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## A NEW RHYNCHOSAUR (REPTILIA, ARCHOSAUIROMORPHA) FROM THE UPPER TRIASSIC OF EASTERN NORTH AMERICA

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**ABSTRACT**—This paper provides a description and analysis of cranial remains of a rhynchosaur from the Upper Triassic Evangeline Member of the Wolfville Formation of Nova Scotia, Canada. This material, primarily comprising jaw elements, represents the first definitive record of Late Triassic rhynchosaurs from eastern North America. All cranial bones can be assigned to Hyperodapedontinae. The dentition of the Nova Scotian hyperodapedontine differs from those of *Hyperodapedon* and *Isalorhynchus*. The maxilla apparently did not have more than two lateral rows and two medial rows of teeth. The teeth of the lateral row closest to the single groove dividing the maxillary tooth plate are more than twice as large as those of the medial row closest to the groove. The lateral and medial tooth-bearing portions of the maxilla become increasingly crest-like during ontogeny. The dentary lacks a lingual row of teeth. Based on this combination of features, the hyperodapedontine material from the Evangeline Member is assigned to a new taxon, *Oryctorhynchus bairdi*, gen. et sp. nov., which is the sister species to an unnamed hyperodapedontine taxon from Wyoming. This clade was recovered as the sister taxon to *Hyperodapedon* spp. in the phylogenetic analysis. The late Carnian or earliest Norian tetrapod assemblage from the Evangeline Member represents a mixture of faunal elements from a wide paleolatitudinal range, suggesting a more cosmopolitan distribution for continental tetrapods during the early Late Triassic than previously assumed.

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**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

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### INTRODUCTION

Rhynchosauria is a clade of probably herbivorous archosauromorph reptiles that was an important element in many Middle and Late Triassic tetrapod communities (Chatterjee, 1974; Benton, 1983; Whatley, 2005; Schultz et al., 2016; Langer et al., 2017). Diagnostic features for Rhynchosauria include the presence of a single median external narial opening, the contact between the premaxilla and the prefrontal, the presence of multiple tooth rows on the maxilla and the dentary, and the fusion of the parietals (Dilkes, 1998; Whatley, 2005; Butler et al., 2015; Ezcurra et al., 2016). Most rhynchosaurs, grouped together as Rhynchosauridae, have beak-like, edentulous premaxillae and maxillary tooth plates with two or more lateral and medial rows of teeth divided by a longitudinal groove for the reception of the dentate dentary blade. They attained a wide geographic distribution during the Middle and Late Triassic (Anisian–Norian) and were particularly abundant in Gondwana, with records from Argentina, Brazil, India, Madagascar, Tanzania, and Zimbabwe (Huene, 1938, 1940, 1942; Sill, 1970; Chatterjee, 1974; Azevedo, 1984; Dilkes, 1998; Langer and Schultz, 2000; Langer et al., 2000, 2017; Montefeltro et al., 2010; Butler et al., 2015; Mukherjee and Ray, 2015; Ezcurra et al., 2016; Schultz et al., 2016). In

Europe, the clade is known from the Middle Triassic (Anisian) of England (Benton, 1990; Hone and Benton, 2008; Langer et al., 2010) and the Upper Triassic (?Carnian) of Scotland (Benton, 1983) to date. The more derived rhynchosaurs form a subclade Hyperodapedontinae, which is characterized by synapomorphies including the extensive lateral overlap of the maxilla by the jugal, the lateral tooth-bearing area of the maxilla being equal in width to or broader than the medial tooth-bearing area, and the presence of enlarged teeth with angular cross-sections (= pyramidal; Chatterjee, 1969) in the first lateral row (L1) on the maxilla (Whatley, 2005; Langer et al., 2017). Huxley (1869, 1887) described the first known hyperodapedontine, *Hyperodapedon gordonii*, from the Upper Triassic Lossiemouth Sandstone Formation of Scotland; Benton (1983) provided a detailed anatomical study of this taxon. In his description of *Hyperodapedon huxleyi* from India, Lydekker (1885) first placed *Hyperodapedon* in its own subfamily Hyperodapedontinae to distinguish it from *Rhynchosaurus* from the Middle Triassic of England.

Lucas et al. (2002) proposed a global *Hyperodapedon* biochron for tetrapod-bearing continental strata of late Carnian age and correlated with the Otischalkian-Adamanian Land Vertebrate Faunachron in the American Southwest. However, the taxonomic diversity of Hyperodapedontinae remains in need of a comprehensive reassessment (Whatley, 2005; Langer et al., 2017). Thus, it appears premature at this point to designate *Hyperodapedon* as the index fossil for an eponymous global biochron.

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Late Triassic rhynchosaurs are uncommon in North America. No undisputed records of these reptiles have been reported from the Chinle Formation and Dockum Group in the American Southwest, both of which have yielded a wealth of Late Triassic tetrapod fossils. Only two definitive occurrences in North America have been recorded to date. Baird (1963) announced the discovery of rhynchosaurian remains in the Upper Triassic (Carnian) Wolfville Formation of Nova Scotia, which, at that time, represented the first record of these reptiles from North America. Sues and Olsen (2015) briefly reviewed these finds and published photographs of a right premaxilla, a right maxilla of a juvenile, and a basicranium (Sues and Olsen, 2015:fig. 14b–d). Various authors (e.g., Langer et al., 2017) have commented on aspects of this material, which is documented in detail here for the first time.

Lucas et al. (2002) reported jaw fragments, especially a piece of a left maxilla preserved still in occlusion with part of the dentary, from the Upper Triassic (Carnian) Jelm Formation of Wyoming. A.J.F. is currently studying additional jaw remains from this stratigraphic unit. Lucas et al. (2002) tentatively identified the Nova Scotian and Wyoming specimens as *Hyperodapedon* cf. *H. sanjuanensis* based on the shared absence of teeth on the lingual surface of the dentary. *Hyperodapedon sanjuanensis* is otherwise known only from the Upper Triassic (Carnian) Ischigualasto Formation of northwestern Argentina (Sill, 1970) and correlative strata of the Santa Maria Formation of southern Brazil (Azevedo, 1984). Langer et al. (2017) cited the absence of a lingual row of teeth on the dentary (recently confirmed in the holotype; Gentil and Ezcurra, 2018), along with the crest-like medial tooth-bearing portion of the maxilla and the reduced number of teeth on the anterior portion of that bone, as evidence for assigning the North American specimens to *Hyperodapedon sanjuanensis*.

