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## Amniote faunal revision of the Pictou Group (Permo-Carboniferous), Prince Edward Island, Canada

*Révision des amniotes du groupe de Pictou (Permocarbonifère), Île du Prince-Édouard, Canada*Kirstin S. Brink<sup>a,b,\*</sup>, Nicolás E. Campione<sup>b</sup>, Jessica R. Hawthorn<sup>a,b</sup><sup>a</sup> Department of Biology, University of Toronto Mississauga, 3359, Mississauga road N, Mississauga, L5L 1C6 Ontario, Canada<sup>b</sup> Department of Ecology and Evolutionary Biology, University of Toronto, 25, Willcocks Street, Toronto, M5S 3B2 Ontario, Canada

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## ABSTRACT

The amniote faunal assemblages from the Pictou Group (Prince Edward Island, Canada) are re-evaluated for the first time in 50 years. Fossils recovered from formations within this group (Orby Head, Hillsborough River, and Kildare Capes) indicate the presence of a parareptile, representing the first occurrence of a non-synapsid amniote from the PEI redbeds. The amniote taxa from PEI are re-described within the context of current research, providing the basis for an updated faunal list for the vertebrate-bearing formations within the Pictou Group. The presence of a parareptile, diadectid, and possibly two synapsids (caseid and/or varanopid), together with the absence of edaphosaurids and definitive ophiacodontids, suggests similarities with the upland Bromacker and Richards Spur localities of Germany and Oklahoma, respectively. However, more research and new fossil discoveries are needed to confidently resolve the systematics and palaeoecology of amniotes from the Lower Permian of Atlantic Canada.

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## R É S U M É

Les assemblages faunistiques d'amniotes du groupe de Pictou (Île du Prince-Édouard, Canada) sont réévalués pour la première fois en 50 ans. Les fossiles collectés dans les formations au sein de ce groupe (Orby Head, Hillsborough River et Kildare Capes) indiquent la présence d'un parareptile, ce qui représente la première occurrence d'un amniote non synapside dans les couches rouges de l'ÎPÉ. Les taxons amniotes de l'ÎPÉ sont redécrits dans le contexte de la recherche actuelle, fournissant la base d'une liste faunistique actualisée pour les formations qui contiennent des vertébrés au sein du groupe de Pictou. La présence d'un parareptile, d'un diadectidé et de deux synapsidés possibles (un caséidé et/ou un varanopidé), ainsi que l'absence définitive d'édaphosauridés et d'ophiacodontidés suggèrent des similarités avec les localités de hautes terres de Bromacker et de Richards Spur, respectivement en Allemagne et en Oklahoma. Cependant, des recherches et de nouvelles découvertes de fossiles sont nécessaires pour résoudre avec confiance la systématique et la paléoécologie des amniotes du Permien inférieur du Canada atlantique.

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## Mots clés :

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## 1. Introduction

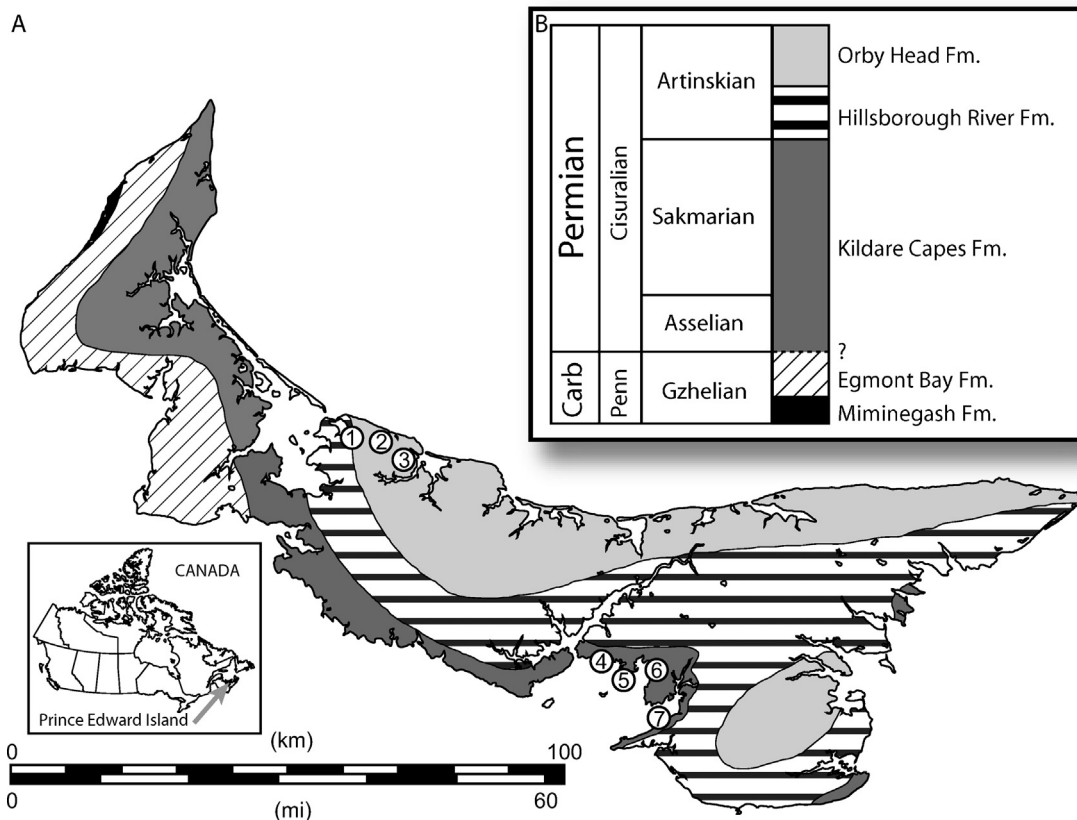
The Permo-Carboniferous Pictou Group redbeds of Prince Edward Island (PEI), Canada, have yielded vertebrate, plant, and trace fossils (Brink et al., 2012; Dawson and Harrington, 1871; Langston, 1963; Ziegler et al., 2002). Most of the vertebrate material is fragmentary (preserved skeletal pieces no larger than 50 mm), making identification difficult. A rigorous study conducted 50 years ago by Langston (1963) provided initial descriptions and occurrence data for 10 chondrichthyan, osteichthyan, and tetrapod taxa from various localities spanning three formations (Fig. 1).

The terrestrial non-amniote tetrapods are represented by a possible left premaxilla (CMN 9990) assigned to the temnospondyl *Eryops megalcephalus* from Lobster Point (Fig. 1A: Locality 4); fragmentary skull bones (CMN 10012, partial right maxilla and partial palatine) of an unknown temnospondyl that shares affinities with *Eobrachyops* (now *Isodectes*; Sequeira, 1998) from Spring Valley (Fig. 1A: Locality 1); a partial right femur (CMN 9989) assigned to *Seymouria* sp. from Irishtown, near French River (Fig. 1A: Locality 2); and a fragmentary left dentary with teeth (CMN

9918) and a postzygapophysis (CMN 9919) of a diadectid from Lord Selkirk Provincial Park (Fig. 1A: Locality 7).

