



The lower actinopterygian fauna from the Lower Carboniferous Albert shale formation of New Brunswick, Canada – a review of previously described taxa and a description of a new genus and species

Kathryn E. Mickle^{1,2}

¹College of Science, Health, and the Liberal Arts, Philadelphia University, 4201 Henry Ave, Philadelphia, PA 19114, USA

²University of Kansas Biodiversity Institute, 1345 Jayhawk Blvd, Lawrence, KS 66045, USA

Correspondence to: Kathryn E. Mickle (micklek@philau.edu)

Received: 7 September 2016 – Revised: 21 November 2016 – Accepted: 21 November 2016 – Published: 31 January 2017

Abstract. The Lower Carboniferous Albert shale formation of New Brunswick, Canada, is well-known for the preservation of countless articulated lower actinopterygian palaeoniscoid fishes. This site is at the boundary between the Devonian and the Lower Carboniferous, making the lower actinopterygians preserved at this site important. The taxonomic history of previously described Albert shale formation actinopterygians is reviewed here. Many of the earliest described actinopterygian taxa from the Albert Formation are represented by poorly preserved type specimens and have the distinction of being moved from one paraphyletic genus to another paraphyletic genus. While these taxa are in need of major redescriptions, such work is premature until the large paraphyletic or polyphyletic genera they have been placed in, *Palaeonicus*[*m*], †*Rhadinichthys*, and †*Elonichthys*, are redescribed. But there is new diversity within the Albert shale formation. Here, a new lower actinopterygian species, †*Lambeia pectinatus*, is described from one well-preserved specimen. This new species is characterized by dorsal ridge scales with pectinated posterior margins, body scales inserted between adjacent dorsal ridge scales, body scales with pectinated posterior and ventral margins, the presence of a ventral rostro-premaxilla and a median rostral bone, a separate and distinct antorbital bone, and a single supraorbital bone. This newly described species is distinct from previously described fishes from the Albert Formation, and the morphology of this newly described species is more similar to later Carboniferous fishes rather than Devonian fishes. This suggests that morphological features commonly seen in Carbonifer-

ous fishes and rarely seen in Devonian fishes were present early in the Carboniferous.

1 Introduction

1.1 The Albert shale formation

For over 150 years, lower actinopterygian, or palaeoniscoid, fishes have been described from the Albert shales of southeastern New Brunswick, Canada (Fig. 1). The term Albert shales has been used informally to refer to the Albert shale formation, the middle formation of the Horton Group between the basal Memramcook Formation and the overlying Weldon Formation (Gussow, 1953; Greiner, 1962) (Fig. 2). Greiner (1962) and Utting (1987) present the Albert Formation itself as being composed of three members – the Dawson Settlement, Frederick Brook, and Hiram Brook members (Fig. 2). St. Peter (1993) presents the Albert Formation as being composed of six stacked lithofacies – conglomerate, sandstone, mudstone, mudstone/sandstone, kerogenous mudstone, and evaporate facies.

Since the 1800s, there has been controversy over the age of the Albert Formation. While an Early Carboniferous age was supported by the fossil fish and plants (Bailey and Eells, 1878; Lambe, 1909, 1910), some cautioned that the Albert Formation could be Devonian in age (Bailey et al., 1880; Eells, 1903). This trend continued into the late 1900s. Greiner (1962, 1974) had originally described the Albert Formation as Lower Carboniferous in age, but after the descrip-

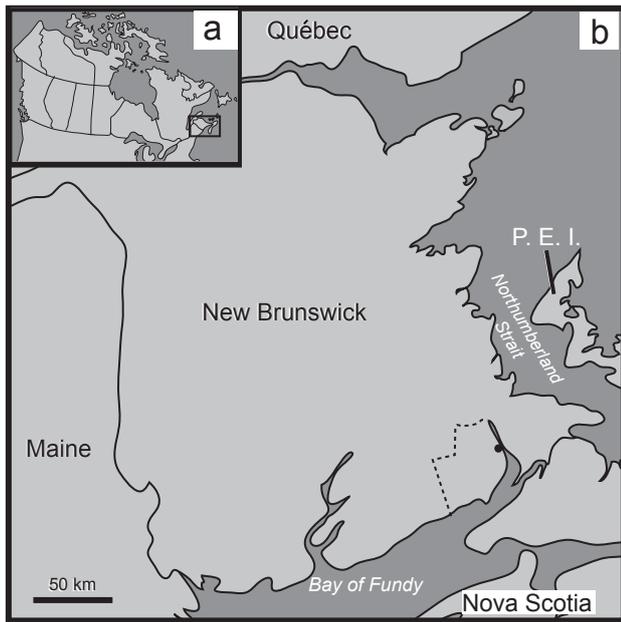


Figure 1. Map of locality. (a) Map of North America; box highlights area enlarged in (b). (b) Close up of New Brunswick, Canada. Dashed line indicates Albert County, where the majority of the specimens were collected. Black dot indicates Hillsborough, the site at which the original material described by Jackson was collected. Scale bar equals 50 km; (a) not to scale. Map modified from Google Maps, Map Data: © 2015 Google.

tion of an osteolepid, †*Latvius porosus* from basal beds, he considered the lower part of the Albert Formation to be Devonian (Greiner, 1977). Recent reassessments of the Albert Formation sarcopterygian material do not support Greiner's assignment of the material to the Devonian genus †*Latvius*, but rather suggest megalichthyid and Carboniferous affinities (Miller and Brazeau, 2007). This, combined with spore analyses, has put an end to the controversy regarding the age of the Albert Formation. The Albert Formation is Tournaisian (Lower Carboniferous) in age, near the Devonian and Lower Carboniferous boundary (Utting, 1987; St. Peter, 1993; Miller and Brazeau, 2007).

The Albert Formation is paleontologically famous for its countless articulated lower actinopterygian specimens (Greiner, 1977). These actinopterygians are important because with the supported Early Carboniferous age of the Albert Formation, they potentially bridge morphological gaps between Devonian and Carboniferous forms. Unfortunately, these fishes have not been dealt with in great detail for over a hundred years. The taxonomic history of the Albert Formation fishes is discussed here.

SERIES	GROUP	FORMATION	MEMBER
Upper Carboniferous			
	Hopewell		
Lower Carboniferous	Windsor		
	Moncton	Hillsborough	
		Weldon	
	Horton (Nova Scotia)	Gautreau	
			Hiram Brook
		Frederick Brook	
		Dawson Settlement	
Devonian		Memramcook	
Pre-Horton			

Figure 2. Stratigraphic column of the Lower Carboniferous of New Brunswick, Canada. Figure modified after Utting (1987, fig. 2).

1.2 Review of the taxonomic history of the Albert Formation palaeoniscoids

The palaeoniscoid fishes from the Albert Formation of New Brunswick have been a taxonomic nightmare for over 150 years. Lambe (1909, 1910) provided a taxonomic history of these fishes in his redescription of some of the New Brunswick fishes. This information is reviewed and updated below.

In 1851, Jackson described the first palaeoniscoid fishes from the Albert shales in papers entitled “Report on the Albert Coal Mine” (Jackson, 1851a) and “Descriptions of five new species of fossil fishes” (Jackson, 1851b). Though the second title claims to include the descriptions of five new taxa, only three new species were described and named – †*Palaeoniscus[m] alberti*, †*P. brownii*, and †*P. cairnsii*. Four additional specimens were described but never named. No type material was designated, and though plates and figures are referenced in this publication, they were never included with the text (Lambe, 1909, 1910).

Eastman (1908) and Lambe (1910) concluded that though Jackson's plates and figures were never published with the original descriptions, a few must have existed and been distributed to paleontologists because the plates were referenced by other scientists (see Traquair, 1877, p. 49; Dawson, 1877, p. 338). Dawson (1877) described two new palaeoniscoid species from the Albert Formation – †*Palaeoniscus[m] modulus* and †*Palaeoniscus[m] jacksonii*. Again, no type material was designated. Dawson (1877) also provided additional comments on Jackson's original species and referenced particular specimens figured by Jackson (1851a, b).

