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First record of the tritylodontid cynodont *Oligokyphus* and cynodont postcranial bones from the McCoy Brook Formation of Nova Scotia, Canada

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Abstract: A fragment of a right dentary with one postcanine tooth from the Upper Triassic (Rhaetian) Scots Bay Member of the McCoy Brook Formation at Wasson Bluff, Nova Scotia, Canada, represents the first record of the tritylodontid cynodont *Oligokyphus* from the early Mesozoic of eastern North America. In addition, three dissociated postcranial bones from the same horizon and locality are referable to derived cynodont therapsids. One of these elements, a nearly complete right humerus, can be assigned to Tritylodontidae. Two other bones, an ulna and incomplete ischium, belong to indeterminate derived cynodonts but show no features allowing more precise taxonomic identification. The presence of *Oligokyphus* in the McCoy Brook Formation provides additional evidence for the remarkably wide geographic distribution of many latest Triassic and Early Jurassic continental tetrapods.

Résumé : Un fragment d'os dentaire droit comprenant une dent postcanine récupéré du Membre de Scots Bay du Trias supérieur (Rhétien) de la formation de McCoy Brook, à Wasson Bluff (Nouvelle-Écosse, Canada), représente le premier spécimen signalé du cynodonte tritylodontidé *Oligokyphus* du Mésozoïque précoce de l'est de l'Amérique du Nord. En outre, trois os postcraniens dissociés provenant du même horizon et de la même localité peuvent être renvoyés à des thérapsides cynodontes dérivés. Un de ces éléments, un humérus droit presque complet, peut être affecté aux tritylodontidés. Deux autres os, un ulna et un ischion incomplet, appartiennent à des cynodontes dérivés indéterminés, mais ne présentent aucune caractéristique en permettant l'identification taxinomique plus précise. La présence d'*Oligokyphus* dans la Formation de McCoy Brook fournit des preuves supplémentaires de la répartition géographique remarquablement grande de nombreux tétrapodes continentaux de la fin du Trias et du Jurassique précoce. [Traduit par la Rédaction]

Introduction

The Fundy rift basin in Nova Scotia and New Brunswick, Canada, is the largest and most northern of the exposed rift basins of the Newark Supergroup in eastern North America (Olsen et al. 2005). Four stratigraphic units have been recognized in the basin (from bottom to top): the Wolfville Formation (?Middle to Late Triassic), Blomidon Formation (Late Triassic: Norian), North Mountain Basalt (Late Triassic: Rhaetian), and McCoy Brook Formation (latest Triassic to earliest Jurassic) (Olsen et al. 2005; Sues and Olsen 2015). The extrusion of the vast Central Atlantic Magmatic Province, which is represented in the Fundy basin by the North Mountain Basalt (201.564 ± 0.054 Ma), slightly post-dates the initiation of the end-Triassic extinction event by a few thousand years (Blackburn et al. 2013). The overlying McCoy Brook Formation was deposited during the final, latest Triassic (Rhaetian) phase of the extinction and the earliest Jurassic post-extinction recovery period. Exposures of this unit at Wasson Bluff near Parrsboro (Cumberland County, Nova Scotia) have yielded an important, stratigraphically well-constrained record of continental vertebrates present immediately following the end-Triassic global mass extinction (Sues and Olsen 2015).

The base of the McCoy Brook Formation at most locations is composed of the largely lacustrine mudstones and limestones of the Scots Bay Member (Tanner 1996; Sues and Olsen 2015). At what Olsen et al. (1989) designated as site J and Sues and Olsen (2015) termed site c at Wasson Bluff (latitude: 45.393483°N, longitude: 64.237833°W), a distinctive unit in the upper portion of the Scots Bay Member known as the "Fish Bed" laps onto the North Mountain Basalt (Fig. 1). It comprises a purple or greenish-grey mudstone adjacent to the basalt and contains countless bones and scales of semionotid and redfieldiid fishes, but also teeth and fin spines of hybodont sharks and well-preserved bones and teeth of tetrapods including protosuchid crocodyliform reptiles (*Protosuchus micmac* Sues et al., 1996) and unidentified basal ornithischian and, possibly, small theropod dinosaurs. Olsen et al. (2005) interpreted this deposit as a wave-sorted lag that accumulated between basalt boulders along a lake shoreline.