Amniote taxa, according to Langston (1963), are limited to non-therapsid synapsids, including: a nearly complete dentary (CMN 10000) referred to cf. *Mycterosaurus* within Nitosauridae, a family currently of uncertain validity (Reisz, 1986), from Spring Valley (Fig. 1A: Locality 1); a partial pterygoid and epipterygoid (CMN 9914) referred to the now invalid (Reisz, 1986) suborder Ophiacodontia from the Tea Hill Park locality (Fig. 1A: Locality 5); and an articulated metatarsal and phalanx (CMN 9991) of the caseid *Trichasaurus* from Spring Valley (Fig. 1A: Locality 1). Perhaps the most notable specimen from PEI, described by Leidy (1854), is the partial snout of *Bathygnathus borealis* (ANSP 9524), a sphenacodontid similar to *Dimetrodon* and *Sphenacodon*, collected from the bottom of a well near French River (Fig. 1A, Locality 3). Finally, as an addendum, Langston (1963) mentions a proximal end of a tibia (CMN 10019) referred to *Ophiacodon* from a locality along the shoreline between Pownal and Cherry Valley (Fig. 1A: Locality 6).

Together with the plant and spore data already known from PEI (e.g., Barss et al., 1963; Dawson, 1854), the



**Fig. 1.** Geological map of Prince Edward Island, Canada. A. Localities. B. Approximate ages of formations. Locality 1: Spring Valley; Locality 2: Irishtown; Locality 3, French River; Locality 4: Lobster Point; Locality 5: Tea Hill Park; Locality 6: shoreline between Pownal and Cherry Valley; Locality 7: Lord Selkirk Provincial Park. Abbreviations: Carb: Carboniferous; Penn: Pennsylvanian.

**Fig. 1.** Carte géologique de l'Île du Prince-Édouard, Canada. A. Localités. B. Âges approximatifs des formations. Localité 1: Spring Valley; Localité 2: Irishtown; Localité 3: French River; Localité 4: Lobster Point; Localité 5: Tea Hill Park; Localité 6: Rivage entre Pownal et Cherry Valley; Localité 7: Lord Selkirk Provincial Park. Abréviations: Carb: Carbonifère; Penn: Pennsylvanie.

After Ziegler et al. (2002) and Brink et al. (2012).

description of the PEI vertebrate assemblages anchored the age of the redbeds in the Early Permian (Langston, 1963; Mossman and Place, 1989; Ziegler et al., 2002), and allowed for comparisons of the assemblages with roughly equivalent (temporally and depositionally) global Permo-Carboniferous localities. In general, the taxa found on PEI were considered similar to those of the Early Permian of Texas (Olson and Vaughn, 1970). The footprint localities of PEI have been compared to contemporaneous strata in Europe (Mossman and Place, 1989), and, recently, the Early Permian, “upland” (Eberth et al., 2000) Bromacker locality in Germany (Brink et al., 2012).

Since Langston’s (1963) study, our understanding of vertebrates from the Pennsylvanian and Permian has vastly increased, in large part thanks to Robert Reisz’ prolific research programme dedicated to understanding the taxonomy, phylogeny, anatomy, and diversity of taxa during this important interval in the history of life (e.g., Berman and Reisz, 1982; Campione and Reisz, 2010; Maddin et al., 2008; Modesto and Reisz, 2008; Modesto et al., 2009; Reisz, 1986; Reisz and Dilkes, 2003; Sullivan and Reisz, 1999). Given these advances, we reassess the amniote taxa from PEI within the context of current knowledge of Permo-Carboniferous tetrapods, provide an updated faunal list for this region, figure specimens that were described but not figured by Langston (1963), and compare the assemblage to other major coeval localities from North America and Europe.

### 1.1. Geological setting

The repeated fining-upward fluvial megasequences of the Pictou Group were divided into five formations by van de Poll (1989). The Gzhelian Miminégash Formation consists of orange- and red-coloured mudstones interbedded with fine or very fine-grained wacke, and is overlain by the Egmont Bay Formation, a fining-upward sequence also of Gzhelian age (van de Poll, 1989). The contact between the Egmont Bay and Kildare Capes formations approximates the transition from Pennsylvanian to Permian strata, and the latter formation, of Asselian–Sakmarian age (and possibly the Latest Gzhelian), is represented by a fining-upward megacyclic sequence with small-scale, generally fluvial-dominated cycles within the formation (van de Poll, 1989). The overlying Artinskian-aged Hillsborough River Formation consists of two laterally-equivalent subunits: the western Malpeque Member, composed of finer-grained sediments similar to the distal platform lithofacies of New Brunswick, and the eastern Wood Islands Member, which is more coarsely grained and similar to the sediments of the more proximal Cumberland Sub-basin of Nova Scotia (van de Poll, 1989). The youngest formation, the Orby Head Formation, is Artinskian in age and composed of sediments ranging from medium-grained wackes to conglomerates. Van de Poll (1989) also suggested that these five formations be recognized as components of a separate group, the Prince Edward Island Group, but this designation has not been adopted by subsequent authors (e.g., Calder et al., 2004; Ziegler et al., 2002). Due to overlap with mainland sequences, the Pictou Group was retained as the designation for the PEI strata. The Permo-Carboniferous ages for

the Pictou Group formations are based largely on plant and spore data (Barss et al., 1963; Hacquebard, 1972; Ziegler et al., 2002).

### 1.2. Institutional abbreviations

**AMNH FR**, American Museum of Natural History, New York, New York, USA; **ANSP**, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA; **TMM**, Texas Memorial Museum, University of Texas, Austin, Texas, USA.

## 2. Systematic palaeontology

REPTILIA Laurenti, 1768

PARAREPTILIA Olson, 1947

*Parareptilia* indet.

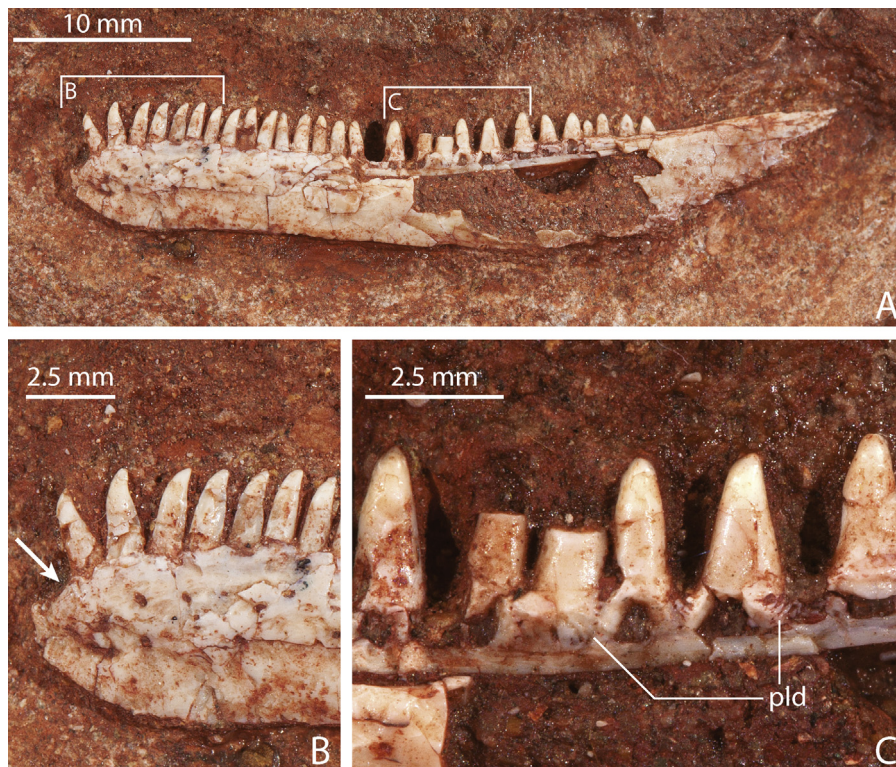
(Fig. 2)

**Material:** CMN 10000, left dentary

**Locality and Age:** Locality 1, Spring Valley (Fig. 1). Hillsborough River Formation (Artinskian). Referred to as Locality P-6108 by Langston (1963).