Other purported Late Triassic rhynchosaurs from North America cannot be assigned to this clade. Pritchard et al. (2018) interpreted *Colobops noviportensis*, based on a partial, dorsoventrally crushed cranium (length about 2.5 cm) from the Upper Triassic (Norian) New Haven Formation of the Newark Supergroup in Connecticut, as the basal-most member of Rhynchosauria. Sues and Baird (1993) originally identified this specimen as a sphenodontian. All features listed by Pritchard et al. (2018) as unambiguous synapomorphies for *Colobops noviportensis* and Rhynchosauria are also shared by sphenodontians. Reassessment of the unique specimen recently confirmed its identification as a sphenodontian (Scheyer et al., 2020).

Hunt and Lucas (1991) placed several isolated limb bones and a fragment identified as a partial premaxilla from the Norian-age Cooper Canyon Formation of Texas in a new taxon of rhynchosaur, *Otischalkia elderae*. However, the holotypic humerus, a referred humerus, and two femora lack diagnostic features that would support this identification (Schultz et al., 2016). The alleged premaxilla fragment does not closely resemble premaxillae of other, undisputed rhynchosaurs examined by us, and its identity must remain uncertain at present. Subsequently, Spielmann et al. (2013) referred three partial humeri from the Norian-age Bull Canyon Formation of New Mexico to *Otischalkia elderae*, but again there is nothing that suggests rhynchosaurian affinities for these finds (Schultz et al., 2016).

Between 1958 and 1985, the late Donald Baird (then at the Princeton University Museum of Natural History) and his associates collected numerous mostly dissociated skeletal remains of tetrapods from outcrops of the Wolfville Formation along the southern shores of the Minas Basin, including most of the specimens described in this paper. The Wolfville Formation is part of the Fundy Group in the Fundy basin of the Newark Supergroup in New Brunswick and Nova Scotia. The Fundy basin is a half-graben that formed during the continental rifting of Pangaea during the late Permian and early Mesozoic, and its thick sedimentary and igneous fill accumulated during this time interval

(Fig. 1; Sues and Olsen, 2015). The Wolfville Formation unconformably overlies the possibly Permian Honeycomb Point Formation and underlies the Norian–Rhaetian Blomidon Formation. Sues and Olsen (2015) divided this formation into the Economy Member and Evangeline Member. Isolated bones and teeth of tetrapods typically occur as clasts in calcite-cemented, pebbly intraformational conglomerates of the Evangeline Member. Most are fragmentary and often water-worn. However, a few partial skulls and skeletons of tetrapods have been recovered from mudstones and sandstones of this unit. To date, strata of the Evangeline Member have yielded a diverse assemblage of continental tetrapods, including the traversodontid cynodont *Arctotraversodon plemmyridon*, an unidentified kannemeyeriiform dicynodont, three taxa of procolophonid parareptiles, the temnospondyl stem amphibian *Metoposaurus bakeri*, and several taxa of non-archosaurian archosauromorph and archosaurian reptiles (Sues and Olsen, 2015). The geological age of this unit is poorly constrained. *Metoposaurus bakeri* is elsewhere known only from the Camp Springs Formation of the Dockum Group in Texas (Hunt, 1993). The latter formation has generally been dated as late Carnian (Tuvanian; Lucas et al., 2002; Sues and Olsen, 2015), but Martz and Parker (2017) considered it earliest Norian (early Lacion) in age. None of the other well-documented tetrapod taxa known from the Evangeline Member has been reported outside the Fundy basin to date.

**Institutional Abbreviations**—NSM, Nova Scotia Museum of Natural History, Halifax, Nova Scotia, Canada; YPM VPPU, former Princeton University collection now housed at the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

**Anatomical Abbreviations**—**at**, additional tooth; **bo**, basioccipital; **bpt**, basipterygoid process; **bt**, basal tuber; **cp**, cultriform process; **en**, margin of external naris; **eof**, facet for exoccipital; **f**, possibly pneumatic foramen; **fl**, flange on L1 tooth; **fs**, facet for squamosal; **icc**, foramen for internal carotid canal; **L1,2**, lateral tooth row 1,2; **M1**, medial tooth row 1; **mf**, metotic foramen; **mg**, median groove on maxillary tooth plate; **oc**, occipital condyle; **pbs**, parabasisphenoid; **pmf**, facet for contact with left premaxilla; **sp**, splenial; **stu**, sella turcica.

## MATERIALS AND METHODS

The holotype, NSM018GF009.012, and the referred specimens were found dissociated, except for the basicranial elements, and are for the most part fragmentary and often water-worn. We refer all cranial remains to a single taxon of hyperodapedontine rhynchosaur because, based on the available maxillae and dentaries, there is no evidence for the presence of more than one taxon.

The fused parietals (NSM018GF009.001) and the basicranium (NSM018GF009.002) both compare closely in size to the homologous elements in a skull of *Hyperodapedon gordonii* reconstructed by Benton (1983) with a length of 17.5 cm; the estimated total length for the individual with that skull is ca. 1.3 m.

This paper follows Chatterjee (1974) in referring to the tooth rows lateral to the groove dividing the maxillary tooth plate as L1 and L2 and to those medial to this groove as M1 and M2, with L1 and M1 each positioned closest to the groove. Directional terms follow the standard nomenclature used in comparative anatomy.

## SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768

DIAPSIDA Osborn, 1903, sensu Benton, 1985

ARCHOSAUIROMORPHA Huene, 1946, sensu Benton, 1985

RHYNCHOSAURIDAE Cope, 1871, sensu Dilkes, 1998

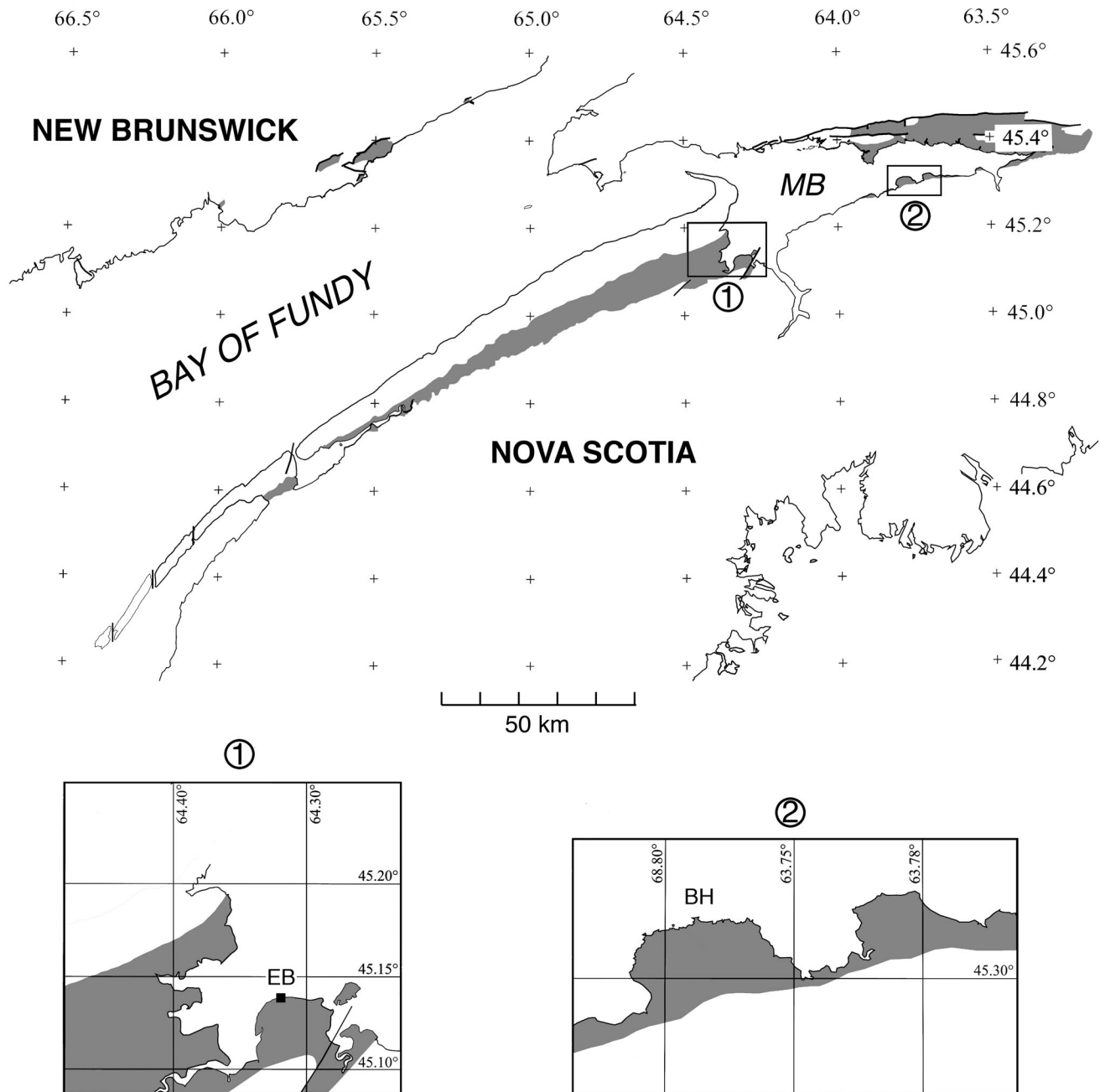


FIGURE 1. Map of the Fundy basin of Nova Scotia and New Brunswick, with the distribution of strata of the Wolfville Formation in gray. The inserts show the two areas from which the hyperodapedontine remains described in this paper have been recovered: **1**, Evangeline Beach, Kings County, Nova Scotia; **2**, Burntcoat headland, Hants County, Nova Scotia. Modified from Sues and Olsen (2015). **Abbreviations:** **BH**, Burntcoat headland; **EB**, Evangeline Beach; **MB**, Minas Basin.

HYPERODAPEDONTINAE Lydekker, 1885, sensu Schultz, Langer, and Montefeltro, 2016

*ORYCTORHYNCHUS BAIRDI*, gen. et sp. nov.

(Figs. 2–7)

**Diagnosis**—Diagnosed by the following combination of character states: maxilla with no more than two lateral and two medial rows of teeth; lateral and medial portions of the tooth-bearing part of the maxilla becoming increasingly crest-like during ontogeny; teeth of the lateral tooth row L1 more than twice as large as those of the medial tooth row M1 and with prominent

anterolingual flanges; and dentary without a row of lingual teeth. A possible autapomorphy is the presence of a single median foramen between the basal tubera, which has not been previously reported in any hyperodapedontine.

**Holotype**—NSM018GF009.012, fragment of a left maxilla (Fig. 3C). Although most of the teeth are damaged on this specimen, it clearly shows the flanges on the teeth of the L1 row and teeth of the M1 row that are shorter mesiodistally than wide labiolingually.

**Referred Specimens**—NSM018GF009.001, incomplete fused parietals of large individual (Fig. 5); NSM018GF009.002, basicranium of large individual (Fig. 6); NSM018GF009.003, incomplete



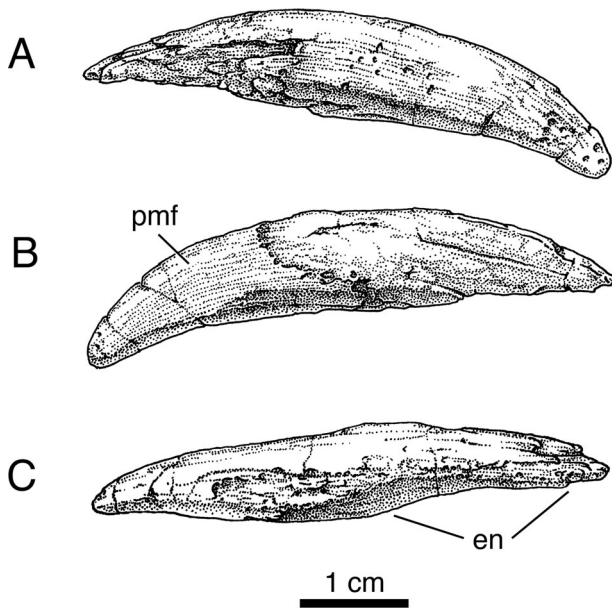


FIGURE 2. *Oryctorhynchus bairdi*, gen. et sp. nov., NSM018GF009.004, right premaxilla, in **A**, lateral, **B**, medial, and **C**, anterior views.

left maxilla of large individual (Fig. 4C–E); NSM018GF009.004, right premaxilla (Fig. 2); NSM018GF009.005, fragment of left dentary with attached piece of splenial (Fig. 7); NSM018GF009.006, poorly preserved piece of dentary; NSM018GF009.007, poorly preserved fragment of left maxilla; NSM018GF009.008, fragment of left maxilla; NSM018GF009.009, fragment of left maxilla; NSM018GF009.010, nearly complete left maxilla of juvenile individual; NSM018GF009.011, anterior portion of left maxilla; NSM018GF009.013, small piece of left dentary; NSM018GF009.014, anterior portion of left dentary of juvenile individual; NSM018GF009.015, nearly complete right maxilla of juvenile individual (Fig. 4A, B); NSM020GF005.001, left premaxilla; YPM VPPU 020587, fragment of right dentary.