In the late 1800s and early 1900s, many scientists commented on how the Albert Formation palaeoniscoids were more similar to species within the genera †*Rhadinichthys* and †*Elonichthys*. As detailed by Lambe (1910), Traquair (1877) commented that †*Palaeoniscus[m] alberti* and †*P. cairnsii* are closely allied to †*Rhadinichthys carinatus* (Agassiz). This reassignment was later upheld by Traquair (1911). Traquair (1877) referred †*Palaeoniscus[m] brownii* to †*Elonichthys brownii*. Newberry (1899) upheld Traquair's (1877) reassignments. In Woodward's catalogue (1891), †*Palaeoniscus[m] alberti*, †*P. cairnsii*, and †*P. modulus* were referred to †*Rhadinichthys alberti*, †*R. cairnsii*, and †*R. jacksoni* (1891). Woodward (1891) also assigned †*Palaeoniscus[m] brownii* to †*Elonichthys brownii*, but also noted that he felt this was a "doubtful" and ill-defined species (Lambe, 1910). Eastman (1908) also referred the New Brunswick species to the genera †*Rhadinichthys* and †*Elonichthys*. In the same publication, Eastman described a new species from the Albert shales – †*Elonichthys elegantulus* – but no type specimen was designated (1908). All of the reassignments by Traquair (1877), Newberry (1889), Woodward (1891), and Eastman (1908) were done without justifications for these reidentifications.

Sometime before 1908, Jackson's original unpublished plates were discovered by Eastman in the Yale Peabody Museum (Eastman, 1908; Lambe, 1910). Using these plates, it was possible for Lambe (1909, 1910) to identify some of Jackson's original type and figured specimens in the collections of the Museum of Comparative Zoology, Harvard, and the Boston Society of Natural History. Using this new information, Lambe (1909, 1910) was able to redescribe the Albert Formation fishes and describe a new taxon, †*Elonichthys elli*. Agreeing with Traquair (1877, 1911), Woodward (1891), and Newberry (1908), Lambe (1909, 1910) referred †*Palaeoniscum alberti* to †*Rhadinichthys alberti* and †*P. brownii* to †*Elonichthys brownii*. Lambe (1909, 1910) also determined that †*Palaeoniscum cairnsii* (Jackson, 1851a, b) was not a valid species, nor was †*Elonichthys* (†*Palaeoniscum*) *jacksoni* (Dawson, 1877). Lambe (1909, 1910) also referred †*Palaeoniscum modulus* (Dawson, 1877) to †*Canobius modulus*, and the validity of †*Elonichthys elegantulus* (Eastman, 1908) was called into question.

Reassignments of Albert shale fishes continued in the later 1900s. Moy-Thomas (1938) commented that Westoll considered †*Canobius modulus* to be †*R. alberti* and agreed with Westoll that †*C. modulus* is synonymous with †*R. alberti*. Sternberg (1939) studied newly collected specimens from the Albert Formation and assigned these specimens to †*R. alberti*. Sternberg (1939) cautioned though that there were differences in measurements and ratios between the specimens designated as †*R. alberti*, suggesting that there is more than one species within this taxon or that the species is characterized by a great degree of variation. Gardiner commented on the Albert Formation fishes in his catalog of Canadian fossil fishes (Gardiner, 1966). Miller and McGovern (1996)

published a preliminary report describing palaeoniscoids tentatively identified as †*Elonichthys* from the Albert shales in Norton, New Brunswick, Canada. This has been the last work that has investigated the actinopterygian fauna of the Albert shale formation until this current work.

Jackson's original taxa – †*Rhadinichthys alberti*, †*R. cairnsii*, and †*Elonichthys brownii* – are discussed here. Some of these specimens have a long history of moving from one museum collection to another and have changed catalog numbers over the years. This makes identifying specimens mentioned in older literature difficult. Tables 1 and 2 detail the numerous identities of the original Jackson and Lambe specimens, respectively. Two questionable taxa from the Albert Formation – †*Rhadinichthys elegantulus* (Gardiner, 1966, states that the type is in the Museum of Comparative Zoology, Harvard (MCZ); no number given) and †*Canobius modulus* (Gardiner, 1966, states that the type is in Redpath Museum, McGill University; no number given) have never had type specimens designated. The statuses of these taxa are examined here as well.

1.3 Problem of generic assignment of the Albert Formation palaeoniscoids

The majority of the actinopterygians described from the Albert Formation have been placed within the poorly defined and paraphyletic genera †*Palaeoniscum*, †*Elonichthys*, or †*Rhadinichthys*. This problem is intensified by the fact that the type specimens of some of these genera are poorly preserved and uninformative. The specific problems with these genera are described below, as well as suggestions on how to deal with these problems.

1.3.1 † *Palaeoniscum*

Originally described in 1818 by Ducrotay de Blainville, the genus † *Palaeoniscum* has been a problematic one. After Ducrotay de Blainville's original description, Agassiz (1833) found no distinction between †*Palaeoniscum* and another genus described by Ducrotay de Blainville, †*Paleothrissum*. Agassiz (1833) combined the two genera into a new genus, †*Palaeoniscus*, keeping the same type species as Ducrotay de Blainville (1818). Jordan (1917) regarded Agassiz's use of the term †*Palaeoniscus* as a misspelling and called for the use of the name †*Palaeoniscum* and authority going to Ducrotay de Blainville (1818). It should be noted that Ducrotay de Blainville's original specific epithet was †*Palaeoniscum freieslebenense* (Ducrotay de Blainville, 1818), not the spelling that is used today, †*Palaeoniscum freieslebeni*.

Troschel (1857) recognized that Agassiz's †*Palaeoniscus[m]* could probably be divided into two different genera based on scale morphologies. After Agassiz, many species of † *Palaeoniscus[m]* were described, though

Table 1. Identities of Jackson's figured specimens. Plate and figure numbers, past and present museum catalog numbers, Jackson's (1851a, b) and Lambe's (1910) identifications, and type status included. Abbreviations: BSNH, Boston Society of Natural History; MCZ, Museum of Comparative Zoology. Genera abbreviated: *E.*, *Elonichthys*; *P.*, *Palaeoniscus*; *R.*, *Rhadinichthys*.

Plate and fig. no. Jackson (1851a, b)	BSNH no.	Former MCZ no.	Current MCZ no.	Jackson (1851) ID	Lambe (1910) ID	Type status
Plate I, fig. 1	7899	1960	5082	† <i>P. alberti</i>	† <i>R. alberti</i>	Holotype
Plate I, fig. 2	7900	1961	5083	† <i>P. brownii</i>	† <i>E. brownii</i>	Holotype
Plate I, fig. 3	7899a	1956	5084	† <i>P. cairnsii</i>	† <i>R. alberti</i>	Holotype † <i>P. cairnsii</i> (Jackson)
Plate I, fig. 4	Lost?	X	X	† <i>Palaeoniscus</i> sp.	† <i>E. brownii</i>	Holotype † <i>P. jacksoni</i> (Dawson)
Plate I, fig. 5	7901	1957	5085	Not mentioned	† <i>E. brownii</i>	Plesiotype
Plate II, fig. 1	7902		6150	† <i>Palaeoniscus</i> sp.	† <i>E. brownii</i>	
Plate II, fig. 2, 2 bis	7987	1959	5086	† <i>Palaeoniscus</i> sp.	† <i>R. alberti</i>	
Plate II, fig. 3	7987a	1958	5087	† <i>Palaeoniscus</i> sp.	† <i>R. alberti</i>	
Plate II, fig. 4	Lost?	X	X	Not mentioned	X	
Plate II, fig. 5	7898		6151	Not mentioned	† <i>R. alberti</i>	
Plate II, fig. 6	Lost	X	X	X	X	
Plate II, fig. 7	7903	1953	5088	† <i>Palaeoniscus</i> sp.		
Plate II, fig. 8	7898a		6152	Not mentioned	† <i>R. alberti</i>	

Table 2. Identities of Lambe's (1910) figured specimens. Plate and figure numbers, past and present museum catalog numbers, and identifications included when known. Abbreviations: BSNH, Boston Society of Natural History; MCZ, Museum of Comparative Zoology. Genera abbreviated: *E.*, †*Elonichthys*; *R.*, †*Rhadinichthys*.