Based on the time scale of Blackburn et al. (2013), U–Pb dates from CAMP igneous units linked to the astrochronology of Whiteside et al. (2007), and the palynological data of Cirilli et al. (2009), the "Fish Bed" is latest Rhaetian in age, about 201.45 Ma (Fig. 1). This age is consistent with U–Pb dates from latest Rhaetian marine strata in the Pucara basin in Brazil (Wotzlaw et al. 2014).

The past five years have witnessed rapid erosion of the exposure of the "Fish Bed", and this prompted more detailed documentation of the sediments and fossils from the site. In 2008, erosion exposed an area of approximately 2 m² of "Fish Bed" strata on a cliff outcrop usually concealed by talus. Approximately 3 kg of fossil-bearing matrix were collected from the actively eroding

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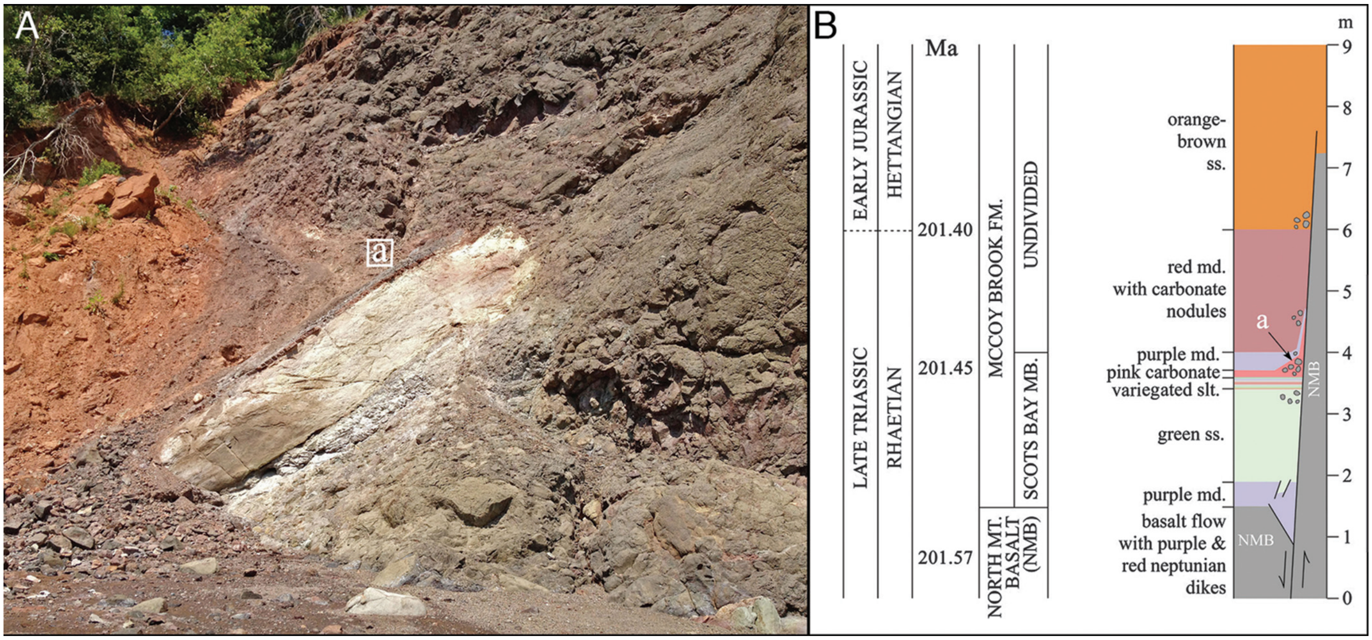
Fig. 1. Faulted onlap relationship between strata of the Scots Bay Member of the McCoy Brook Formation and the North Mountain Basalt (modified from Sues and Olsen 2015). (A) Photograph looking north towards outcrop of onlap at 45.393483°N, 64.237833°W with locality indicated by the boxed letter a. (B) Measured section at same location with strata of the Scots Bay Member that produces tetrapods. All McCoy Brook deposits contain basalt-clast talus adjacent to the fault, and the “Fish Bed” portion of the Scots Bay Member that produced tetrapod remains is rich in basalt clasts at site a and is ‘smeared out’ on the fault plane. Abbreviations: FM., formation; MB., member; md., mudstone; slt., siltstone; ss., sandstone. Chronology based on Blackburn et al. (2013).



mid-cliff section. This sample was processed with particular focus on recovering skeletal remains of reptiles and other tetrapods.