**Horizon and Locality**—Evangeline Member of the Wolfville Formation (Newark Supergroup); Upper Triassic (late Carnian or earliest Norian). The holotype and most other specimens were collected at Evangeline Beach, Kings County, Nova Scotia, Canada. NSM018GF009.015, the juvenile maxilla, was recovered from the Burntcoat headland, Hants County.

**Etymology**—From Greek *oryktos*, dug, mined, alluding to the inferred digging habits of rhynchosaurs and the derivation of the name ‘Minas Basin’ from the French ‘les mines,’ and Greek *rhynchos*, snout. The specific epithet honors the late Donald Baird for his pioneering work on Triassic tetrapods from Nova Scotia.

## DESCRIPTION

**Premaxilla**—Positioned in its articular context, a right premaxilla (NSM018GF009.004; Fig. 2) gently curves anteroventrally and tapers distally to a point. Its mediolaterally flattened proximal portion was inserted between the maxilla and the nasal posteriorly and forms the lateral margin of the median external narial opening. The medial surface of the distal half of the premaxilla is flat and striated where it contacted (but was not sutured to) its antimeres to form a transversely narrow, superficially incisor-like bony ‘beak’ overhanging the mandibular symphysis. This portion of the bone is triangular in transverse section. A nearly

complete left premaxilla (NSM020GF005.001) is closely similar in size.

**Maxilla**—Maxillae (Figs. 3, 4) are the most common cranial remains collected to date. Most specimens are fragmentary, and the teeth are often worn or damaged.

The (in occlusal view) roughly triangular tooth plate is convex in side view, labiolingually widest posteriorly, and tapers anteriorly. Only the base of the plate-like ascending process of the bone is preserved on NSM018GF009.003 and NSM018GF009.015. The maxilla bears a posterodorsal surface for contact with the jugal; this contact forms a slight lateral ledge (NSM018GF009.003) or knob-like lateral thickening (NSM018GF009.009). In NSM018GF009.011 and NSM018GF009.015, a longitudinal groove extends parallel to the alveolar margin along the lateral surface of the maxilla, becoming deeper anteriorly. Ventral to this groove, a distinct ridge (= anteroventral ridge; Nesbitt and Whatley, 2004) is present above the alveolar margin of the maxilla. The alveolar margin is convex in lateral view, curving upward anteriorly. A longitudinal groove divides the maxillary tooth plate into a lateral and a narrower medial portion (Figs. 3, 4). It becomes increasingly wider transversely and shallower toward the anterior end of the maxilla in NSM018GF009.003 where the teeth and some bone were worn away. The groove is narrower on other maxillae (e.g., NSM018GF009.011) that show little wear. In NSM018GF009.009, the lateral tooth row extends to the anterior end but the medial tooth row terminates anteriorly a short distance behind the lateral one (Fig. 3A, B). The longitudinal groove on the maxilla received the dentate dentary blade when the jaws closed. The teeth of M1 are closely spaced, more numerous than those of L1, and, for the most part, anteroposteriorly narrow in basal cross-section. Only the juvenile maxilla NSM018GF009.015 has a few teeth with conical crowns. The closely spaced teeth of the lateral row are more than twice as large as those of the medial row; this size disparity is particularly pronounced in NSM018GF009.011 (Fig. 3A, B). Most lateral teeth are roughly triangular in transverse section (‘pyramidal’ sensu Chatterjee, 1974), and each has a distinct lingual flange extending anteriorly along the lingual surface of the preceding tooth, as in *Isalorhynchus genovefae* and most specimens of *Hyperodapedon*. Most crowns of the teeth bordering the groove laterally and medially have steep wear surfaces that resulted from contact with the dentate dorsal ridge of the dentary (e.g., NSM018GF009.011). If not worn away, the narrow anterior portion of the maxilla has the smallest teeth in either row. None of the maxillae has teeth on the lingual surface, unlike in more basal rhynchosaurs such as *Ammorhynchus navajoi* (Nesbitt and Whatley, 2004).

The largest available maxilla, a heavily worn left element (NSM018GF009.003; Fig. 4C, D), has two lateral rows of teeth. The teeth have been heavily abraded and are mainly visible in section, with L1 extending along the medial surface of the lateral maxillary ridge. The lateral and the posteriorly incomplete medial portion of the maxilla form crests rather than ‘cushions’ as in most other hyperodapedontines (Langer et al., 2017). A partial left maxilla (NSM018GF009.011) preserves an M2 row with largely abraded teeth lingual to M1. The M1 row of NSM018GF009.015 has a single additional tooth just lingual to one of its posterior teeth (Fig. 3A).

**Parietal**—The fused parietals are represented by an incomplete element lacking most of its anterior portion and the distal end of the right lateral process (NSM018GF009.001; Fig. 5). It has an estimated posterior width of about 12 cm. As in other derived rhynchosaurs, the fused parietals are triradiate, with anterolaterally curving lateral processes at the posterior end. The latter bear deeply incised dorsal notches on their slightly ventrally deflected distal ends for the reception of the medial processes of the squamosals, as in *Hyperodapedon gordonii* (Benton, 1983) and