Plate and fig. no. Lambe (1910)	Original BSNH no.	Former MCZ no.	Current MCZ no.	Current CMN no.	Lambe (1910) ID
Plate III, fig. 1	?	?	?	?	† <i>R. alberti</i>
Plate III, fig. 2	?	?	?	?	† <i>R. alberti</i>
Plate III, fig. 3	?	?	?	?	† <i>R. alberti</i>
Plate III, fig. 4	7899a	1956	5084	X	† <i>R. alberti</i>
Plate III, fig. 5	7987a	1958	5087	X	† <i>R. alberti</i>
Plate III, fig. 6	7987a	1958	5087	X	† <i>R. alberti</i>
Plate IV, fig. 1	7900	1961	5083	X	† <i>E. brownii</i>
Plate IV, fig. 2	7900	1961	5083	X	† <i>E. brownii</i>
Plate IV, fig. 3	7902		6150	X	† <i>E. brownii</i>
Plate IV, fig. 4	7901	1957	5085	X	† <i>E. brownii</i>
Plate V, fig. 2, 3, 5, 6	7900	1961	5083	X	† <i>E. brownii</i>
Plate V, fig. 4	7902		6150	X	† <i>E. brownii</i>
Plate VI, fig. 1	?	?	?	?	† <i>E. brownii</i>
Plate VII, fig. 1	?	?	?	?	† <i>E. brownii</i>
Plate VIII, fig. 1	?	?	X	4384	† <i>E. brownii</i>
Plate IX, fig. 1	?	?	?	?	† <i>E. brownii</i>

as Traquair (1877) pointed out, many of these species are dubious.

Traquair (1877) recognized the problem with the genus †*Palaeoniscus*[*m*] early on and concluded that the genus †*Palaeoniscus*[*m*] was composed of a large number of species that were referable to more than one genus. Traquair (1877) further commented that it seemed that any small fusiform, rhombic-scaled actinopterygian from Paleozoic rocks seemed to be placed in this genus without comparison with the original type specimen. Traquair attempted to remedy the problem by restricting the species included in this genus to †*Palaeoniscus freieslebeni*, †*P. magnus*, †*P.*

macropomus, †*P. elegans*, †*P. comptus*, †*P. longissimus*, and †*P. macrophthalmus* (Traquair, 1877).

Though a step towards constraining and defining just what constitutes †*Palaeoniscus*, Traquair's (1877) diagnosis is problematic in that it provides a list of characteristics that are not diagnostic, not even when taken as a unit. The diagnosis of †*Palaeoniscus* includes characters common to Paleozoic actinopterygians such as a fusiform body, jointed fin rays in the pectoral fin, small fulcra on the pectoral fin, the dorsal fin originates anterior to the anal fin, oblique suspensorium, and small conical teeth (Traquair, 1877). Even with restricting which species are included within †*Palaeoniscus*, the genus

is still in need of redescription. Woodward (1891) followed Traquair (1877) by restricting which species were included in the genus †*Palaeoniscum*. While Traquair recognized the problem with †*Palaeoniscum* early, his conclusions reviewed above still describe the situation today. A conservative approach would be to restrict †*Palaeoniscum* to †*P. freieslebeni* and to reinvestigate and redescribe the other species placed within this genus.

1.3.2 † *Rhadinichthys*

The genus †*Rhadinichthys* was erected by Traquair (1877) to house species that were once considered to belong to the genus †*Palaeoniscum*. The type species of †*Rhadinichthys*, †*R. ornatissimus*, was originally described as a species of †*Palaeoniscus*[*m*] by Agassiz (1835). Traquair's original 1877 diagnosis of †*Rhadinichthys* includes characteristics such as a slender body, very oblique suspensorium, a dorsal fin originating almost opposite the anal fin, and the principal rays of the pectoral fin being unarticulated until close to their terminations. Again, these characters are not diagnostic and quite general among lower actinopterygians.

After describing four species of †*Rhadinichthys* from the Carboniferous of Glencartholm, Moy-Thomas and Bradley Dyne (1938) remarked that the genus could be divided into two different types – one with long thin bodies and small fins and the other with deeply fusiform bodies with large fins. They concluded that †*Rhadinichthys* “requires complete revision” and that the forms that they discussed would be more accurately described after revisionary work was done (Moy-Thomas and Dyne, 1938, p. 457). Romer (1945) erected a family, the Rhadinichthyidae, for which †*Rhadinichthys* is the type genus. This work was done without the reinvestigation of the genus called for by Moy-Thomas and Bradley Dyne (1938).

Gardiner and Schaeffer (1989) attempted to divide lower actinopterygians into different generic groups. Different †*Rhadinichthys* species were placed in different generic groups. When this was done, Gardiner and Schaeffer (1989) followed the convention of Wiley (1981) and placed the genus name in shutter quotes to signify its paraphyletic state. For example, “†*Rhadinichthys*” *canobiensis* is placed in the †*Australichthys* group, whereas “† *Rhadinichthys*” *carinatus* is placed within the †*Belichthys* group and the type species of †*Rhadinichthys*, †*R. ornatissimus*, is placed within the †*Amblypterus* group (Gardiner and Schaeffer, 1989).

Lund and Poplin (1997) reappraised the Rhadinichthyidae and the genus which gives this family its name, primarily based on newly described Bear Gulch fishes they placed within the Rhadinichthyidae. They recognized the following features as diagnostic of Rhadinichthyidae: a prominent snout and subterminal mouth; two suborbital bones; operculum higher but narrower than suboperculum; a triangular dorsal fin with an origin almost equal to that of the anal fin; a deeply cleft and inequilobate caudal fin, fin rays distally

bifurcated in all fins; a reverse L-shaped “antorbital” bone; rostromostrostral not contributing to the rim of the mouth, no premaxillae; absence of premaxillae results in a rostral notch below the rostromostrostral and between the antorbitals; no supraorbital bones; anamestic anocleithrum; elongated clavicles; and low ventrolateral abdominal scale rows (Lund and Poplin, 1997). While this was a step in the right direction, the redescription of †*Rhadinichthys*, the type genus of the family Rhadinichthyidae, had not been done prior to Lund and Poplin's (1997) redescription of the Rhadinichthyidae. †*Rhadinichthys* should be viewed as a paraphyletic genus and should be the focus of future revisionary work.

1.3.3 † *Elonichthys*

The genus †*Elonichthys* was described by Giebel (1848). The type species of †*Elonichthys*, †*E. germari*, is represented by a poor type specimen (Schultze and Bardack, 1987; Malabarba, 1988; Long, 1988; Schindler, 1993). As pointed out by Schultze and Bardack (1987), the type specimen of † *Elonichthys germari* does not allow for confirmation of generic designation. Malabarba (1988) also commented on the poor quality of the type species of this genus and our poor understanding of the genus as a whole. Schindler (1993) described †*Elonichthys* as being a “summary” genus that cannot be clearly defined.

Schultze and Bardack (1987) and Malabarba (1988) have both discussed the paraphyletic/polyphyletic nature of the genus †*Elonichthys*. Long (1988, p. 39) cautioned that many Carboniferous species of †*Elonichthys* have been erected on characters of “dubious phylogenetic value” and that the genus could be paraphyletic. Long (1988) also identified a further problem with this genus, primarily that many of the specimens assigned to this genus are too poorly preserved.

Gardiner and Schaeffer (1989) placed various species of †*Elonichthys* in different groups and have shutter quotes around the genus name, suggesting they also thought that the genus was paraphyletic. Recognizing the problems with this genus, Schindler (1993) avoided phylogenetic discussion of †*Elonichthys* and also placed the name in shutter quotes. A further problem with this genus is the fact that according to Malabarba (1988) and Gardiner (cited as personal communication in Malabarba, 1988) †*Elonichthys serratus* is more similar to †*Palaeoniscum freieslebeni* than to †*Elonichthys germari*.