**Remarks:** Langston (1963) referred CMN 10000 to cf. *Mycterosaurus*, which at the time belonged to the edaphosaurian family Nitosauridae (Romer and Price, 1940). *Mycterosaurus* is now placed within Varanopidae (Reisz, 1986). Current interpretations consider the holotype of *Nitosaurus jacksonorum* (AMNH FR 4782), the only other nitosaurid species, to be a possible composite of two taxa (*Aerosaurus* and *Oedaleops*). Accordingly, Reisz (1986) considered both the genus and species, as well as the family Nitosauridae, *incertae sedis*, as no lectotype was designated for *N. jacksonorum*. Furthermore, Edaphosauria, originally erected by Romer and Price (1940) to include edaphosaurids and caseids, has never been recovered within a phylogenetic context (e.g., Benson, 2012; Reisz, 1986; Sidor, 2003) and is no longer in use.

Langston’s (1963) referral of the dentary to cf. *Mycterosaurus* was based on the supposition that an isolated tooth (CMN 10017, assumed by Langston to pertain to the same taxon as the dentary) conformed to the expected morphology for a ‘primitive’ edaphosaur. In addition, Langston (1963) noted that the posterior ascending process of the dentary was identical to that figured by Romer and Price (1940) for *Mycterosaurus*. *Mycterosaurus* dentary teeth were not well known at that time, and the genus has since been re-described as a mycterosaurine varanopid (Berman and Reisz, 1982), a hypothesis that is well supported by subsequent phylogenetic analyses (Benson, 2012; Campione and Reisz, 2010; Maddin et al., 2006; Reisz et al., 2010). The dentary of mycterosaurines, and varanopids in general, is thin relative to its length, and tapers towards the symphysis; their teeth are labiolingually thin, highly recurved along the entire length of the tooth row, and the mesial-most teeth are not angled forward (Campione and Reisz, 2010; Reisz and Berman, 2001; Reisz and Dilkes, 2003). Mycterosaurine teeth are particularly notable for their serrated carinae (Evans et al.,



**Fig. 2.** CMN 10000, left dentary, labial view. A. Complete dentary. B. Subset of A showing anterior margin of dentary with light sculpturing, with arrow indicating first tooth position. C. Subset of A showing tooth roots. Abbreviation: pld: plicidentine.

**Fig. 2.** CMN 10000, dentaire gauche, vue labiale. A. Dentaire complet. B. Sous-ensemble de A) montrant la marge antérieure du dentaire avec sculpture légère et une flèche indiquant la première position des dents. Abréviation : pld : plicidentine.

2009). These morphological features are not present in CMN 10000 and hence we do not support the assignment of the dentary to cf. *Mycterosaurus*.

**Description and comparisons:** the dentary is slender and elongate, with a jagged, posterodorsally-angled posterior margin for articulation with the angular and surangular (Fig. 2A). Pitted ornamentation and nutritive foramina are subtly present on the lateral surface, mostly in the anterodorsal region of the bone (Fig. 2B). In lateral view, the tooth-bearing margin is strongly rounded anteriorly, and so the first two dentary teeth are anteriorly procumbent relative to the remaining teeth (Fig. 2B). From approximately the third tooth position, the margin of the dentary becomes nearly straight, with a slight dorsal angle starting at the 16th tooth position (Fig. 2A).

There are 29 tooth positions, exceeding the number known in any other parareptile, with the possible exception of lanthanosuchoids and *Nyctiphruetus* (Chudinov, 1957; Efremov, 1946; Säilä, 2010). The most mesially positioned teeth taper gently towards their apex, and exhibit a distally directed curve that terminates in a pointed tip (Fig. 2). The teeth decrease in length and become less recurved posteriorly along the tooth row; a triangular-shape typifies the distal-most tooth positions. Distal teeth are slightly bulbous near their attachment with the tooth row. Small, non-serrated carinae are present along the mesial and distal margins of the tooth and are limited to the apices of the teeth.

A fortuitous break in the specimen below the level of the jawbone exposes the shape of the tooth root, which is 1 mm in height and flared where it attaches to the dentary (Fig. 2C). A low shelf of dentary bone borders the tooth roots labially and lingually, suggesting a protothecodont tooth attachment, as in other parareptiles (MacDougall and Modesto, 2011; Modesto and Reisz, 2008). No replacement pits or replacement teeth are visible. The tooth roots show an infolding of the dentine (plicidentine [Fig. 2C]), a condition suggested to be present in other parareptilian taxa (Modesto and Reisz, 2008). However, the infolding in CMN 10000 is restricted to the tooth root only, whereas the extent to which the folds on the teeth of *Colobomycter* or *Macroleter* extend below the level of the jawbone is not known. These dentine folds in transverse view in CMN 10000 (Fig. 2C) are similar to those of the parareptile *Soturnia* (Cabreira and Cisneros, 2009; fig. 1C), which are also restricted to the tooth root. There is minute fluting on the posterior teeth of the dentary of CMN 10000, which differs from the well-defined and large flutes on the teeth of *Colobomycter* and *Macroleter* (Modesto and Reisz, 2008; Tsuji, 2006).

An isolated tooth (CMN 10017) found in the same nodule as CMN 10000 is two times larger than any of the dentary teeth (Fig. 6D). The tip is recurved as in the dentary teeth, and has a slight-shovel shaped morphology, creating minute carinae near the tip of the tooth, as in the expanded maxillary teeth of *Macroleter* (Tsuji, 2006).

Langston (1963) compared CMN 10000 to several contemporaneous taxa, including edaphosaurids, captorhinids, *Nitosauros*, and parareptiles, and suggested that it was most similar to the dentary of *Nitosauros jacksonorum* described by Romer and Price (1940). However, given that the dentary of *N. jacksonorum* was described from an impression in matrix and the affinities of the specimen are uncertain (Reisz, 1986), it is difficult to confidently compare the two specimens. CMN 10000 and AMNH FR 4782 exhibit conical teeth, and the mesial-most tooth of *N. jacksonorum* is slightly procumbent (Romer and Price, 1940).