While inspecting rock samples under a dissecting microscope, one of us (T.J.F.) discovered a dentary fragment of a tritylodontid cynodont (Fig. 2). This fossil was subsequently extracted by mechanical preparation. In addition, Sterling L. Nesbitt and Alan H. Turner, then graduate students at Columbia University, collected three postcranial bones of cynodonts from the “Fish Bed” during a field trip with P.E.O. in March 2005. Olsen et al. (2005, figs. 20G–20H) previously figured two of these bones, a right humerus and a right ulna, as cynodont (Figs. 3, 4A–4B). Subsequently, H.-D.S. identified the third specimen as a partial right ischium of a small cynodont (Fig. 4C). The dentary fragment represents the first definite record of the tritylodontid cynodont *Oligokyphus* from eastern North America. The purpose of this paper is to describe it and the cynodont postcranial bones and assess their significance.

The institutional abbreviation NSM denotes the Nova Scotia Museum.

Systematic paleontology

Synapsida
Cynodontia
Tritylodontidae Cope, 1884
Oligokyphus Hennig, 1922
Oligokyphus sp.

Description: A fragment of a right dentary, NSM012GF014.006 (preserved length: 13.5 mm) contains a single molariform postcanine tooth and empty alveoli for two additional teeth behind the former (Figs. 2A–2B). The broken and abraded nature of the bone and the abraded apices of the tooth cusps are consistent with postmortem transport of the specimen.

The crown of the single preserved molariform postcanine tooth is longer anteroposteriorly than wide buccolingually (Table 1; Figs. 2C–2E). It has two rows of three cusps that decrease in size posteriorly and are separated by a median groove. The number of cusps is diagnostic for *Oligokyphus* among tritylodontid cynodonts (Kühne 1956). Individual cusps are crescent-shaped in occlusal view, with convex anterior and concave posterior surfaces and steeply inclined buccal and lingual flanks. A median ridge is present on the concave posterior surface of each cusp. The buccal cusps are slightly larger than the lingual ones. Small accessory cuspules are present along the anterior margin of the tooth crown, similar to those in *Oligokyphus major* (including *Oligokyphus minor*) from Liassic fissure fillings of Windsor Hill Quarry in Somerset, England (Kühne 1956) and *Oligokyphus* sp. from the Kayenta Formation of Arizona (Early Jurassic; Sues 1985). *Oligokyphus lufengensis* from the Lower Lufeng Formation of Yunnan (China; Early Jurassic) lacks such cuspules (Luo and Sun 1994). A distinct ridge extends from the apex of each posterior cusp toward the median groove. The outer surface of the enamel bears distinct ridging (perikymata) as previously reported for *Oligokyphus* (Sues 1985). The posterior third of the buccal surface of the anterobuccal cusp shows well-defined wear.

The anterior root of the molariform tooth is exposed by breakage (Fig. 2A). It has a pronounced vertical depression on its anterior face and a slight vertical depression along its lingual edge. The apical end of the root curves strongly backwards (Fig. 2B). CT scanning of the dentary fragment showed that the tooth also has a longitudinal depression on its posterior surface, resulting in a figure-eight shape of the anterior root in transverse section, as in other tritylodontid cynodonts (Cui and Sun 1987). The buccolingual width of the anterior root is almost twice its anteroposterior length. The posterior root of the preserved tooth is only visible on the CT images. It is more or less round in transverse section, with a longitudinal depression on its anterior surface and a rounded posterior edge. The two roots are separated by a space approximately equivalent to the anteroposterior width of the anterior root. CT imaging revealed alveoli for anterior and posterior roots of a second tooth immediately behind the preserved tooth as well as the alveolus for the anterior root of a third tooth (Fig. 2B). The

Fig. 2. *Oligokyphus* sp. (NSM012GF014.006), right dentary fragment with postcanine tooth. (A) Lingual view of jaw fragment. (B) CT image of jaw fragment in lingual view, showing alveoli for the two roots of next posterior tooth and for the anterior root of the tooth succeeding the latter (indicated by arrows). (C) Buccal view of postcanine tooth in jaw fragment. (D)–(E) Photograph and drawing of postcanine tooth in occlusal view. Hatched areas indicate wear or abrasion. Scale bars = 2 mm.

