lingual turn, the ridge bears a small cusp. The basin reaches its greatest depth just in front of the notch between the buccal and central cusps. The ridge forming the anterior margin of the tooth crown is distinctly convex in occlusal view and is crenulated near its buccal end. A posterior cingulum extends along the posterior margin of the tooth crown from the principal buccal to the lingual cusp and, along with the transverse row of cusps, encloses a very narrow posterior basin. Anteriorly, the crown slightly projects into the posterior margin of its predecessor.

The last alveolus in each maxilla contains a sectorial tooth. Only fragments of two displaced cusps of this tooth were preserved on the left side and were removed during preparation to expose the still unerupted molariform crown. The right sectorial tooth (Fig. 2A), implanted in the lingual portion of the last alveolus, has lost all of its cusps due to breakage, and a molariform postcanine is preserved above it in the same alveolus. The three cusps are more or less longitudinally arranged, with the central one being the largest. The crown has an inverted D-shape in occlusal view, with a convex buccal margin, which bears a well-developed cingulum, and an almost straight lingual margin. Its greatest buccolingual width is 2.2 mm, and its anteroposterior length is 3.4 mm.

DISCUSSION

Phylogenetic Relationships

Until work currently in progress (Hopson, pers. comm.) has further resolved the interrelationships of gomphodont cynodonts, it is difficult to assess the phylogenetic position of the traversodont from the Deep River basin more precisely. We consider it a new taxon, *Plinthogomphodon herpetairus*, based on its distinctive combination of dental features, but we are aware that the polarities of some of these character-states still remain uncertain. The following comparisons are based on the published accounts by Crompton (1972), Hopson (1984, 1985), and Kemp (1980) as well as first-hand examination of specimens referable to *Boreogomphodon*, *Exaeretodon*, and *Masseognathus* by H.-D.S.

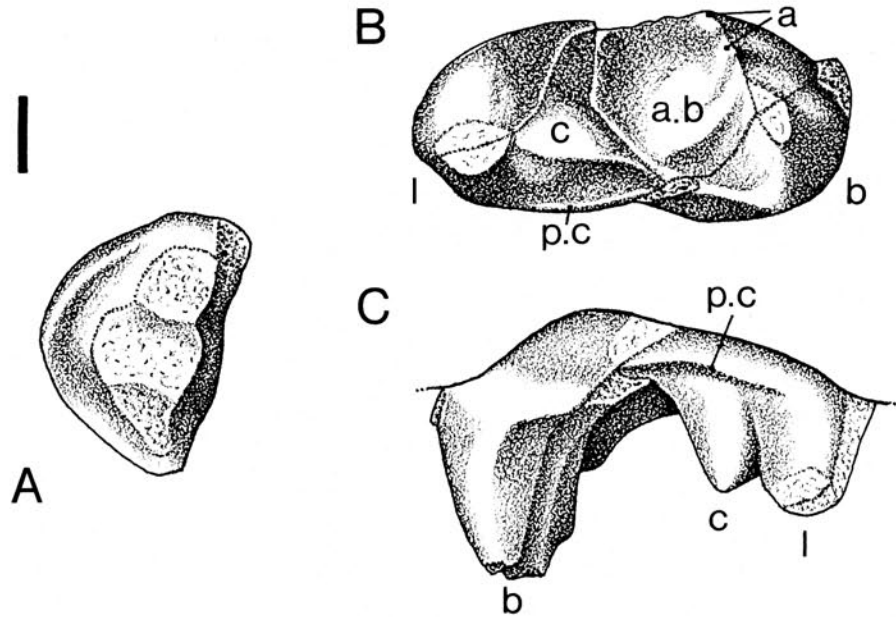


FIGURE 2. *Plinthogomphodon herpetairus*, UNC 15567 (holotype). A, sectorial postcanine tooth in last alveolus of right maxilla in occlusal view. Anterior is toward the top of the figure. B, C, molariform postcanine tooth in last alveolus of left maxilla in occlusal (B) and posterior (C) views. The buccal cusplule is broken off. Anterior is toward the top of the figure in B. Abbreviations: a, accessory cusps; a.b, anterior basin; b, buccal cusp; c, central cusp; l, lingual cusp; p.c, posterior cingulum. Scale bar equals 1 mm.