Langston (1963) also noted similarities in general morphology with the parareptiles *Nycteroleter* and *Nyctiphruetus acudens*. However, *Nycteroleter* bears more extensive sculpturing on the dentary and the lingual sides of the teeth are nearly straight, and *Nyctiphruetus* exhibits a shorter and deeper mandibular morphology, greater spacing between teeth, and unexpanded tooth root bases (Ivakhnenko, 1997).

CMN 10000 also resembles the dentary of *Limnoscelus paludis* in that the teeth are conical, have cutting edges and apically recurved tips, and decrease in size posteriorly along the dentary (Berman et al., 2010). The differences between CMN 10000 and *L. paludis* relate to an enlargement of the dentary symphysis and associated teeth in the latter; also, the teeth of *L. paludis* are fluted at the base, above the level of the jaw.

In overall shape, these teeth are most similar to those described for the parareptiles *Delorhynchus* (Fox, 1962) and *Colobomycter* (Modesto, 1999; Modesto and Reisz, 2008), although their marginal teeth are known from specimens that only preserve the upper jaw. *Delorhynchus* (Fox, 1962) was also originally assigned to Nitosauridae based on the shape of the teeth and maxilla, but has since been re-identified as a parareptile (Modesto, 1999). The teeth also bear some resemblance to those of millerettids in being conical, slightly recurved, and possessing minute cutting edges (Gow, 1972). However, the mesial-most tooth is not procumbent in *Milleretta*. The similarities outlined above, along with the occurrence of a virtually identical lower jaw of a yet unnamed acleistorhinid parareptile from the Richards Spur locality in Oklahoma (OMNH 73363, Modesto et al., 2009), provide strong evidence that CMN 10000 pertains to a parareptile. The similarity of the isolated tooth, CMN 10017, to the teeth of *Macroleter* suggests that it may also pertain to a parareptile, but given its isolated nature any interpreted affinities with the dentary should be considered tentative.

#### SYNAPSIDA Osborn, 1903

*Synapsida* indet.

(Figs. 3 and 4)

**Material:** CMN 9914, incomplete left pterygoid and epipterygoid.

**Locality and age:** Locality 2, near Alexandra. Kildare Capes Formation (Asselian–Sakmarian). Referred to as Locality P-6004 by Langston (1963).

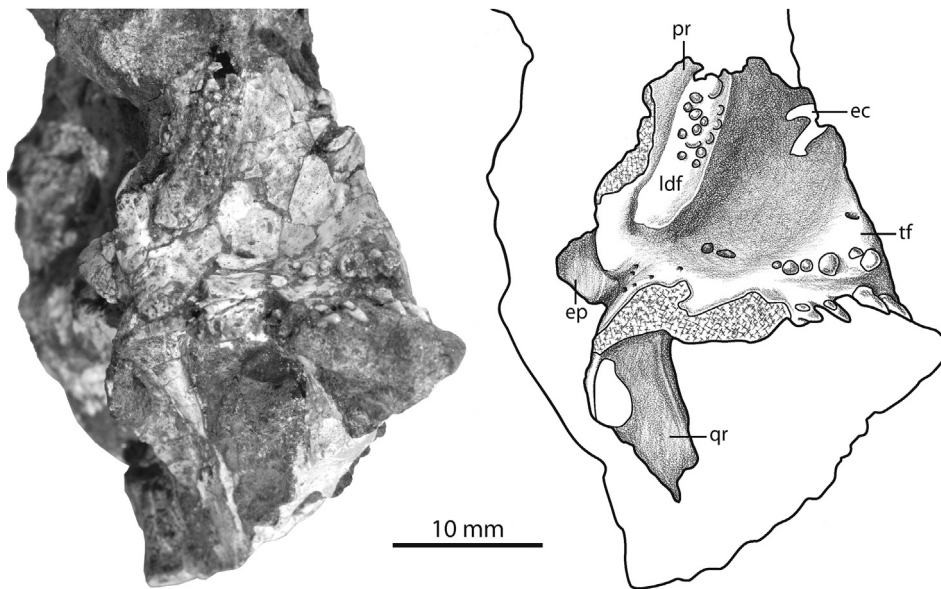
**Remarks:** CMN 9914 was referred to *Ophiacodon* based on the following five characters (Langston, 1963): 1) a long,

narrow interpterygoid vacuity; 2) the low position of the basal articular process in relation to the palatal surface; 3) the absence of an interlocking union between pterygoid and quadrate; 4) a cartilaginous basal part of the epipterygoid; and 5) the absence of a thickened transverse flange of the pterygoid. Olson and Vaughn (1970) remarked that the pterygoid more closely resembled that of an “advanced” caseid, but did not provide any specific reasons for this assignment.

**Description and comparisons:** the pterygoid has a tri-radiate shape created by the posteriorly directed quadrate ramus, the ventrolaterally directed transverse flange, and the anteriorly directed palatal ramus (Fig. 3). The quadrate ramus is incomplete, and the posterior-most extent has been reconstructed based on an impression left in the matrix. This ramus is narrow and convex ventrally, with a thickened medioventral ridge. Langston (1963) stated that the absence of an interlocking union between the pterygoid and quadrate is an ophiacodontid characteristic, but this anatomy is not preserved adequately enough to comment on the articulation between the quadrate and the quadrate ramus. There is no evidence for the development of a medial flange from the quadrate ramus that would form the floor of a cavity for the middle ear, as in ophiacodontids (Romer and Price, 1940).

Anterodorsal to the quadrate ramus is the epipterygoid (Fig. 3). A thin, broken process, much thinner than the epipterygoid process of sphenacodontids (Brink and Reisz, 2012), but similar to that of caseids (Maddin et al., 2008), extends dorsally lateral to a cupped process dorsal to the body of the pterygoid. This cup serves as the articulation for the basiptyergoid process of the basisphenoid. The extent of cartilage that may have supported these structures in life is not known. The basicranial articulation is low relative to the palatal surface, which is similar to all eupelycosaur (Campione and Reisz, 2010), with the possible exception of *Dimetrodon* (Brink and Reisz, 2012). New preparation of CMN 9914 indicates that the epipterygoid slightly overlaps the quadrate ramus dorsally. There is no indication of an articulation between the epipterygoid and the quadrate.

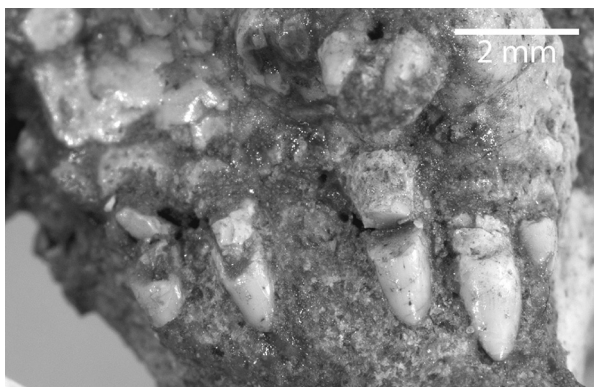
Ventral to the epipterygoid is the transverse flange of the pterygoid. The transverse flange is distinct and triangular shaped in lateral view, as in most eupelycosaur, with the exception of *Edaphosaurus* (Reisz, 1986). The pterygoid bears a primary row of at least 10 teeth along the thickened ventral edge of the transverse flange, and a secondary row of six teeth anterior to the first. The secondary row runs posteromedially from the lateral margin of the transverse flange toward the central body, where the three rami of the pterygoid intersect. The large teeth of the primary row are near conical in shape, with rounded, spatulate tips, bulging anteriorly to create a slight posterior curve (Fig. 4). These teeth increase in height laterally along the row, with the exception of the most labially-positioned tooth (1.42 mm tall, 0.9 mm wide at base), which is slightly smaller than the second most labial tooth (2.98 mm tall, 1.02 mm wide at base). The teeth of the secondary row are nearly the same size but slightly smaller than those of the primary row, and also increase in height labially along the row.