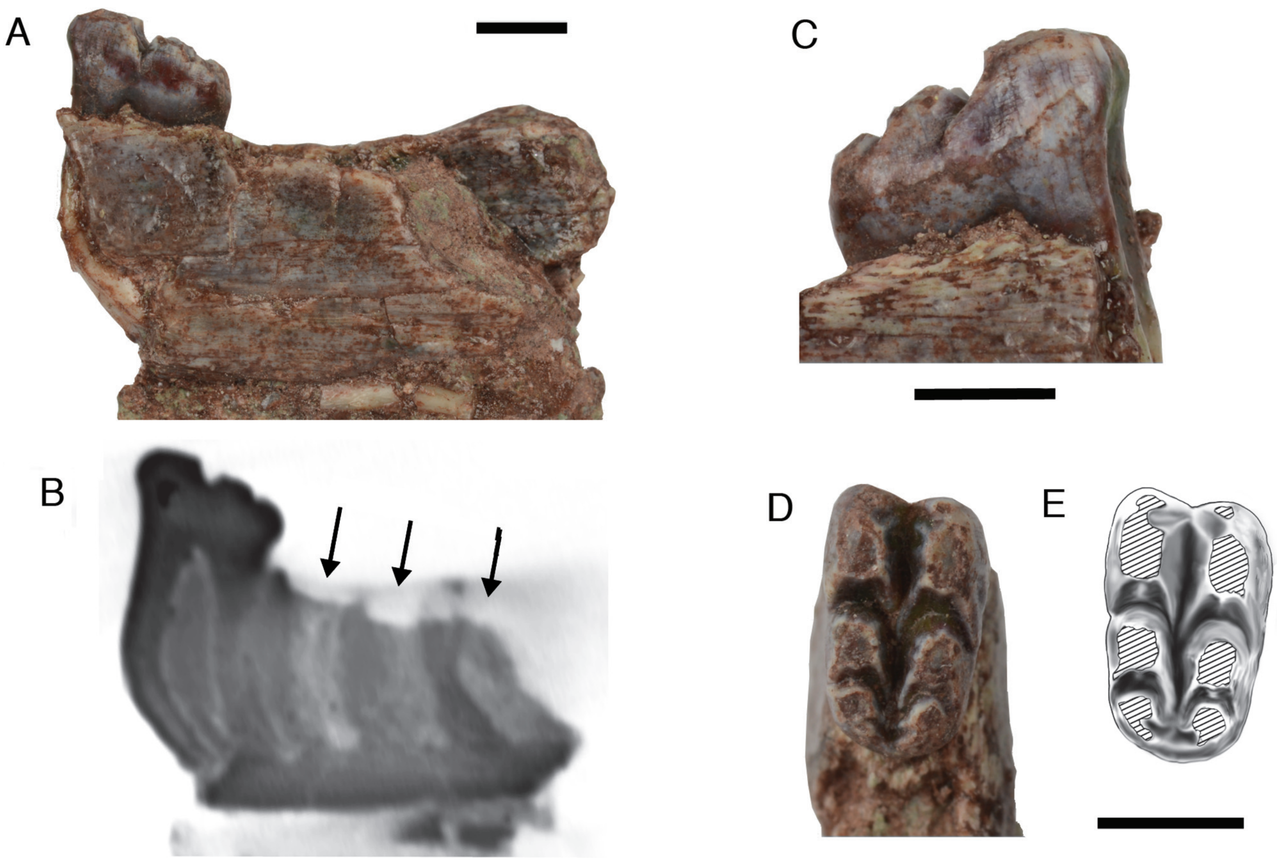


Fig. 3. Right humerus of an unidentified tritylodontid cynodont (NSM014GF014.002) in (A) dorsal, (B) ventral, (C) anterior, and (D) posterior views. Abbreviations: bf, bicipital fossa; dpc, deltopectoral crest; ec, ectepicondyle; en, entepicondyle; fe, entepicondylar foramen; h, head of humerus; ti, origin for lateral head of M. triceps brachii and (or) insertion for M. teres major.