More recently, progress has been made regarding *Elonichthys*. Poschmann and Schindler (2004) revised the family Elonichthyidae. Schindler (2009) concluded that all specimens recovered from the type locality of *Elonichthys germari* belong to *E. germari*. These newly found specimens include disarticulated remains, scales, as well as partially articulated remains (Schindler, 2009). These specimens, as well as the original type material, are the basis of an ongoing revision of the genus *Elonichthys* that will be published

soon (Schindler, 1993; Schindler, personal communication, 15 November 2016).

Overall, †*Palaeoniscum*, †*Rhadinichthys*, and †*Elonichthys* represent paraphyletic genera that are in need of revision. This revisionary work is beyond the scope of this study. Recognizing the problems with these genera, and the high likelihood that revisionary work may lead to the erection of multiple new genera, it has been decided to not place any new species from the Albert Formation or elsewhere within these genera. Species cannot be confidently assigned to these taxa because it is unclear what defines these genera to begin with. This also hinders redescrptions of the New Brunswick fishes, which have been moved from one poorly understood genus to another.

1.4 Previous descriptions of Albert Formation palaeoniscoids

Overall, the original taxa described from the Albert Formation are represented by poorly preserved type specimens, undiagnostic descriptions, and reassignments from one paraphyletic genus to another paraphyletic genus. These difficulties are reviewed below for †*Rhadinichthys alberti*, †*Rhadinichthys cairnsii*, †*Elonichthys ellsii*, †*Elonichthys* (†*Rhadinichthys*) *elegantulus*, and †*Canobius modulus*.

1.4.1 †*Rhadinichthys alberti*

Jackson's original description of †*Palaeoniscum alberti* is based on the specimen depicted in plate I, fig. 1 (Jackson, 1851a, b). This specimen was later identified as BSNH 7899, which was changed to catalog number MCZ 1960 and then MCZ 5082 (Table 1). Accordingly, the holotype is currently housed in the Museum of Comparative Zoology, Harvard, as MCZ 5082. The type specimen is illustrated in Fig. 3a.

There are many problems with Jackson's (1851a, b) original description. First, many of the features included in the description are common to lower actinopterygians (such as a single triangular dorsal fin and bifurcated caudal fin) and therefore uninformative. Other details, such as the color of the scales and absence of information on the gill plates or the vertebral column, do not add relevant information to the description.

Another problem deals with the holotype itself. As pointed out by Lambe (1909, 1910), MCZ 5082 is a poorly preserved specimen. There is no information about the skull. The holotype consists of a body with poorly preserved fins – pelvic fins are absent and the pectoral, dorsal, and anal fins are incomplete. Though the fulcrum of the caudal fin are preserved, the caudal fin itself is highly fragmentary. Even the scales are poorly preserved – the posterior margins of the majority of the scales are broken and the ganoine ornamentation on these scales is hard to determine. The type specimen itself barely preserves any diagnostic characters (Fig. 3a).

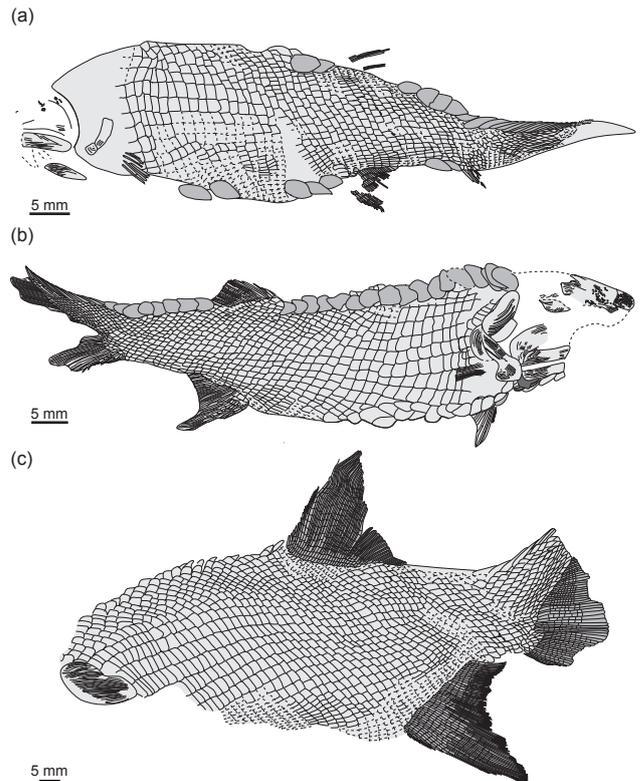


Figure 3. Illustrations of type specimens of Jackson's (1851) original species from the Albert Formation of New Brunswick, Canada. (a) †*Rhadinichthys* (†*Palaeoniscum*) *alberti*, illustration of MCZ 5082; (b) †*Rhadinichthys* (†*Palaeoniscum*) *cairnsii*, illustration of MCZ 5084; (c) †*Elonichthys brownii*, illustration of MCZ 5083. Dashed lines represent areas of ambiguity that have been reconstructed. Scale bars equal 5 mm.

The reassignment of †*Palaeoniscus*[*m*] *alberti* to †*Rhadinichthys alberti* by Traquair (1877, 1911), Woodward (1891), Hay (1902), Eastman (1908) and Lambe (1909, 1910) was not justified or explained other than by the statement that the specimens seemed to be more closely aligned to †*Rhadinichthys* (Traquair, 1877). It is assumed that it is the placement of the dorsal and anal fins that justified the movement of this species to †*Rhadinichthys*. Lambe's (1909, 1910) redescription does provide more diagnostic characters, but these characters are not based on what is preserved in the type specimen itself. Lambe (1909, 1910) does not identify the other specimens included in this species, nor did he detail which specimens preserve these new diagnostic characters. This reclassification also has problems because of the questions of what defines the genera †*Palaeoniscum* and †*Rhadinichthys*. In the redescription of †*R. alberti*, Lambe (1909, 1910) concluded that there were no differences between †*R. alberti* and †*R. cairnsii*. Jackson (1851a, b) had identified differences in the ganoine ornamentation of the scales that distinguish †*R. alberti* from *R. cairnsii*. Lambe (1909, 1910) said these differences

did not exist, and so †*R. cairnsii* was dismantled and the specimens originally described in this species were placed into †*R. alberti*. Nevertheless, the type specimen of †*R. cairnsii* is more complete than the type specimen of †*R. alberti*. The type of †*R. cairnsii* preserves cranial information, including a tuberculated snout. Using information from the type specimen of †*R. cairnsii* to redescribe the taxon †*R. alberti* is problematic, especially when the character that is supposed to join the two taxa, ganoine ornamentation, is so unclear and poorly preserved in the type of †*R. alberti*.

Gardiner (1966) stated that †*Rhadinichthys alberti* may belong to the genus †*Rhadinoniscus* because of features of the branchiostegal rays. This is problematic because the type specimen of †*R. alberti* does not preserve any clear information about the branchiostegal rays.

1.4.2 † *Rhadinichthys cairnsii*

Jackson's (1851a, 1851b) original type for †*R. cairnsii* is illustrated in Fig. 3b based on MCZ 5084. The distinction between †*P. cairnsii* and †*P. alberti* was attributed to differences in the ganoine ornamentation of the flank scales; the scales of †*P. cairnsii* were described as having striae running parallel to the anterior and lower margins of the scales (Jackson, 1851a, b). Though the scales are not well preserved in the type of †*R. alberti*, Lambe determined that the same striation pattern existed in †*R. alberti* and †*R. cairnsii*, and so †*R. cairnsii* was not a separate species. Lambe included the former type specimen of †*R. cairnsii* in †*R. alberti* (1909, 1910). The problems with this have been discussed above.

1.4.3 † *Elonichthys brownii*

The type specimen of †*E. brownii* is illustrated in Fig. 3c. Though the type specimen of †*E. brownii* is incomplete, the fins and scales are well preserved, (Fig. 3c). The Albert Formation specimens were most likely placed within this genus by Traquair (1877) on the basis of the large size of the fins in comparison to the other Albert Formation specimens that were placed within the genus †*Rhadinichthys*. As mentioned above, there is a large problem with this assignment to †*Elonichthys* because of our understanding of what this genus represents.