**Fig. 3.** CMN 9914, left pterygoid, ventral view. Left, photograph; right, interpretive drawing. Abbreviations: ec: sutural surface of the ectopterygoid; ep: epipterygoid; ldf: lateral dental field; pr: palatal ramus; qr: quadrate ramus.

**Fig. 3.** CMN 9914, ptérygoïde gauche, vue ventrale. Gauche, photographie, droite, dessin interprétatif. Abréviations: ec: surface suturale de l'ectoptérygoïde; ep: épityptérygoïde; ldf: domaine dentaire latéral; pr: branche palatine; qr: branche du carré.

The palatal ramus of the pterygoid has been damaged since its original description by Langston (1963: fig. 4). Previously, the ramus bore two anteriorly directed dental fields, but the medial field is no longer present. Therefore, the shape and extent of the interpterygoid vacuity cannot be determined, although the vacuity is long and narrow in most non-therapsid eupelycosaur (Reisz, 1986). The teeth of the dental field are not arranged linearly as in ophiacodontids, but rather form a small field of irregularly spaced teeth (Fig. 3). This palatal tooth field extends posteriorly to the level of the basicranial articulation, which is not typical of ophiacodontids (Benson, 2012). The sutural contact for the overlapping ectopterygoid articulation is located on the lateral surface of the posterior portion of the palatal ramus, anterodorsal to the transverse flange (Fig. 3).



**Fig. 4.** CMN 9914, teeth of the transverse flange of the pterygoid in anterior view.

**Fig. 4.** CMN 9914, dents du rebord transversal du ptérygoïde en vue antérieure.

Langston compared CMN 9914 to edaphosaurids, caseids, and ophiacodontids, and decided that the pterygoid most closely resembled ophiacodontids for the five reasons stated earlier. However, the extent of the interpterygoid vacuity, the presence and extent of cartilage, and the articulation between the quadrate and the pterygoid cannot be determined. The low position of the basicranial articulation is common in eupelycosaur and most likely primitive (Benson, 2012; Reisz, 1986; Reisz et al., 2009), and therefore cannot be used to identify this specimen as an ophiacodontid. New preparation of CMN 9914 has revealed that the transverse flange is thickened laterally, and is generally more robust overall than other ophiacodontid pterygoids.

The secondary row of teeth, anterior to the enlarged primary teeth of the transverse flange, is not typical of ophiacodontids, or of many eupelycosaur. Teeth situated anterior to those of the transverse flange are typically smaller than the teeth of the flange, and are arranged irregularly, as in caseids (Olson, 1968; Reisz et al., 2009), and some sphenacodontians, such as *Haptodus* (Currie, 1979), or in a radial pattern, as in *Varanops* (Campione and Reisz, 2010). The distribution of palatal teeth resembles that of some caseids in having patches of small teeth anterior to the prominent row of teeth of the transverse flange (Maddin et al., 2008; Olson, 1968; Reisz et al., 2009). The two rows of teeth along the transverse flange are very similar to those of the caseosaur *Eothyris* (Reisz et al., 2009), and to the mycterosaurine *Mesenosaurus romeri*, although the teeth anterior to the main tooth row in the latter are smaller than those in CMN 9914 (Reisz and Berman, 2001).

The overall robusticity of CMN 9914, the slender shape of the quadrate process, the fields of numerous palatal teeth that extend posteriorly to the level of the basicranial

articulation, and the presence of two rows of teeth on the transverse flange of the pterygoid do not support an affinity of CMN 9914 with ophiacodontids. It is possible that the presence of two rows of teeth on the transverse flange of the pterygoid is autapomorphic, regardless of its taxonomic status.

SYNAPSIDA Osborn, 1903

CASEASAURIA Williston, 1912

CASEIDAE Williston, 1911

Caseidae indet.

**Material:** CMN 9991, incomplete metatarsal.

**Locality and Age:** Locality 1, Spring Valley. Hillsborough River Formation (Artinskian). Referred to as Locality P-6108 by Langston (1963).

**Remarks:** Langston (1963) referred CMN 9991 to the caseid *Trichasaurus* based on a comparison with a similar metatarsal from the holotype of *Trichasaurus texensis* (FMNH 652). Given the short, squat nature of the metatarsal (Langston, 1963: fig. 7), it likely pertains to a caseid (Olson, 1968); however, it is not necessarily diagnostic to a specific genus, and may also be *Casea*, as mentioned by Langston (1963); instead we refer to it to an indeterminate caseid.

SYNAPSIDA Osborn, 1903

EUPELYCOSAURIA Kemp, 1982

Eupelycosauria indet.

(Fig. 5)

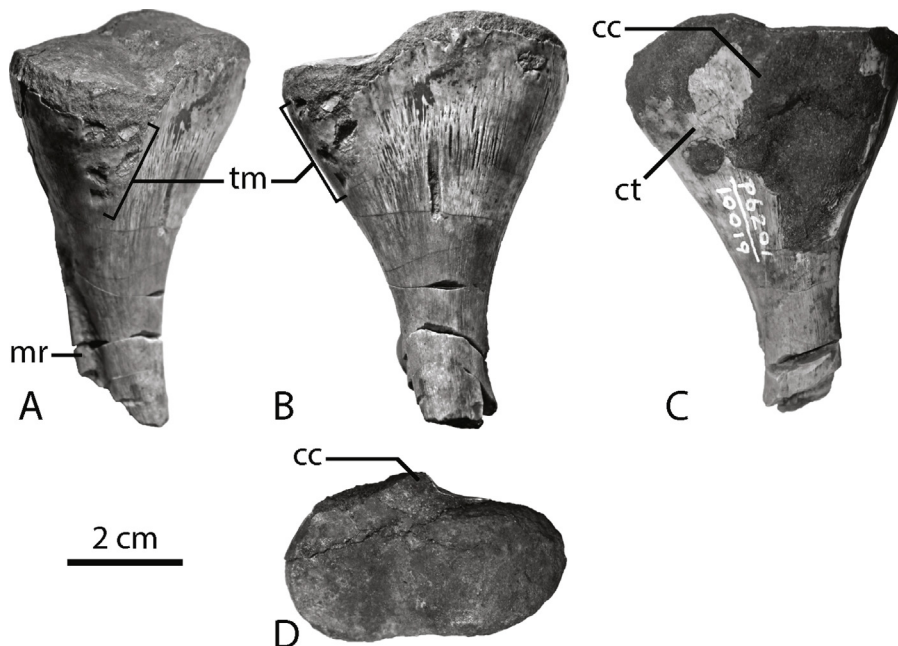
**Material:** CMN 10019, proximal end of right tibia.