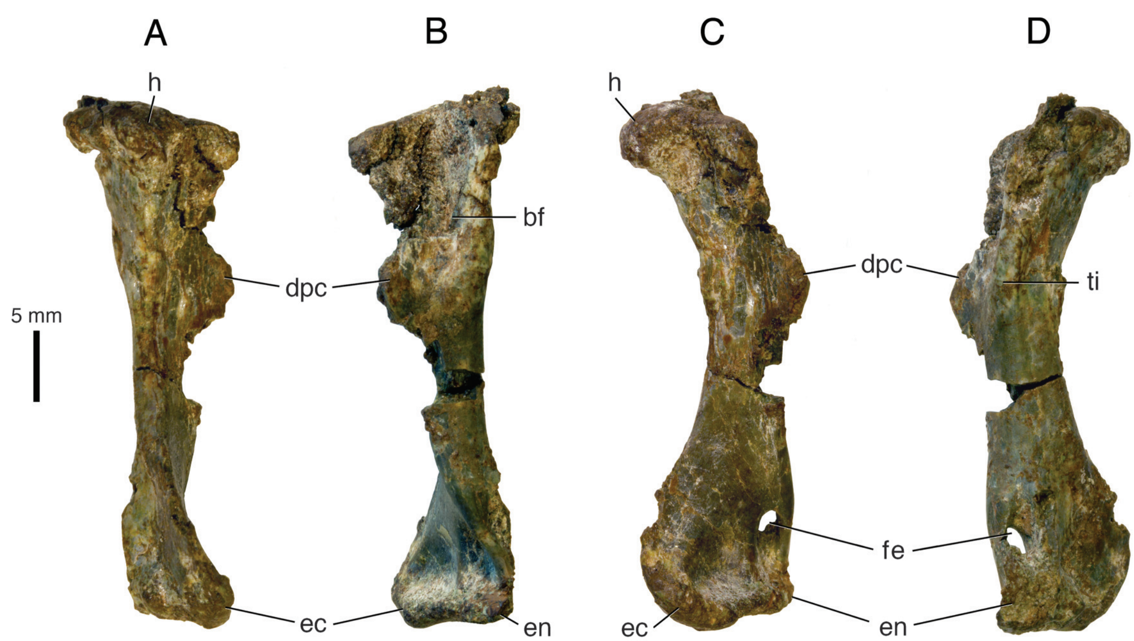


Fig. 4. Partial right ulna of an unidentified derived cynodont (NSM014GF014.003) in (A) lateral and (B) anterior views. (C) proximal portion of a right ischium of an unidentified derived cynodont (NSM014GF014.004) in lateral view. Abbreviations: af, acetabular facet of ischium; an, acetabular notch; bi, insertion for M. brachialis; cp, coronoid process; ol, olecranon; sln, semilunar notch.