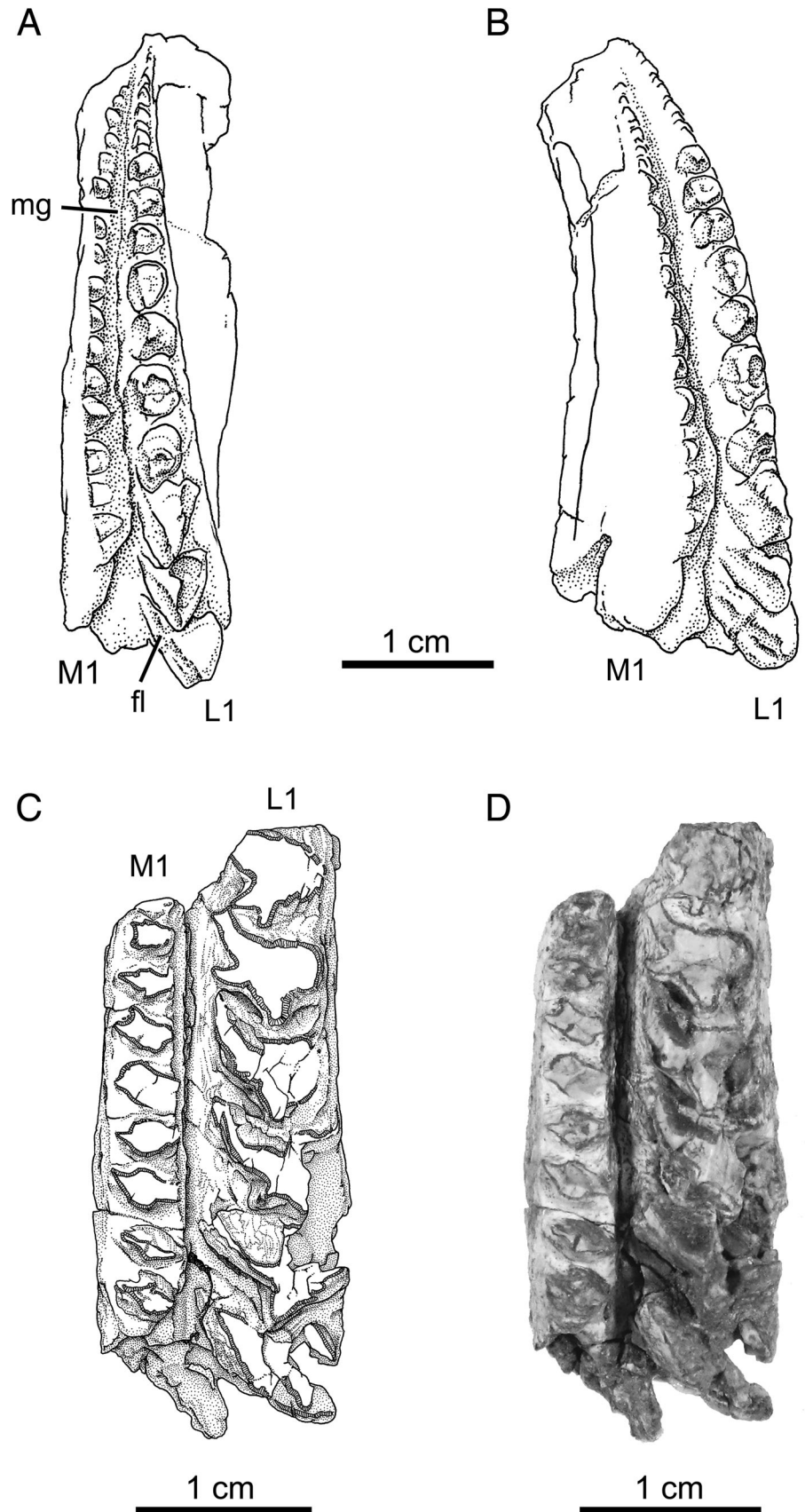


FIGURE 3. *Oryctorhynchus bairdi*, gen. et sp. nov., maxillae. **A**, **B**, NSM018GF009.011, partial left maxilla, in **A**, occlusal and **B**, oblique medial views. **C**, **D**, NSM018GF009.012, holotype, partial left maxilla in occlusal view: **C**, drawing and **D**, photograph. Anterior is to top of page.

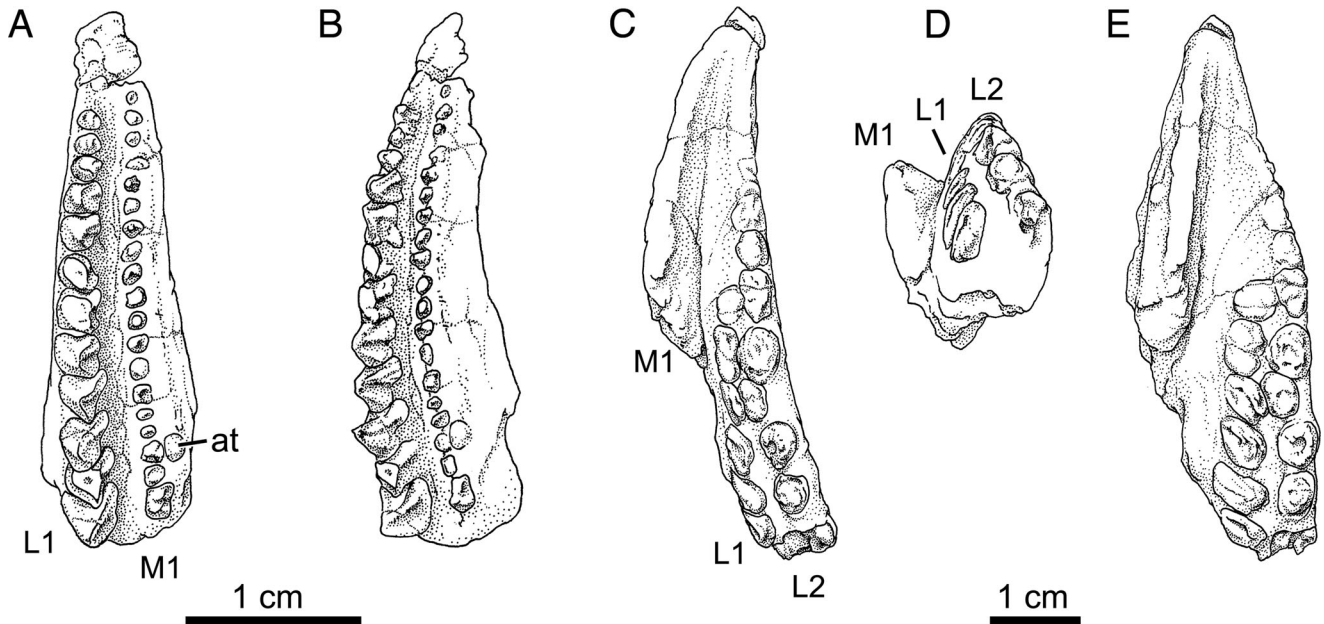


FIGURE 4. *Oryctorhynchus bairdi*, gen. et sp. nov., maxillae. **A, B**, NSM18GF009.015, small right maxilla, in **A**, occlusal and **B**, oblique medial views. **C–E**, NSM018GFF009.003, large left maxilla, in **C**, occlusal, **D**, posterior, and **E**, oblique medial views. Its medial tooth row has been largely obliterated. In **A–C, E**, anterior is to top of page.