**Locality and Age:** Locality 3, along the shoreline between Pownal and Cherry Valley. Kildare Capes Formation (Asselian–Sakmarian). Referred to as Locality P-6201 by Langston (1963).

**Remarks:** Langston (1963) did not fully describe CMN 10019, but provided a brief comment in an addendum, noting the slender shaft and referring the specimen to *Ophiacodon* within the size range of *O. retroversus*. This specimen is notable for the presence of tooth marks on the ventrolateral surface, and is described in detail here for the first time.

**Description and comparisons:** the tibia is broken approximately midshaft, and only the proximal end is preserved. The maximum width of the proximal end is 47.8 mm, and the circumference of the shaft at its narrowest point is 52 mm. The two areas for articulation of the femoral condyles are weakly distinguished from one another by a shallow depression with no accompanying ridge, as the finished surface of the articular area is not preserved, and the cnemial trough of the dorsal surface and the ventral surface of the element are only shallowly concave at their most proximal limits (Fig. 5).

The dorsal surface is less well preserved than the ventral surface, as there are several areas of missing bone surface. The cnemial crest and trough are both weakly expressed (Fig. 5C, D). The weakly concave ventral surface of the tibia exhibits one large nutritive foramen amongst several smaller foramina (Fig. 5B). A strong, sharp ridge is present on the medial side of the shaft, extending from the medial side of the cnemial crest in a posteromedial direction (Fig. 5A).



**Fig. 5.** CMN 10019, eupelycosaurian right tibia. A. Medial view. B. Ventral view. C. Dorsal view. D. Proximal view. Abbreviations: cc: cnemial crest; ct: cnemial trough; mr: medial ridge; tm: tooth marks.

**Fig. 5.** CMN 10019, tibia droit d'eupélycosaurien. A. Vue médiale. B. Vue ventrale. C. Vue dorsale. D. Vue proximale. Abréviations : cc : crête cnémiale ; ct : creux cnémial ; mr : crête médiane ; tm : marques de dents.

CMN 10019 bears five small, puncture-and-scrape tooth marks forming short, shallow furrows on the ventrolateral surface (Fig. 5A, B). They are arranged in two rows, indicating either two separate bites or the upper and lower dentition of a single bite. The close spacing of these marks suggest that the vertebrate feeding on CMN 10019 was small, and thus the tooth marks are likely the result of scavenging. The tooth marks are, in overall shape, similar to those identified on a skeleton of *Varanops* (Reisz and Tsuji, 2006). Evidence of scavenging by tetrapods in Early Permian communities is exceedingly rare, with this specimen representing only the second published occurrence. Three xenacanthiform teeth were found in close association with this specimen, with one reportedly wedged against the articular surface of CMN 10019 (Langston, 1963). However, orientation of the tooth marks suggests that they were unlikely to have been made by the diplodont teeth of a xenacanthiform. There is insufficient evidence to attribute these tooth marks to any specific vertebrate scavenger, although they likely pertain to a tetrapod.

The morphology of the tibia is not consistent with that of a caseid. CMN 10019 shares with caseids the weak expression of the cnemial crest and a weakly concave ventral surface of the tibial head (Olson, 1968). However, CMN 10019 is less robust than typical caseid tibiae, and the head of the tibia is not as broad as would be expected for a caseid with a shaft of similar circumference (Olson, 1968; Reisz et al., 2011). The weak division between the two articular surfaces for the femoral condyles also differs from the deep groove present on the proximal surface in caseids (Reisz et al., 2011). Caseids also lack the sharp ridge present on the medial side of CMN 10019.

CMN 10019 is more elongate and slender in morphology than edaphosaurid tibiae, which are generally short and broad, with strongly-developed cnemial crests (Romer and Price, 1940); however, this specimen cannot be conclusively differentiated from the tibia of any other large eupelycosaur. CMN 10019 is similar to varanopids in its gracile morphology, level of development of the cnemial crest (Campione and Reisz, 2010), and the shape of the outline of the tibial head in proximal view, which has been previously described as reniform (Maddin et al., 2006) or C-shaped (Campione and Reisz, 2010). The development of the medial crest, however, is variable in the varanopid *Varanops*; it is weakly developed in TMM 43628-1 and more greatly developed in OMNH 73175 (Campione and Reisz, 2010; Maddin et al., 2006).

The cnemial crest and medial ridge are most strongly developed in sphenacodontids, such as *Dimetrodon* (Romer and Price, 1940: pl. 32C), although ontogenetically earlier specimens tend to exhibit weaker development of crests and ridges in limb elements relative to those of ontogenetically later specimens (Brinkman, 1988). Based on similarities in the cnemial crest and medial ridge, we cannot reject the possibility that CMN 10019 is a sphenacodontid. Sphenacodontid material is known from PEI (ANSP 9524, *Bathygnathus borealis*); however, CMN 10019 is from the Kildare Capes Formation, whereas ANSP 9524 is known from the younger Orby Head Formation.

The features of CMN 10019 also closely resemble those of *Ophiacodon*. The weakly concave ventral surface,

rounded lateral margin of the proximal end, and the weak development of the cnemial crest is consistent with the ophiacodontid condition, where the skeleton is more poorly ossified than other eupelycosaur, even in adult specimens (Romer and Price, 1940). The medial ridge is also commonly, but not consistently, expressed in *Ophiacodon* (OMNH 55220, Kissel and Lehman, 2002: fig. 8.9; FMNH UC 671, Williston and Case, 1913: fig. 34a).

Though CMN 10019 may well represent *Ophiacodon* as suggested by Langston (1963), we cannot reject the possibility that it may instead pertain to an immature sphenacodontid or a large varanopid. As a result, we assign the tibia to an indeterminate eupelycosaurian.

SYNAPSIDA Osborn, 1903

EUELYCOSAURIA Kemp, 1982

SPHENACODONTIA Romer and Price, 1940

SPHENACODONTIDAE Marsh, 1878

*Bathygnathus borealis* Leidy, 1854

**Material:** ANSP 9524, partial snout including portions of the maxilla and nasal.

**Locality and age:** Locality 3, French River. Orby Head Formation (Artinskian).

**Remarks:** *Bathygnathus borealis* has a long and interesting taxonomic history (see Spalding, 1995). Originally thought to be the dentary of a Triassic reptile, it was not until 50 years after its discovery that Case (1905) and Huene (1905) independently concluded that *B. borealis* was a sphenacodontid. *Bathygnathus borealis* is similar in overall morphology to *Dimetrodon* and *Sphenacodon* in possessing a maxilla with a rounded ventral margin, a maxillary step posterior to the premaxilla-maxilla suture, teeth that are tear-drop shaped in lateral view, recurved, and serrated, and an elongate nasal-maxillary suture (Leidy, 1854: pl. 1).