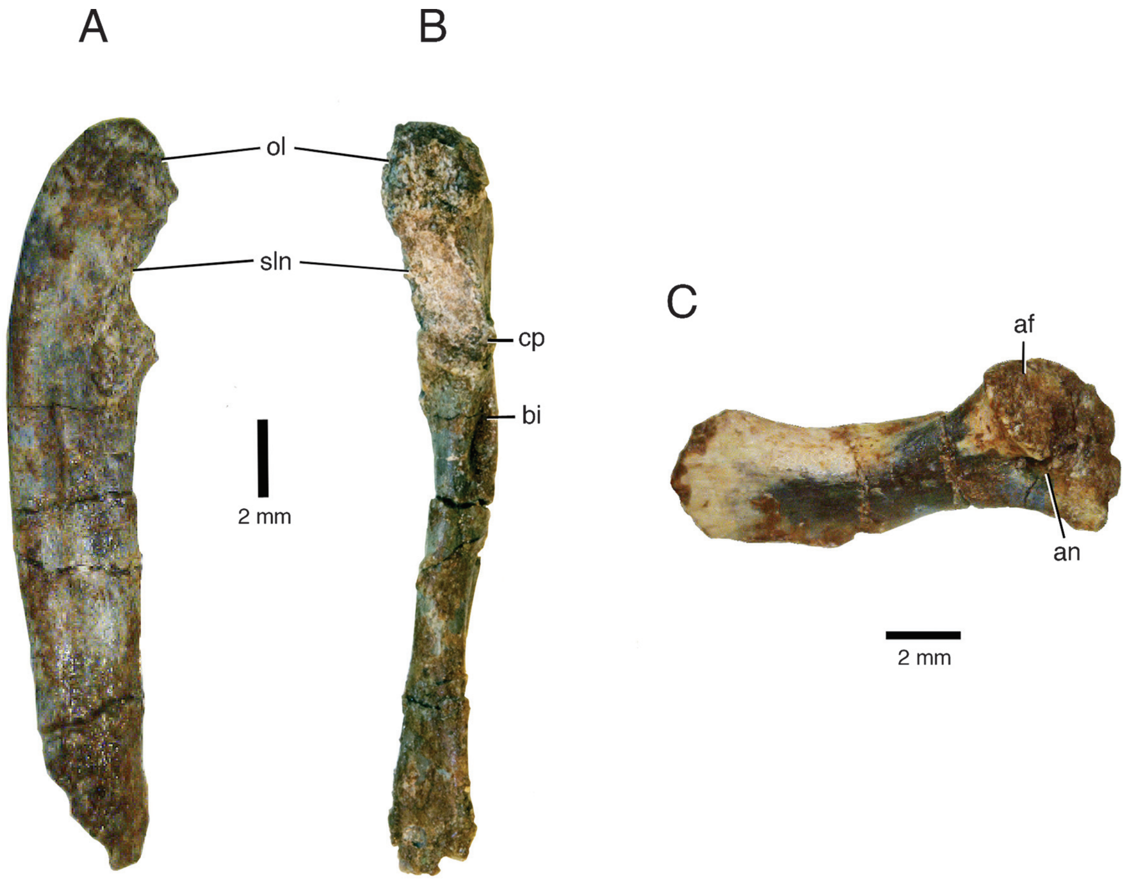


Table 1. Measurements and width/length ratios for lower postcanine teeth of *Oligokyphus*.

Specimen	Postcanine tooth	Width (mm)	Length (mm)	Width/ length	Source
Oligokyphus sp. NSM012GF014.006	3?	2.6	3.8	0.68	Present study
Oligokyphus triserialis	?	3.9	4.3	0.91	Kühne 1956, p. 95
Oligokyphus "*biserialis*"	?	2.2	3.6	0.61	Kühne 1956, p. 95
Oligokyphus lufengensis, IVPP 4008	1	2.4	3.8	0.63	Luo and Sun 1994, fig. 2
Oligokyphus lufengensis, IVPP 4008	2	2.3	3.8	0.61	Luo and Sun 1994, fig. 2

Note: Underlined values are measured from published figures. The abbreviation IVPP denotes Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing.

apical portions of all roots curve distinctly backwards. The bending of the tooth roots shows that the postcanine crowns underwent anterior (mesial) migration during development, much more so at the crowns than at the apices of the roots. The longer anterior root of the tooth is more distinctly bent than its shorter posterior root. Cui and Sun (1987) described this condition in several taxa of tritylodontid cynodonts from China, and the specimen from Wasson Bluff establishes its presence in *Oligokyphus*.

Synapsida
Cynodontia
Tritylodontidae Cope, 1884
Gen. et sp. indet.