The type specimen of †*Palaeoniscum jacksonii* (Dawson) could not be located, but based on Jackson's (1851a, 1851b) fig. 4, plate 1, which illustrates the type of †*P. jacksonii*, Lambe (1909, 1910) determined it to be the same as †*Elonichthys brownii*.

1.4.4 † *Elonichthys elli*

Lambe (1909, 1910) described a new species from the Albert shales based on the type and only specimen, CMN 4379. Lambe (1909, 1910) describes a unique pattern of ganoine on the anterior flank scales that defines this species. The anterior flank scales bear ridges of ganoine that "have the appear-

ance of rows of connected tubercles" (Lambe, 1909, p. 171). Again, its placement within †*Elonichthys* is dubious, but the ganoine ornamentation makes it clear that this specimen is unique and different from the other previously described Albert Mine fishes. This pattern of ganoine ornamentation has not been seen in any other specimen.

1.4.5 † *Elonichthys* (†*Rhadinichthys*) *elegantulus*

The most abundant fish from the Albert shales is represented by small fusiform fishes that preserve much information regarding the scales but not much regarding the head (Lambe, 1910). These fishes were originally described by Eastman in 1908, but Lambe (1909, 1910) found this description problematic. Lambe (1910) proposed that these small and abundant specimens represent the young of one of the taxa represented by the larger specimens. Lambe (1910) concluded this on the basis of its small size and imperfect preservation, especially in regard to the head. Lambe proposed that these specimens were more similar to the body shape of †*Rhadinichthys alberti* than †*Canobius modulus* and warned that these specimens may be juvenile †*R. alberti* (Lambe, 1909, 1910), a statement Gardiner (1966) supported. Regardless, this species was later listed as †*Rhadinichthys elegantulus* by Hay (1929) and Gardiner (1966).

Also problematic is the lack of type material for this species. Though there are countless small fishes with well-preserved scales, prominent lateral lines, and poorly preserved heads, we do not know which specimen Eastman used in his description. In the description of †*E. elegantulus*, Eastman refers to an "extensive suite of material from the Lower Carboniferous of Albert County" as well as Jackson's original descriptions, but no specific specimens are mentioned (1908, p. 274). There are no illustrations of †*E. elegantulus* figured; therefore, we cannot determine which small fish specimens were studied by Eastman or which is the holotype. Gardiner (1966) mentions that the type specimen is in the Museum of Comparative Zoology, Harvard, but does not give a specimen number.

1.4.6 † *Canobius modulus*

Originally described by Dawson (1877, 1878) as †*Palaeoniscus* (†*Rhadinichthys*) *modulus*, this species is figured by Dawson in 1877 as fig. 1 and 1878 as fig. 18. Dawson (1877) stated that the specimen figured in Jackson's plate II, fig. 5, "probably belongs" to this species (p. 338). Important characters noted by Dawson (1877) include 10 large oval dorsal ridge scales between the head and the dorsal fin.

Woodward (1891) and Eastman (1908) reassigned †*Palaeoniscum modulus* to †*Rhadinichthys modulus* because of the reassignment of the other Albert Formation palaeoniscoids to the genus †*Rhadinichthys*. Eastman (1908) stated that Dawson's original description is a composite based upon

two individuals preserved on the same slab of shale. One of the specimens is incomplete and poorly preserved in comparison to the second specimen. The more complete specimen is figured by Dawson (1878), but this specimen does not preserve the dorsal ridge scales that are illustrated and described in the description. The information on the dorsal ridge scales comes from the more incomplete second specimen. Eastman (1908) provided a photograph of two specimens on a single slab of shale and described them as cotypes of †*Rhadinichthys modulus*. Eastman (1908) also mentioned that this specimen is housed in the Peter Redpath Museum of McGill University. Attempts to locate this specimen have so far failed.

Lambe (1909, 1910) redescribed this species as †*Canobius modulus*. He placed the species in the genus †*Canobius* on the basis of the near vertical suspensorium, blunt snout, and dorsal ridge scales complete to the occiput that are seen in †*Canobius* but not in †*Rhadinichthys*. Three specimens from the Redpath Museum were examined by Lambe (1909, 1910). Moy-Thomas (1938) discussed how Westoll considered †*Canobius modulus* to be †*R. alberti*. Gardiner (1966) agreed with this and stated that †*C. modulus* is considered to be a “peculiarly preserved specimen of †*Rhadinichthys alberti*” and then synonymized the two taxa (1966, p. 61). While Eastman (1908), Lambe (1909, 1910), and Gardiner (1966) agree that the type specimen of †*C. modulus* is in the Redpath Museum, McGill University, there is no record of a specimen number.

1.5 Concluding remarks on redescrptions of the Albert Formation palaeoniscoids

Six species have been described from the Albert Formation, but the validity of the majority of these species has been questioned. The type specimens are either unknown, or poorly preserved. On top of this, the Albert Formation palaeoniscoids have been assigned to genera that are poorly understood, represented by poor type material, and are known to be paraphyletic. Even more problematic is how every described species has been moved from one poorly described genus to another without much justification. What we are left with is a situation where the palaeoniscoids from the Albert shale formation cannot be redescrbed at this time.

There are hundreds of specimens of Albert Formation palaeoniscoids in museums such as the Museum of Comparative Zoology, Harvard; the Yale Peabody Museum; the Canadian Museum of Nature; and the New Brunswick Natural History Museum. Some of these specimens are well preserved and have been previously placed within †*Rhadinichthys alberti*, †*Elonichthys brownii*, or even †*Rhadinichthys cairnsii*. The problem with this is that these better preserved specimens show features that are not visible in the types of the species they have been assigned to. Compounding the problem is that the features they do preserve have been used in redescrptions of the taxa. It is not possible

to confidently determine if these forms belong to any species within †*Rhadinichthys*, †*Palaeoniscum*, or †*Elonichthys*.

Problems with the paraphyly of †*Rhadinichthys*, †*Elonichthys*, and †*Palaeoniscum* have far-reaching effects beyond understanding the palaeoniscoids from the Albert Formation. It also impairs our understanding of the systematics of lower actinopterygians overall. Multiple species have been placed within these genera, meaning we do not understand a large portion of the lower actinopterygian diversity. Also, though many species have been described as belonging to †*Rhadinichthys*, †*Elonichthys*, and †*Palaeoniscum*, investigations into the relationships of lower actinopterygian fishes may include one representative species from each genus, if any. Including only one taxon from a genus known to be paraphyletic excludes a large amount of diversity and impedes recognizing problems with these genera. Future work on lower actinopterygians will necessitate redescrptions of †*Rhadinichthys*, †*Elonichthys*, and †*Palaeoniscum*. Until such work is done, we do not understand a large portion of the Carboniferous and Permian actinopterygian diversity.

Problems with these genera have been known since the late 1800s. A concerted effort must be made to address the problems with †*Rhadinichthys*, †*Elonichthys*, and †*Palaeoniscum*. The condition of the type specimens may necessitate that the types are the type and only specimen of each genus. The other species placed within †*Rhadinichthys*, †*Elonichthys*, and †*Palaeoniscum* may need to be reevaluated and placed in new genera that can be described on the basis of informative type species. This may be the only prudent way to deal with large cosmopolitan genera described on the basis of uninformative type species. Such an undertaking is beyond the scope of this study but must be done in the near future.

Rhadinichthys, *Elonichthys*, and *Palaeoniscum* were the three main Paleozoic palaeoniscoid genera in the mid-1800s. *Palaeoniscum* is a Permian genus and should not be considered for Early Carboniferous specimens independent of the problems of defining this genus. As for *Rhadinichthys*, some of the specimens from the Albert shales may belong to this genus; nevertheless, the preservation of the type specimen is so poor that assignment of this specimen to *Rhadinichthys* is not prudent. Future work should identify a new well-preserved specimen from museum collections and start from the beginning with the description of a new taxon.

Though the fishes from the Albert Formation subscribed to the genera †*Rhadinichthys*, †*Elonichthys*, or †*Palaeoniscum* cannot be commented on further here, a new specimen and taxon can be described. While examining specimens of palaeoniscoids from the Albert Formation, a specimen that represents a form quite different from the type specimens of the previously described fishes was uncovered. This specimen is well preserved and can be differentiated from the previously described taxa, regardless of the condition of

those type specimens. One specimen, which constitutes a new taxon from the Albert Formation, is described below.