### 3. Discussion

#### 3.1. Revised faunal list

Langston (1963) provided the first comprehensive assessment of the Permo-Carboniferous faunal assemblages from PEI. Here, we provide a revised interpretation of the fauna based on current taxonomic and anatomical descriptions. In particular, Langston (1963) assigned generic and specific designations to several of the specimens, despite their highly fragmentary and hence taxonomically ambiguous nature. A recent study by Nesbitt and Stocker (2008) stressed the importance of apomorphy-based comparisons when assessing the taxonomic status of fragmentary material. Although the methodology described by the authors is more objective compared to traditional anatomical comparisons, it is unfortunately of limited use here. In particular, current character matrices that include both early reptile and synapsid OTUs (e.g., Laurin and Reisz, 1995; Reisz et al., 2010) either do not code characters that pertain to the anatomical regions described in this study or include characters that, when coded for the specimens examined here, are plesiomorphic. Similar issues occur within more exclusive clades, including Parareptilia (MacDougall and Reisz, 2012; Tsuji, 2006)



and non-therapsid synapsids (Benson, 2012; Sidor, 2003). Given the limitations of current phylogenetic matrices with regard to the data afforded by the vertebrate fossils from PEI, we opt for a more traditional comparative approach. However, unlike Langston's (1963) original interpretations we are more conservative and assign specimens to higher taxonomic groupings so as to better reflect their taxonomic uncertainty, which can have important effects on subsequent meta-analyses (e.g., diversity patterns; Benton, 2012; Benson and Upchurch, 2013).

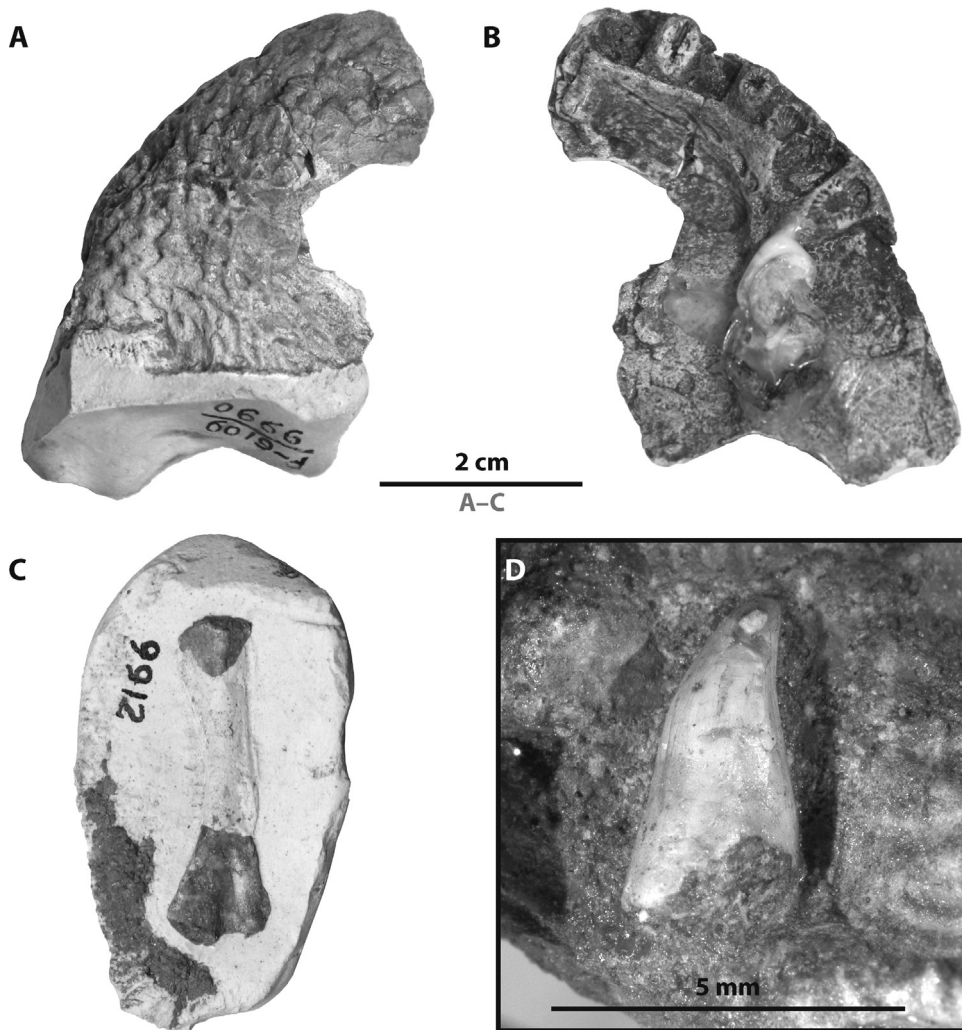
The amniote taxa from PEI described and compared in the previous section form the majority of the revised faunal list (Table 1). The dentary previously described as cf. *Mycterosaurus* is here interpreted as an indeterminate parareptile. Parareptiles are common components of other Lower Permian amniote faunas (e.g., Berman et al., 2000; MacDougall and Reisz, 2012), but were previously unknown from the Pictou Group. Thus, our interpretation represents the first documentation of a non-synapsid amniote from PEI. Re-assignment of the pterygoid and tibia from 'Ophiacodontia' to Synapsida indeterminate and Eupelycosauria indeterminate, respectively, eliminates any definitive body fossil evidence of ophiacodontids from the Pictou Group. Ambiguous evidence of ophiacodontids may

lie in the presence of two species of '*Gilmoreichnus*' (Calder et al., 2004; Mossman and Place, 1989), an ichnotaxon from the Kildare Capes and Hillsborough River formations, assigned to Ophiacodontidae by Haubold (1971). However, this ichnotaxon is in need of re-evaluation (Brink et al., 2012; Voigt, 2005), as it has been subjectively synonymized with multiple other ichnotaxa, and may represent a captorhinomorph or other eupelycosaurian trackmaker (Calder et al., 2004; Mossman and Place, 1989). Although the pterygoid does not pertain to an ophiacodontid, it is a synapsid and likely represents a caseid or a varanopid, given similarities with a yet unnamed caseid from Bromacker (Martens et al., 2005; Reisz et al., 2011) and *Mesenosaurus romeri* (Reisz and Berman, 2001). The metatarsal previously assigned to *Trichasaurus* likely pertains to a caseid, but cannot be confidently assigned to a genus at this time. These interpretations suggest the occurrence of at least two different synapsids from PEI, a possible caseid and at least one non-therapsid eupelycosaur. One final specimen (CMN 9912, from near Locality 5, Fig. 1A) not described by Langston (1963) is a small femur, preserved only by its proximal and distal ends (Fig. 6C); it is too incomplete to allow for taxonomic identification and thus was not included in the faunal list.