'*Teyumbaita*' *sulcognathus* (Montefeltro et al., 2010). A dorsal ridge divides each lateral process into a narrow flat dorsal and an anteroventrally curving anterior portion. The ridges converge anteromedially and become the sagittal ridge on the intertemporal portion of the parietals (most of which is not preserved). The ventral surface of the lateral process is deeply concave at the junction with the median portion of the parietals. The posterior margin of the fused parietals is formed by a transverse ridge. It has a shallow median embayment and overhangs a distinct groove, which is delimited by a second transverse ridge posteroventrally.

**Basicranium**—A well-preserved basicranium (NSM-018GF009.002; Fig. 6) comprises the basioccipital and the basisphenoid (which is indistinguishably fused with the parabasisphenoid), with a partially preserved cultriform process and lacking most of the left basipterygoid process. Its ventromedial length up to the base of the cultriform process is 5.2 cm. The two bones are clearly separated from each other, with the basioccipital being longer than the parabasisphenoid along the midline. The basioccipital forms the large occipital condyle except for its dorso-lateral corners, which were made up by the exoccipitals. The articular surface of the condyle extends anteroventrally close to the basal tubera. The large, dorsolaterally facing articular facets for the exoccipitals almost contact each other medially on the dorsal surface of the basioccipital but are separated posteriorly, not completely excluding the basioccipital from the margin of the foramen magnum. The robust basal tubera are formed by the basisphenoid anteriorly and the basioccipital posteriorly. They are wider transversely than long anteroposteriorly. The basisphenoid portion of each tuber is longer than wide. An elongate ventral opening between the basal tubera possibly corresponds to pneumatic foramina in a similar position in the basal rhynchosaur *Mesosuchus browni*, which open into a pneumatic sinus in the basal tuber (Sobral and Müller, 2019:fig. 3). On the dorsal surface of the basioccipital, the ventral margin of the metotic foramen is visible between the facet for the exoccipital and the basipterygoid process. The small sella turcica in the

parabasisphenoid has two posterior openings, which represent the anterior exits of the internal carotid canals. These passages enter the parabasisphenoid posteriorly through paired foramina on the ventral surface between the basipterygoid processes. The complete right basipterygoid process is directed posterolaterally and extends farther ventrally than the basal tuber in lateral view. It has an anterolaterally facing surface for contact with the pterygoid. The cultriform process extends anterior and dorsal to the basipterygoid processes. It increases in depth antero-dorsally and forms a distinct ventral ridge.

**Dentary**—Several fragments of dentaries are available, but none preserves the anterior tip or the posterior contacts with the postdentary bones. The largest and best-preserved dentary in the sample is the partial left element NSM-018GF009.005 (Fig. 7). Its lateral surface is concave anteroposteriorly. The tightly packed teeth form a nearly straight, palisade-like row along the dorsal margin of the dentary, which probably extended close to the rostral tip anteriorly. Individual teeth are rod-shaped, labiolingually narrow, and show wear on the labial and lingual surfaces of most teeth. The lack of wear on the posterior-most two teeth indicates that these are near the posterior end of the

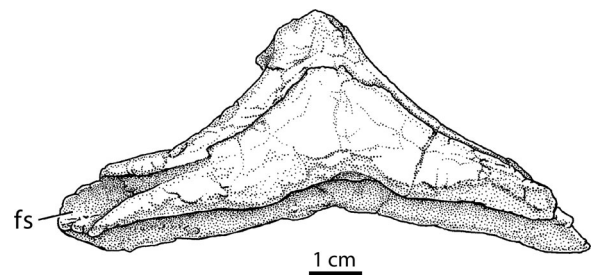


FIGURE 5. *Oryctorhynchus bairdi*, gen. et sp. nov., NSM018GF009.001, incomplete fused parietals, in dorsal view. Anterior is to top of page.