2 Materials and methods

2.1 Material examined and methods

The new taxon is represented by a single specimen collected from the Albert Formation and housed in the Yale Peabody Museum (YPM). The fossil specimen and its latex peel were examined by stereomicroscopy. The latex peel allowed for three-dimensional views of the specimen preserved as a negative impression. The fossil and peel were examined side by side. Photographs were taken with a Canon XSi digital camera equipped with a macro lens. Illustrations were prepared using a camera lucida, and digital illustrations were prepared using Adobe Photoshop and Illustrator programs.

2.2 Nomenclature

Two naming conventions have been used in reference to the two paired bones in the skull roof of actinopterygians – frontal and parietal or parietal and post-parietal. The first set of names is based on tradition, whereas the second is based on homology (Jollie, 1962; Schultze, 2008; Wiley, 2008). For further discussion on the problems the traditional naming convention poses, especially to phylogenetic analyses, see Schultze (2008) and Wiley (2008). The naming convention based on homology, parietal and post-parietal, is used here in the taxonomic description. Bones are identified as the dermosphenotic(s) and dermopterotic following the criteria of Poplin (2004). The bones of the snout are identified following the nomenclatural scheme presented by Mickle (2015).

2.3 Anatomical abbreviations

Ao, antorbital; aop, accessory opercular bone; bsi, inserted body scales; d, dentary; df, dorsal fin; dh, dermohyal; dpt, dermopterotic; drs, dorsal ridge scales; dsp, dermosphenotic; ex, extrascapular; io, infraorbital; lg, lateral gular; mdr, median dorsal rostral; mg, median gular; n, nasal; op, operculum; pop, preoperculum; p, parietal; pp, post-parietal; ps, presupracleithrum; pt, posttemporal bone; sc, sclerotic; scl, supracleithrum; so, suborbital; sop, suboperculum; sup, supraorbital; vr-pmx, ventral rostro-premaxilla.

2.4 Institutional abbreviations

BSNH, Boston Society of Natural History; CMN, Canadian Museum of Nature; MCZ, Museum of Comparative Zoology; YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut.

3 Systematic paleontology

Osteichthyes Huxley, 1880

Actinopterygii Cope, 1871

Lambeia n. gen.

Diagnosis: As for the type and only species

Type and only Species: †*Lambeia pectinatus* n. sp.

Etymology: After Lawrence Lambe, in honor of his work on the Albert Formation fishes.

Lambeia pectinatus n. gen. n. sp. (Figs. 4–10)

Etymology: *pectinatus* in reference to the pectinations on the dorsal ridge scales and ventral and posterior margins of the scales.

Diagnosis (based on the unique combination of characters): large edentulous tuberculated ventral rostro-premaxilla; median dorsal rostral bone; maxilla with broad postorbital plate; complex ganoine ornamentation on maxilla; nasal bones with ganoine ornamentation of tubercles and short ridges ventrally, longer diagonally oriented ridges mid-bone; single rectangular-shaped supraorbital bone; numerous suborbital bones; dermopterotic as long as the parietal plus the post-parietal bones; presupracleithrum; dermohyal; series of accessory opercular bones; 12 branchiostegal rays; two lateral gular plates; six dorsal ridge scales beginning at scale row 20; first three dorsal ridge scales with pectinated posterior margins; dorsal ridge scales occupy the space of two body scale rows; body scales rows intermittently inserted between adjacent dorsal ridge scales; anal fin almost opposite dorsal fin; dorsal and anal fins posteriorly placed on the body; body depth dramatically decreases posterior to dorsal fin; large pectoral and pelvic fins; body scales with pectinated posterior margins and horizontal ganoine ridges; ventrally placed scales from scale row 5 to the end of pelvic fin have pectinated posterior and ventral margins.

Holotype and only specimen: YPM 8664 (Figs. 4–10). The holotype YPM 8664 preserves the anterior two-thirds of a rather large fish in lateral view (Fig. 4). The counterpart is missing. The caudal peduncle and fin are not preserved. Though the distal portion of the dorsal fin is missing, the proximal portion along the body is preserved and appears to be complete. The pectoral, pelvic, and anal fins are large and spectacularly preserved (Fig. 4). Though the specimen is not complete, it is a medium- to large-sized palaeoniscoid with a length of 19.5 cm, minus the caudal peduncle and fin. It is noted that this fish is preserved on a slab with the remains of three other smaller palaeoniscoids.

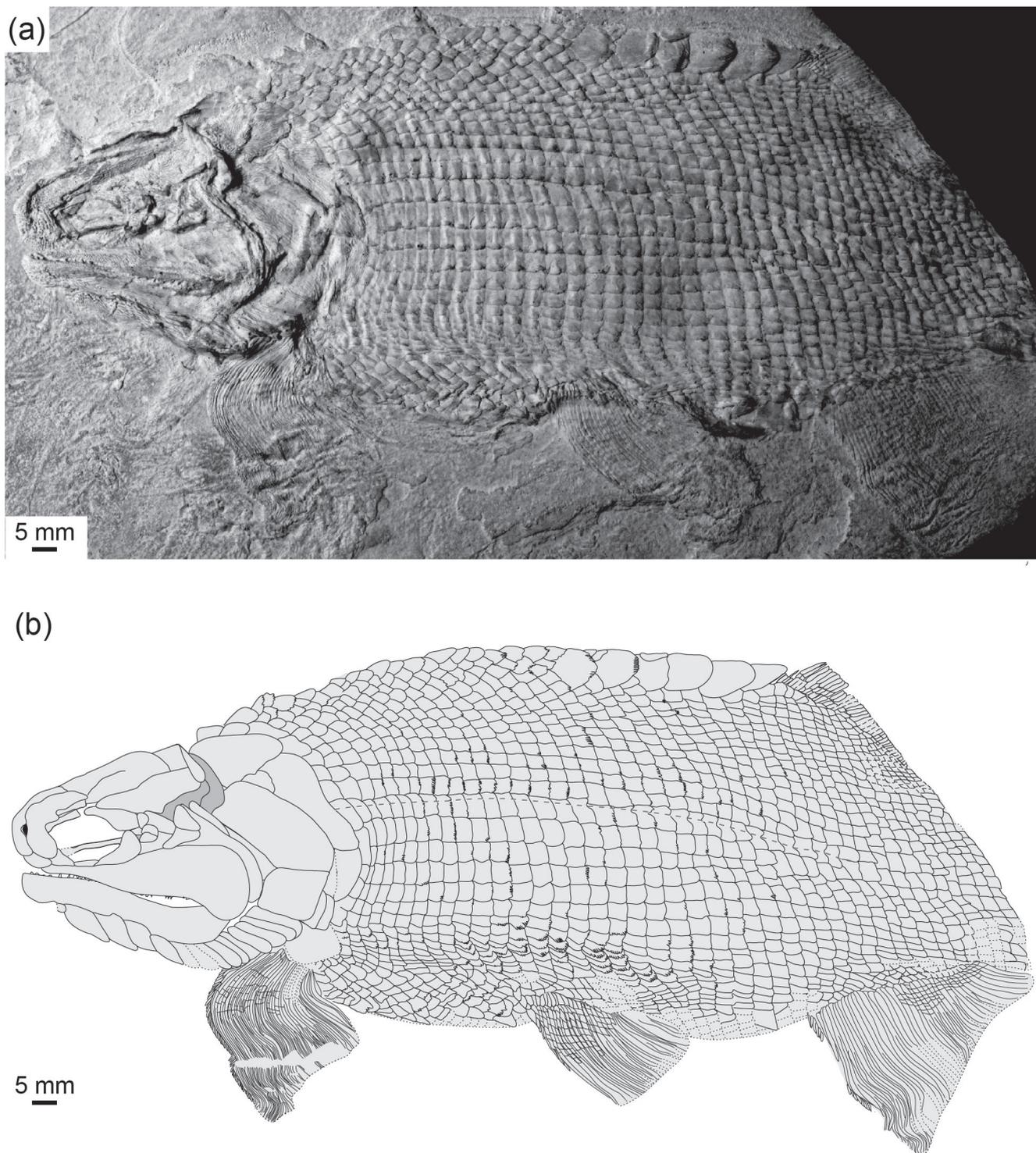


Figure 4. Type and only specimen of †*Lambeia pectinatus*. (a) Photograph of the latex peel of YPM 8664; (b) illustration based on YPM 8664. Dashed lines represent areas of ambiguity that have been reconstructed. Long dark gray dashed line represents lateral-line-bearing scales. Scale bars equal 5 mm.