Description: A right humerus, NSM014GF014.002 (Fig. 3), has a greatest length of 37 mm. The deltopectoral crest and the ectepicondylar region are badly damaged, but the remainder of the bone is, for the most part, well preserved. The humerus has flaring proximal and distal articular ends linked by a rather slender shaft, which is triangular in transverse section. The planes of the proximal and distal ends are twisted relative to one another, their long axes enclosing an angle of about 40°. On the proximal end, the head of the humerus is raised above the adjacent dorsal surface of the shaft and projects anteromedially as well as dorsally. The articular surface of the head is confluent with adjoining areas. A ridge extends from the lateral end of the proximal articular surface to about the mid-shaft of the humerus. Near its distal terminus the ridge forms a slight thickening, which represents the point of origin of the lateral head of M. triceps brachii and (or) insertion for M. teres major. The medial edge of the large deltopectoral crest is mostly broken. Set at a distinct angle to the adjacent proximal portion of the shaft, the crest borders the well-developed bicipital depression, which extends for nearly half the length of the humerus. The medial edge of the deltopectoral crest continues posterodistally as a low, rounded ridge that forms a bar across the large, oval entepicondylar foramen. Although the thin ectepicondylar edge is slightly damaged, enough is preserved to establish the absence of an ectepicondylar foramen. The entepicondyle is thicker and situated farther from the radioulnar articulation than the ectepicondyle. The broad ulnar condyle wraps around the distal end and extends onto both the dorsal and ventral aspects of the humerus. It is less extensive ventrally than dorsally. The radial condyle also wraps around the distal end.

DISCUSSION: NSM014GF014.002 is identifiable as tritylodontid based on its close resemblance to the humerus of *Oligokyphus major* from the Early Jurassic of Somerset, England (Kühne 1956). It differs from tritheledontid humeri in the absence of an ectepicondylar foramen (Gow 2001; Martinelli et al. 2005). The humerus of the basal mammaliaform *Morganucodon* ("*Eozostrodon*") from Early Jurassic fissure fillings in Wales (Jenkins and Parrington 1976) also lacks an ectepicondylar foramen. However, NSM014GF014.002 differs from the latter in having a less bulbous humeral head, a much more extensive deltopectoral crest, and a flatter entepicondyle.

Synapsida
Cynodontia
Gen. et sp. indet.

DESCRIPTION: A partial right ulna, NSM014GF014.003 (Figs. 4A–4B), has a preserved length of 22 mm. It lacks its distal end and the proximal portion of the one has been damaged in several places. The olecranon process is robust and probably was long; its relative size cannot be determined because the olecranon itself is damaged and the distal end of the ulna is not preserved. The large semilunar notch for the ulnar condyle of the humerus is deeply concave proximodistally and slightly concave transversely. The proximal portion of this facet is situated more laterally than the more distal one and also appears less concave. The facet for the radial condyle is not very distinct. The portion of the ulna bearing the facet for the proximal head of the radius has broken off. Just distal to the coronoid process, an elongate pit on the anteromedial edge of the ulnar shaft probably represents the insertion of M. brachialis. The shaft of the ulna is gently sigmoidal and mediolaterally narrow. Either side of the shaft bears a longitudinal groove, especially near the proximal end on the lateral surface. These grooves represent the areas of attachment for extensor and flexor muscles.

DISCUSSION: NSM014GF014.003 closely resembles the ulnae of *Oligokyphus* (Kühne 1956), the tritheledontid *Pachygenelus* (Gow 2001), and *Morganucodon* (Jenkins and Parrington 1976). The shared similarities and the damaged condition of the element do not permit more specific referral to Tritylodontidae, Tritheledontidae, or even Mammaliaformes. (Mammaliaforms are not yet known from diagnostic craniodental remains from the McCoy Brook Formation.)

Synapsida
Cynodontia
Gen. et sp. indet.

DESCRIPTION: NSM014GF014.004 (Fig. 4C) comprises the proximal portion of a right ischium. A slight constriction separates the robust acetabular portion from the thin, ventromedially extending plate of the ischium. The well-developed acetabular facet faces dorsally and anterolaterally. A distinct medial facet contacted the ilium. A ridge extends from the centre of the lateral rim of the acetabular facet posterodorsally toward the ischial tuberosity; a faint groove is situated dorsal to this ridge. The thin anteroventral edge of the ischial plate forms the dorsal margin of an apparently large obturator foramen. A deep acetabular notch extends between the acetabular facet of the ischium and the pubic process.