In features of its dentition, *Plinthogomphodon* is most similar to basal traversodont cynodonts such as *Boreogomphodon* (Sues and Olsen, 1990) and *Luangwa* (Kemp, 1980). It probably had four small upper incisors, unlike the derived condition in *Exaeretodon* and *Scalenodontoides*, which have three (Hopson, 1984). Compared to those of *Exaeretodon* (Crompton, 1972) and *Gomphodontosuchus* (Hopson, 1985), the upper postcanine teeth of *Plinthogomphodon* retain several plesiomorphic character-states: presence of a distinct central cusp, which is situated close to the lingual cusp; a low anterior wall and less developed lingual ridge; a central basin that occupies about half of the anteroposterior length of the tooth crown; a very narrow posterior basin; and transverse orientation of the teeth in the maxilla. Furthermore, upper postcanines of *Plinthogomphodon* lack the "shouldering" of the principal buccal cusp found in *Exaeretodon* and *Massetognathus* (but not in *Gomphodontosuchus*; Hopson, 1985). A posterobuccal cusp is absent, but there is a moderately large anterobuccal cusp, which is preceded by a smaller cusp. Many upper postcanines referable to *Boreogomphodon* have a large posterobuccal cusp, but others lack this cusp (H.-D.S., pers. obs.). *Plinthogomphodon* differs from *Boreogomphodon* consistently in the much larger size of the anterobuccal cusp, which is small in the latter. It resembles *Boreogomphodon* and *Arctotraversodon* (Sues et al., 1992) in that the anterior ridge does not extend onto the anterior face of the lingual cusp; this feature hints at a possible relationship between these three North American taxa, but this hypothesis remains to be tested with better preserved material.

Age of the Vertebrate Assemblage

Based on the shared occurrence of the palaeonisciform fish *Turseodus*, Olsen et al. (1989) correlated the Lithofacies Association II of the Deep River basin of the Newark Supergroup with the Lockatong Formation of the Newark basin and the "upper member" of the Cow Branch Formation of the Dan River basin, and considered the former late Carnian in age. However, Huber et al. (1993:fig. 2) noted that the known strati-

graphic range of *Turseodus* spans almost the entire Late Triassic in the eastern United States, and thus this taxon is of limited biostratigraphic value. Instead they used the presence of the stagonolepidid archosaur *Stegomus arcuatus* (which was recently referred to *Aetosaurus* by Lucas et al. [1998]) to argue for an early to middle Norian age for their "Neshanician land-vertebrate faunachron," which includes the vertebrate assemblage from Lithofacies Association II. *Aetosaurus ferratus* is known only from Norian-age strata in Germany and Greenland as well as mid-Norian marine limestones in the Italian Alps (Lucas et al., 1998). However, regardless of the possible synonymy of *Aetosaurus* and *Stegomus*, the North American material represents a taxon that is distinct from *A. ferratus* and may well have a different stratigraphic range. Furthermore, recent phylogenetic analyses for Stagonolepididae have placed *Aetosaurus* as the sister-taxon to all other members of this clade (Parrish, 1994; Lucas et al., 1998). Therefore, the *Aetosaurus* lineage must predate more derived Carnian-age taxa such as *Stagonolepis*, and its occurrence in pre-Norian strata is to be expected. In the absence of other stratigraphically useful information, it is currently impossible to determine the age of the vertebrate assemblage from Lithofacies Association II of the Deep River basin more precisely than Late Triassic.

ACKNOWLEDGMENTS

We thank the landowner (who does not wish to be identified) for access to the site and other courtesies, and B. Coffey (now at the Virginia Polytechnic Institute, Blacksburg) who found the specimen. Special thanks are due to D. Scott who prepared the illustrations for this paper and to N. C. Fraser (Virginia Museum of Natural History) and J. A. Hopson (University of Chicago) for constructive comments on the manuscript. H.-D.S. gratefully acknowledges financial support from an operating grant from the Natural Sciences and Engineering Research Council of Canada.

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Received 9 April 1998; accepted 14 August 1998.