Type locality: Tournaisian (Lower Carboniferous) Albert Formation, New Brunswick, Canada.

4 Anatomical description

4.1 Snout

The snout is prominent and heavily tuberculated. A median dorsal rostral bone forms the anterior-most portion of the snout (Figs. 5–6). The posterior margin of the median rostral bone contacts the parietal, whereas the ventral margin contacts the ventral rostro-premaxilla (Figs. 5–6). The lateral margin of the median dorsal rostral is notched. This notch forms the median margin of the anterior narial opening. The median dorsal rostral bears tubercles ventrally and short ridges of ganoine dorsally. These ridges are longitudinal to diagonal in orientation (Figs. 5–6).

A large nasal bone lies lateral to the median dorsal rostral and anterior to the orbit (Figs. 5–6). The anterior margin of the nasal is notched. This notch forms the medial margin of the anterior narial opening. The posterior border of the nasal is also notched in two different locations. The ventral-most notch forms the anterior margin of the lateral/posterior narial opening. Dorsal to this notch, there is a protuberance that extends off the posterior margin. Dorsal to this protuberance is the second notch on the posterior margin of the nasal for the supraorbital bone (Figs. 5–6). The nasal bears a complex pattern of ganoine. Unlike many other Carboniferous palaeoniscoids that bear long vertical ridges of ganoine, †*Lambeia pectinatus* has a nasal bone with tubercles and short ridges ventrally and longer diagonally oriented ridges mid-bone (Figs. 5–6).

There is a heavily tuberculated bone ventral to the median rostral and nasal bones (Figs. 5–6). This bone is identified here as the ventral rostro-premaxilla following the terminology of Mickle (2015). The anterior tip of the maxilla is ventral to the posteroventral margin of the ventral rostro-premaxilla. The ventral rostro-premaxilla does not bear teeth, though it is possible that small teeth are obscured by the heavy amount of tuberculations. No canal is visible in this bone, but this could also be because of the heavy ganoine tuberculations. It is termed a ventral rostro-premaxilla because the only criterion that can be used to identify this bone is its placement, information on the placement of canals in any of the snout bones is lacking because of the heavy ganoine ornamentation. The bone lies anterior to the maxilla, ventral to a median rostral bone, and separate from an antorbital bone. The size of this bone and placement suggest that it is not simply a premaxillary bone. This bone is physically located in the area where premaxillary and rostral bones are found.

Posterior to the ventral rostro-premaxilla, posteroventral to the nasal and dorsal to the anterior tip of the maxilla is an antorbital bone. This bone is referred to as an antorbital

because of its position and the putative canals in this bone (Figs. 5–6). The antorbital is roughly triangular in shape and there is a row of sensory pores, illustrated with filled gray circles in Fig. 6. The antorbital forms the anteroventral margin of the orbit.

4.2 Circumorbital series

Ventral to the orbit is a thin rectangular infraorbital bone (Figs. 5–6). This rectangular bone is large enough to bear small tubercles of ganoine. This infraorbital bone contacts the posterior margin of the antorbital bone and the anterior margin of a large crescent-shaped infraorbital bone in the posteroventral corner of the orbit (Figs. 5–6). The crescent-shaped infraorbital bone bears tubercles of ganoine and traces of the main infraorbital canal near the anterior border of the bone. There are pore canals that branch off the main infraorbital canal preserved near the posteroventral margin of the bone. This bone is disturbed and broken in half by the inward collapse of the dorsal half, but it can be reconstructed to its original crescent shape (Figs. 5–6).

A single dermosphenotic is located in the posterodorsal corner of the orbit (Figs. 5–6). The anterodorsal and posteroventral margins of this bone cannot be made out with any confidence, but it appears that this bone is narrower anterodorsally than posteroventrally. There are thin short ridges of ganoine at about mid-bone and elongated tubercles anterodorsally.

4.3 Skull roof

The dermosphenotic abuts against a large dermopterotic (Figs. 5–6). The dermopterotic is ventral to the parietal and post-parietal bones and approximately the length of these bones combined. Dorsal of the orbit and posteroventral to the nasal bone is a rectangular bone (Figs. 5–6). This bone is not a sclerotic bone – a separate sclerotic is preserved ventral to this bone in question (Figs. 5–6). This rectangular bone bears short ridges of ganoine that are different in orientation and size from those on the nasal. This bone fills in the space created by the dorsal-most notch on the posterior margin of the nasal bone. This bone is identified as a supraorbital. The posterior margin of the supraorbital comes in contact with the anteroventral margin of the parietal.

The margins of the parietal bones are difficult to determine. The parietal contacts the nasal, dorsal rostral, and supraorbital bones anteriorly, the dermopterotic laterally, and the post-parietal posteriorly (Figs. 5–6). The parietal bears short ridges of ganoine along the length of the bone and a few elongated tubercles. The post-parietal is trapezoidal in shape, with the medial margin of the bone being longer than the lateral margin (Figs. 5–6). Pit lines are not apparent because of the heavy ganoine ridges present on this bone. The post-parietal is about a third of the length of the parietal.

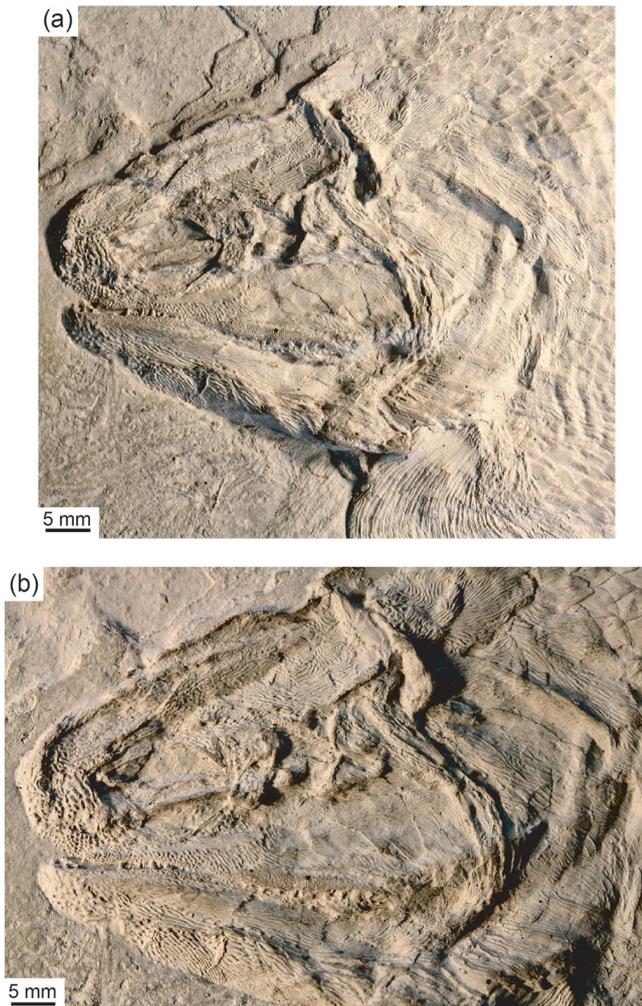


Figure 5. Photographs of the lateral view of the head of the latex peel of type specimen of †*Lambeia pectinatus*, YPM 8664. Scale bars equal 5 mm.

A thin band of bone posterior to the post-parietal and the dermopterotic is an extrascapular bone (Figs. 5–6). There is no ganoine ornamentation on this bone, nor can it be determined if this is a series of bones or a single bone.