DISCUSSION: The preserved portion of the ischium closely resembles the ischia of *Oligokyphus* (Kühne 1956) and *Morganucodon* (Jenkins and Parrington 1976). Although similar to ischia of the aforementioned taxa in overall shape, the ischium of tritheledontid cynodonts has not yet been documented in detail. In view of the similarities shared by the three groups and the fragmentary nature of the bone, it is not possible to assign NSM014GF014.004 to any particular cynodont taxon.

Significance of the new material

Hennig (1922) described *Oligokyphus triserialis* (including *Oligokyphus* "*biserialis*") based on two isolated, waterworn postcanine teeth from the Rhaetian-age Rhaetic Sandstone and possibly the Rhaeto-Liassic bonebed of Baden-Württemberg, Germany (Hennig 1922). Kühne (1956) subsequently described most of the skeleton of *Oligokyphus major* (including *Oligokyphus minor*) based on hundreds of isolated, well-preserved bones and teeth from Early Jurassic fissure fillings in Somerset, England. Since that time, *Oligokyphus* has also been reported from the Lower Jurassic Kayenta Formation of Arizona (Sues 1985) and the Lower Jurassic Lower Lufeng Formation of Yunnan, China (Luo and Sun 1994). The occurrence of *Oligokyphus* in the McCoy Brook Formation is consistent with a wide geographic distribution of this cynodont during the early Mesozoic. It represents the first record of tritylodontid cynodonts from the Newark Supergroup of eastern North America as well as the earliest record of this clade in North America.

Reported records of *Oligokyphus* have an extensive stratigraphic range. The German material of *Oligokyphus triserialis* is latest Triassic (Rhaetian) to earliest Jurassic in age. The specimens of *Oligokyphus major* from England was derived from a marine fissure filling that has been dated as Early Jurassic (Pliensbachian) on the basis of associated marine invertebrates (Kühne 1956). The numerous skeletal remains of *Oligokyphus* sp. from the Kayenta Formation of Arizona (Sues 1985) are Early Jurassic (Pliensbachian) in age (Marsh et al. 2014). The material of *Oligokyphus sinensis* from the Lower Lufeng Formation of Yunnan has not yet been precisely dated. Based on faunal similarities, it is generally assumed that the tetrapod assemblage from the Lower Lufeng is Early Jurassic in age (Luo and Sun 1994).

The presence of *Oligokyphus* in the McCoy Brook Formation at Wasson Bluff provides further evidence for the remarkable faunal similarities among latest Triassic and Early Jurassic assemblages of small continental vertebrates across Pangaea. Another example is the tritheledontid cynodont *Pachygenelus* cf. *P. monus* from Wasson Bluff, which, based on its postcanine dentition, appears to be indistinguishable from *Pachygenelus monus* from the Upper Elliot and Clarens formations (Early Jurassic) of southern Africa (Gow 1980, 2001; Shubin et al. 1991). Furthermore, the skull of the sphenodontian reptile *Clevosaurus bairdi* from Wasson Bluff (Sues et al. 1994) is virtually indistinguishable from that identified as *Clevosaurus* sp. from an unidentified locality in the "Stormberg Group" of southern Africa (Sues and Reisz 1995) and that of *Clevosaurus brasiliensis* from the Caturrita Formation (Late Triassic: Norian) of Brazil (Bonaparte and Sues 2006). First described from Late Triassic fissure fillings in southwestern England (Fraser 1988), *Clevosaurus* has also been reported from the Lower Jurassic Lower Lufeng Formation of Yunnan, China (Jones 2006) and Early Jurassic fissure fillings in Wales (Säilä 2005). Finally, the protosuchid crocodyliform *Protosuchus micmac* from Wasson Bluff (Sues et al. 1996) is closely related to *Protosuchus richardsoni* from the Lower Jurassic Moenave Formation of Arizona (Clark 1986) and *Protosuchus haughtoni* from the Upper Elliot Formation of South Africa (Gow 2000).

The discovery of tritylodontid remains in the Scots Bay Member of the McCoy Brook Formation underscores the potential of continued paleontological exploration of the Triassic–Jurassic boundary strata in the Fundy basin of Nova Scotia.

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