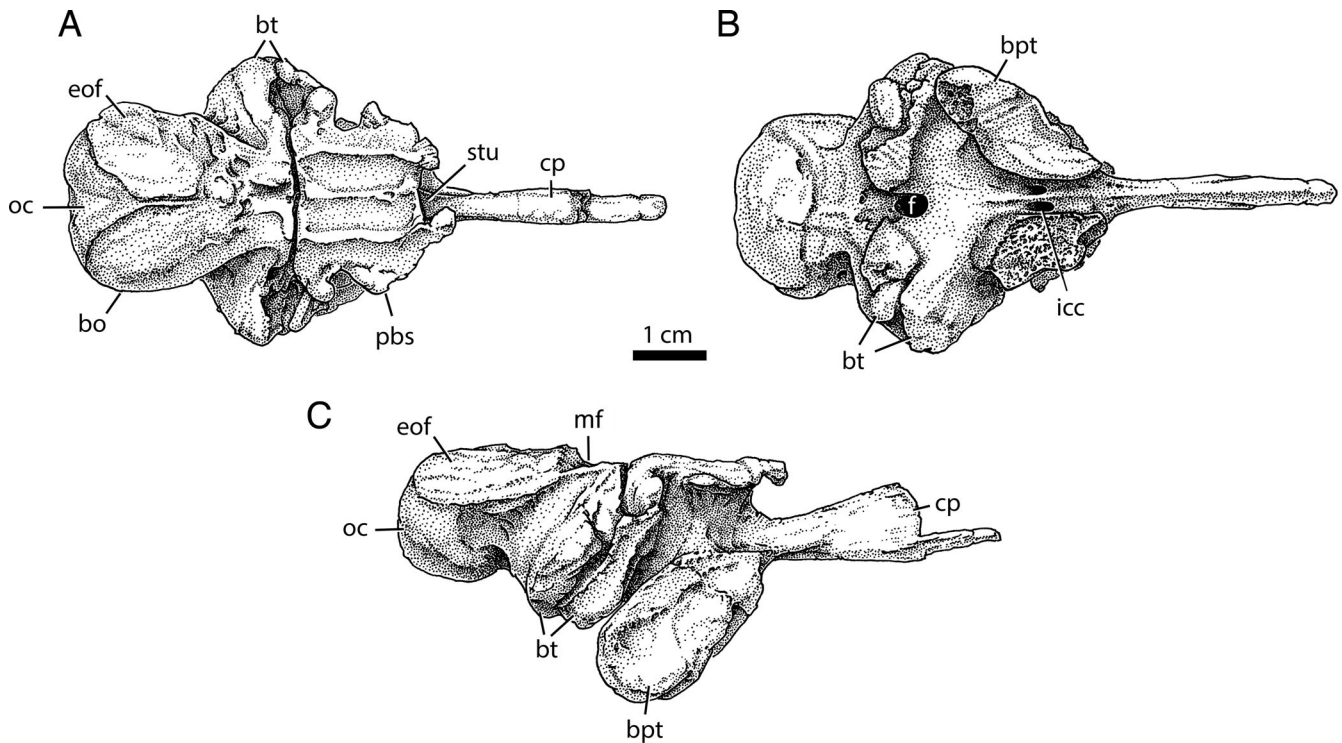


FIGURE 6. *Oryctorhynchus bairdi*, gen. et sp. nov., NSM-018GF009.002, basicranium, in **A**, ventral, **B**, dorsal, and **C**, right lateral views.

dentary, below which any longitudinal row of lingual teeth would be evident if present. Langer et al. (2017) previously noted the absence of this feature in NSM-018GF009.005. The eroded lingual surface of a fragment of a right dentary (YPM VPPU 020587) shows that the teeth are deeply rooted in the jaw. A piece of the splenial adheres to the anteroventral portion of the medial surface of NSM-018GF009.005 (Fig. 7B).

#### PHYLOGENETIC RELATIONSHIPS

All rhynchosaurian cranial bones recovered from the Evangeline Member to date are referable to Hyperodapedontinae based on shared derived features such as the absence of lingual teeth on the maxilla, the lateral portion of the maxillary tooth plate being equal in width to or slightly wider than the medial portion, the presence of a longitudinal groove on the occlusal surface of the maxilla, the combination of conical and pyramidal teeth on the maxilla, the presence of flanges on the teeth forming the L1 row, the basioccipital being longer than the parabasisphenoid along the midline, and the basiptyergoid processes being wider transversely than long anteroposteriorly (Whatley, 2005; Langer et al., 2017). The lateral processes of the posterior portion of the fused parietals gently curve anterolaterally and are distally notched for reception of the medial processes of the squamosals, as in *Hyperodapedon gordonii* (Benton, 1983) and '*Teyumbaita*' *sulcognathus* (Montefeltro et al., 2010). Except for its smaller size, the basicranium closely resembles one referred to *Hyperodapedon huxleyi* from the Upper Triassic Maleri Formation of India (Lydekker, 1885:pl. 3, fig. 1). The currently available dentaries and maxillae of the Nova Scotian hyperodapedontine differ considerably in size and proportions but share features that suggest the presence of only a single taxon in the Evangeline Member. The dentaries lack a lingual row of teeth (which is also variably absent in several species of *Hyperodapedon*; see Whatley [2005] for details). The maxillae have proportionately very large

lateral teeth and a single median groove. None of the known maxillae has more than two lateral and more than two medial tooth rows, resembling the condition in *Isalorhynchus genovefae* (Whatley, 2005) but unlike that in more derived hyperodapedontines, which have at least three anteriorly extending lateral and medial rows of teeth, respectively. The known maxillae, which range in length from 2.8 cm (NSM018GF009.015) to over 6 cm (NSM018GF009.003, which is incomplete at either end), typically have one medial tooth row and one or two lateral tooth rows. Maxillae of *Hyperodapedon* spp., even of small, presumably juvenile individuals, typically have three or more lateral and medial tooth rows, respectively (e.g., Benton, 1983). Langer et al. (2017) suggested that these differences might reflect immaturity of the available specimens from the Evangeline Member, but the number of tooth rows does not further increase in the known growth series. There is no lateral toothless surface, unlike in *I. genovefae* (Langer et al., 2000; Whatley, 2005). The tooth-bearing portions on the maxillae of the Nova Scotian hyperodapedontine become more crest-like as the bone increases in size. The absence of a row of lingual teeth on the dentary is matched by the absence of a secondary groove on the maxilla, which would have resulted from occlusal contact with the former, as observed in various specimens of *Hyperodapedon* spp. (Whatley, 2005).

We scored the character states for the Nova Scotian hyperodapedontine into the character-taxon matrix published by Langer et al. (2017). In the first instance, the cranial bones were individually scored into this matrix (see Supplemental Data). A strict consensus tree generated from 100 most parsimonious trees recovered by an analysis with TNT 1.5 (Goloboff and Catalano, 2016), using the Implicit Enumeration algorithm, showed virtually no resolution among rhynchosaurs more derived than *Mesosuchus browni*, with only the grouping *Hyperodapedon huenei* + '*Teyumbaita*' *sulcognathus*. Coding the entire hypodigm from the Evangeline Member as a single operational taxonomic



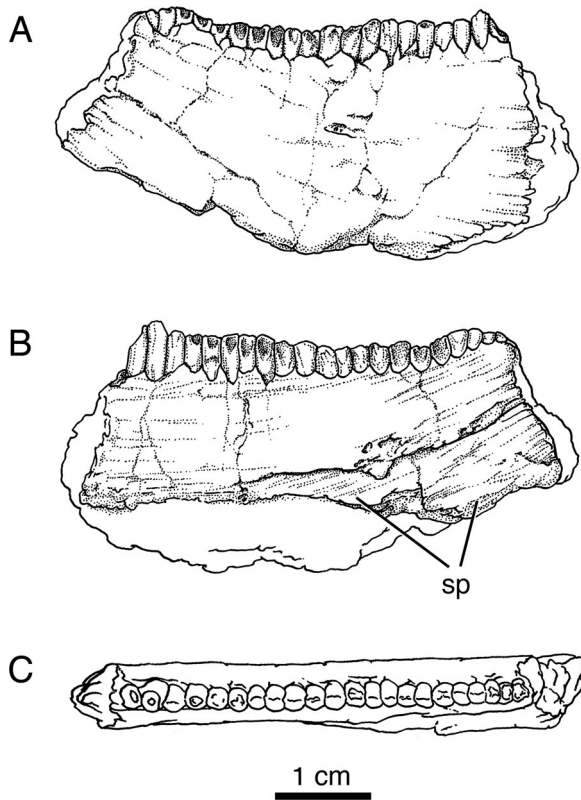


FIGURE 7. *Oryctorhynchus bairdi*, gen. et sp. nov., NSM018GF009.005, partial left dentary with attached fragment of the splenial, in **A**, lateral, **B**, medial, and **C**, dorsal views. In **A**, anterior is to the left.