**Table 1**  
Revised faunal list of vertebrates from Prince Edward Island.

**Tableau 1**  
Liste révisée de la faune de vertébrés de l'île du Prince-Édouard.

Stage	Formation	Specimen	Taxa Langston (1963)	Taxa Present Study
Artinskian	Orby Head	CMN 9989	Temnospondyli Seymouriidae <i>Seymouria</i>	Seymouriamorpha Seymouriidae <i>Seymouria</i> sp.
		ANSP 9524	Synapsida Sphenacodontidae <i>Bathygnathus borealis</i>	Synapsida Sphenacodontidae <i>Bathygnathus borealis</i>
Artinskian	Hillsborough River	CMN 9916	Chondrichthyes Xenacanthidae <i>Xenacanthus</i>	Chondrichthyes Xenacanthiformes indet.
		CMN 10012	Temnospondyli Brachyopidae cf. <i>Eobrachyops</i>	Temnospondyli indet.
		CMN 9990	Temnospondyli Eryopidae <i>Eryops megacephalus</i>	Temnospondyli Eryopidae indet.
		CMN 10000	Synapsida Nitosauridae cf. <i>Mycterosaurus</i>	Parareptilia indet.
		CMN 10017	Synapsida Nitosauridae cf. <i>Mycterosaurus</i>	Unknown
		CMN 9991	Synapsida Caseidae <i>Trichasaurus</i>	Synapsida Caseidae indet.
Asselian–Sakmarian	Kildare Capes	CMN 9918	Anapsida Diadectidae indet.	Diadectomorpha Diadectidae indet.
		CMN 9914	Synapsida Ophiacodontia <i>incertae sedis</i>	Synapsida cf. Caseidae/Varanopidae
		CMN 10019	Synapsida Ophiacodontidae <i>Ophiacodon</i>	Eupelycosauria indet.



**Fig. 6.** Additional tetrapod specimens from PEI. A and B, CMN 9990, partial?left premaxilla of Eryopidae indet., in dorsal and ventral view, orientation as described by Langston (1963); C, CMN 9912, unidentified femur in anterior view; D, CMN 10017, isolated tooth, possibly associated with CMN 10000, parareptile dentary.

**Fig. 6.** Spécimens supplémentaires de tétrapodes de l'ÎPE. A et B, CMN 9990, premaxilla partielle ? gauche de Eryopidae indet, en vues dorsale et ventrale ; orientation telle que décrite par Langston (1963) ; C, CMN 9912, fémur non identifié en vue antérieure ; D, CMN 10017, dent isolée, sans doute associée à un dentaire parareptilien (CMN 10000).

Non-amniotes are not revised in detail here. Nonetheless, descriptions subsequent to Langston's study permit a preliminary review. The elasmobranchian teeth originally assigned to *Xenacanthus* exhibit a bicuspid morphology that is typical of many xenacanthiform species (Ginter et al., 2010). Furthermore, both species that formed the basis for Langston's (1963) comparative context have since been subsumed into the genus *Orthacanthus* (Ginter et al., 2010). As a result, we assign the isolated teeth to Xenacanthiformes indeterminate pending a more detailed comparative study. Similarly, both temnospondyl specimens are assigned to more inclusive clades. The dermal bone previously assigned to cf. *Eobrachyops* cannot be designated to a taxonomic level below that of Temnospondyli, and the premaxilla previously assigned to

*Eryops megacephalus* (Fig. 6A, B) is considered as Eryopidae indeterminate, given that other eryopids exhibit similar sculpturing on the dorsal surface and have similar labiolingually expanded teeth (Boy, 1990; Langston, 1963). Finally, Langston (1963) described the occurrence of two amniote relatives (*Seymouria* and *Diadectes*) based on a partial femur (CMN 9989) and partial dentary (CMN 9918), respectively. The femur, though partial, exhibits a well-developed adductor ridge, deep intercondylar fossa, and prominent fourth trochanter that are characteristic of *Seymouria* (Sullivan and Reisz, 1999). The whereabouts of the partial diadectid dentary are unfortunately unknown at present; however, the specimen figured by Langston (1963: fig. 3B) exhibits the characteristic flattened and labiolingually broad tooth morphology of diadectids (Kissel,

2010). Given the similarities between CMN 9989 and CMN 9918 to *Seymouria* and diadectids, respectively, we agree with Langston's original taxonomic interpretations of these specimens.

### 3.2. Faunal correlations and palaeoecology

Although the taxonomic resolution available for specimens from the Permo-Carboniferous of PEI is limited to higher taxa, the overall faunal list (Table 1) is typical of Early Permian assemblages. In particular, the presence of a large sphenacodontid in the Orby Head Formation suggests similarities to the Early Permian localities of the southern USA, as originally suggested by Langston (1963) and Olson and Vaughn (1970). Olson and Vaughn (1970) suggested that the lower part of the Pictou Group is equivalent to the Wichita Group of Texas and the upper part is equivalent to the Arroyo Formation of the Clear Fork Group (Hentz, 1988), and agreed with Langston's (1963) interpretation of the redbeds of PEI representing an increasingly arid and seasonal climate, similar to the trends observed in the southern USA (DiMichele et al., 2008; Tabor and Montañez, 2004; Tabor et al., 2008).

Brink et al. (2012) suggested that the Kildare Capes Formation (lower Pictou Group) may share more similarities with the Lower Permian Tambach Formation of Germany based on the occurrence of tracks and trackways of diadectids both at the Eldon locality of PEI and at the Bromacker quarry. This is supported by the occurrence of a diadectid within the Kildare Capes Formation (Table 1) and the absence of ophiacodontid and edaphosaurid specimens from the Bromacker quarry (Evans et al., 2009; Martens et al., 2005). Although future data may alter interpreted similarities between the Kildare Capes and Tambach formations, their apparent resemblance in faunal composition is not surprising given their proximity during the Permian (Brink et al., 2012; DiMichele and Hook, 1992).

Eberth et al. (2000) suggested that the Bromacker quarry represents an upland setting, far from coastal environments and coal swamps, which was most likely deposited on an alluvial plain. The sedimentology of the Pictou Group indicates deposition was in major and minor stream channels, probably driven by climatic cyclicity (Tanner et al., 2005). These palaeoenvironmental interpretations and similarities between the ichnofaunas of the Kildare Capes and Tambach formations suggest that the lower Pictou Group sequence may also represent an upland setting (Brink et al., 2012). Similar interpretations and comparisons have been made between the faunal assemblages of Bromacker and the Artinskian-aged (Gradstein et al., 2012; Woodhead et al., 2010) Richards Spur locality in Oklahoma, also considered to represent an upland setting (Evans et al., 2009). Here, edaphosaurids and ophiacodontids are also absent, whereas varanopids and parareptiles comprise the majority of the species richness of the amniote faunal assemblage (Evans et al., 2009; MacDougall and Reisz, 2012).

Given the potential similarity of the faunal assemblages from the Pictou Group with those of Richards Spur and Bromacker, it is possible that the Pictou Group represents a more upland palaeoenvironment. However, this

hypothesis is speculative given the low sample sizes and the level of taxonomic resolution afforded by current PEI specimens, and requires a more detailed comparative analysis of the sedimentology and depositional environment. Future fieldwork in this area, as well as in nearby localities (e.g., Nova Scotia, Canada; Calder, 1998) will be critical for understanding the associations between North American and European fossil assemblages from the Early Permian and interpreting the systematics and palaeoecology of vertebrate taxa from Atlantic Canada during this time.

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