unit (OTU) (Appendix 1), we recovered six most parsimonious trees (each with a length of 223 steps; consistency index [CI] = 0.574; retention index [RI] = 0.783; Fig. 8). The strict consensus of these trees found the OTU as the sister taxon of the unnamed taxon from Wyoming and this clade as the sister group of *Hyperodapedon* spp. including ‘*Supradapedon*’ *stockleyi* and ‘*Teyumbaita*’ *sulcognathus*. Bremer support and bootstrap values for Hyperodapedontinae (including the Nova Scotian taxon) are 5 and 73%, respectively. The Nova Scotian and Wyoming hyperodapedontines share with *Hyperodapedon* spp. the basiptyergoid process being wider anteroposteriorly than long dorsoventrally (character state 52.1), the presence of more than one clear tooth row lateral to the median groove on the maxilla (69.1), and the number of tooth rows lateral to the median groove equal or greater than the number of tooth rows medial to the median groove (121.1). The Nova Scotian and Wyoming hyperodapedontines are distinguished by the presence of only one dentary tooth row (76.0) and the absence of lingual teeth on the dentary (78.0). Because the jaw bones of the Nova Scotian taxon differ from those of other known hyperodapedontines, we propose a new taxon, *Oryctorhynchus bairdi*, for their reception.

In a detailed analysis of the paleobiogeography of Triassic continental tetrapods, Ezcurra (2010) found that Ischigualastian tetrapod assemblages across Pangaea grouped according to paleolatitudes. Langer (2005) first defined the Ischigualastian land vertebrate faunachron for a set of Late Triassic tetrapod assemblages from Argentina and Brazil. Ezcurra (2010) characterized the North American assemblages assigned to this faunachron by the presence of desmosuchine aetosaurs and trilophosaurid archosauromorphs, which he considered restricted to low paleolatitudes (about 10°N). By contrast, he characterized Ischigualastian tetrapod assemblages from mid- to high paleolatitudes by the presence of aetosaurine aetosaurs, rhynchosaurs, and traversodontid cynodonts. The presence of a hyperodapedontine

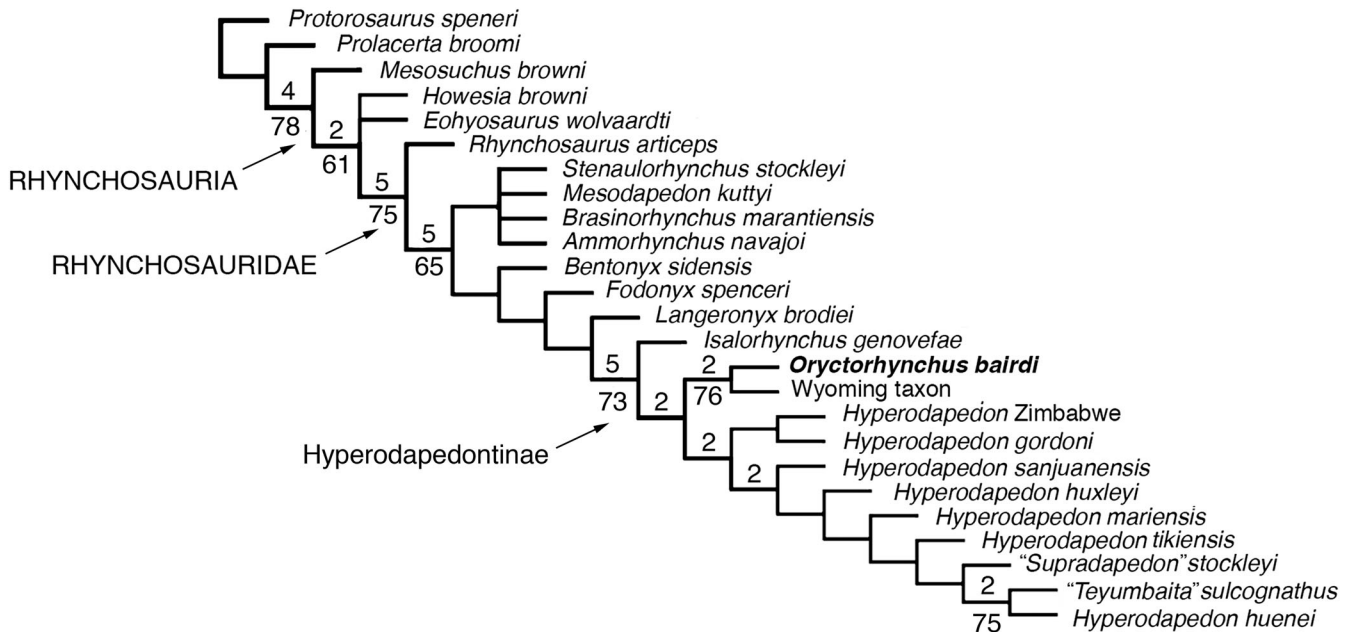


FIGURE 8. Strict consensus from six most parsimonious trees from the TNT analysis of the character-taxon matrix of Langer et al. (2017) with the addition of the hypodigm for *Oryctorhynchus bairdi*. Numbers represent Bremer support (above) and bootstrap value (below). The previously used generic names *Supradapedon* and *Teyumbaita* are listed in quotation marks because they represent constituent taxa in the clade *Hyperodapedon*.

rhynchosaur and a traversodontid cynodont in the low-paleolatitudinal tetrapod assemblage from the Evangeline Member of the Wolfville Formation (Sues and Olsen, 2015) underscores that the latter comprises faunal elements from a wide paleolatitudinal range, suggesting a more cosmopolitan pattern of tetrapod distribution during the early Late Triassic than previously assumed.

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APPENDIX 1. Character states for *Oryctorhynchus bairdi* for the character-taxon matrix published by Langer et al. (2017).

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