4.4 Cheek

Posterior to the circumorbital bones lies a series of suborbital bones (Figs. 5–6). Though this region is disturbed by the inward collapse of the infraorbitals and suborbitals, it is clear that there are numerous suborbital bones. The suborbitals are roughly arranged in vertical rows – the first row is posterior to the circumorbital bones, the second is between the first and third rows of suborbital bones, and the third row contacts the anterior margin of the preoperculum (Figs. 5–6). The third row of suborbitals is composed of two large bones (Figs. 5–6). The dorsal-most of the two large suborbitals has a rounded convex anterior margin. Ventral to this is a triang-

ular suborbital bone with rounded corners. The anterior border of this suborbital bone is slightly concave. Both of these suborbital bones bear fine diagonal ridges of ganoine.

The second row of suborbitals is also composed of large bones. Two large bones with fine ganoine ridges are present and overlain in sections by the suborbital bones in rows 3 and 1 (Figs. 5–6). The first row of suborbital bones is the area with the most disturbance. It seems that multiple smaller suborbital bones are located posterior to the dermosphenotic and infraorbital three (Figs. 5–6).

The maxilla is a large bone with a deep and broad postorbital plate (Figs. 5–6). A posteroventral process off the postorbital plate overlaps the posterodorsal margin of the lower jaw. The maxilla tapers to a narrow arm that extends anterior to the orbit. This narrow arm terminates ventral to the heavily tuberculated ventro–rosto-premaxilla. There are fine, minute, needle-like teeth on the oral margin of this portion of the maxilla. Large conical teeth are seen on the oral rim ventral to the postorbital plate, with small conical teeth inserted between the large ones.

The ganoine ornamentation of the maxilla is complex (Figs. 5–6). The anterior-most portion of the maxilla, up to the anterior-most corner of the infraorbital in the posteroventral corner of the orbit, is heavily tuberculated with closely set tubercles. Below the crescent-shaped infraorbital, the maxilla bears short diagonal ridges of ganoine. The pattern of ganoine on the maxilla then changes to fine, faint, and more horizontally oriented ridges along the postorbital plate. Fine vertical ridges are present along the posteroventral process of the maxilla. Though the anteroventral margin of this process is disturbed, it appears that these vertical ridges of ganoine break down to fine tubercles at this margin. The ventral margin of the postorbital plate has its own ganoine pattern – here ornamentation consists of short, closely set, vermiform ridges that are horizontal to vertical in orientation. Directly ventral and posteroventral to the orbit, there is a narrow band along the dorsal-most border of the maxilla that is smooth and does not bear any ganoine ornamentation. This is an area of articulation between the maxilla and the overlying infraorbitals.

The preoperculum is hatchet shaped, anteriorly inclined, and contacts the dorsal and posterior margins of the postorbital plate of the maxilla (Figs. 5–6). Dorsal to the maxilla, the preoperculum is expanded, whereas posterior to the maxilla, the preoperculum is a tall, narrow arm arched around the posterior margin of the maxilla. The anterior margin of the preoperculum sutures with two suborbitals. These suborbitals are situated within a concavity made by the arms of the expanded region of the preoperculum. There are short ganoine ridges along the posterior margin of the preoperculum and fine horizontal ridges on the expanded region of the preoperculum, dorsal to the maxilla.

Posterior to the preoperculum and anterior to the operculum is a tall and narrow wedge-shaped dermohyal (Figs. 5–6). The dermohyal extends from the anterodorsal corner of

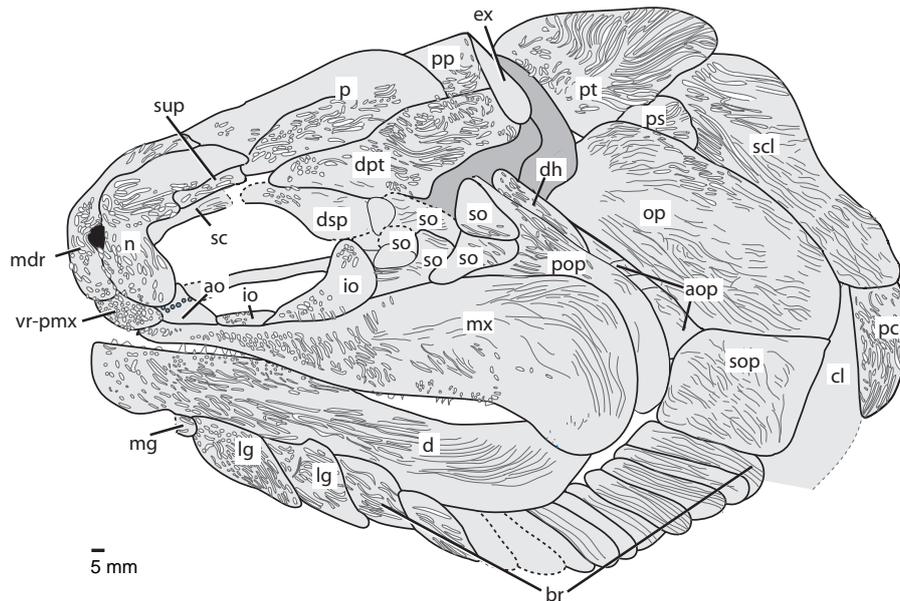


Figure 6. Reconstruction of the head of †*Lambeia pectinatus* detailing bones and ganoine ornamentation. Illustration based on type and only specimen, YPM 8664. Abbreviations: ao, antorbital; aop, accessory opercular bones; br, branchiostegal rays; cl, cleithrum; d, dentary; dh, dermohyal; dpt, dermopterotic; dsp, dermosphenotic; ex, extrascapular; io, infraorbital; lg, lateral gular; mdr, median dorsal rostral; mg, median gular; mx, maxilla; n, nasal; op, operculum; p, parietal; pc, postcleithrum; pop, preoperculum; pp, post-parietal; ps, presupracleithrum; pt, posttemporal; sc, sclerotic; scl, supracleithrum; so, suborbital; sop, suboperculum; sup, supraorbital; vr-pmx, ventral rostro-premaxilla. Dark gray filled circles represent sensory pores; light gray areas represent areas of infilling; dashed lines represent areas of ambiguity and reconstruction.

the operculum to about half the depth of this bone. The dermohyal bears short ridges of ganoine parallel with the anteroventral and posterodorsal margins of the bone. These ridges are similar to those found on the expanded region of the preoperculum. Posterior to the preoperculum, ventral to the dermohyal, and along the anterior border of the operculum is a series of accessory opercular bones. The largest bone of the series is found near the anteroventral corner of the operculum. This bone is wider ventrally than dorsally and bears diagonal ridges of ganoine. There are three accessory opercular bones dorsal to the expanded ventral bone. The dorsal accessory opercular bones are small and rhombic and bear faint ridges of ganoine.

4.5 Lower jaw

Individual bones that make up the lower jaw cannot be distinguished. Overall, the lower jaw is a large bone that is longer than the maxilla (Figs. 5–6). The lower jaw extends slightly anterior to the ventral rostro-premaxilla. Vertically oriented conical teeth are along the oral rim of about the anterior half of the lower jaw. In between these teeth are smaller conical teeth. There are also teeth medial to this series of conical teeth. The medially placed teeth are conical, short, and closely set. Anteriorly, the lower jaw bears ganoine tuberculations. These tubercles are present until about the posterior margin of the ventral rostro-premaxilla. Posterior to the ven-

tral rostro-premaxilla to the posterior margin of the median gular, the lower jaw is ornamented with short diagonal ridges. At the posterior-lateral margin of the median gular, there is a change in ganoine ornamentation on the lower jaw to fine and long horizontal ridges. Near the posterior margin of the lower jaw, these horizontal ridges curve dorsally towards the posteroventral process of the maxilla.

4.6 Operculo-gular apparatus

The operculum is a rectangular bone that is anteriorly inclined and about twice the depth of the suboperculum (Figs. 5–6). The operculum bears fine diagonal ridges of ganoine that are not as closely packed as the ganoine ornamentation on other bones. The suboperculum is vertically oriented and rhombic in shape (Figs. 5–6). There are short diagonal and vertical ganoine ridges on this bone. The suboperculum is taller posterodorsally than anterodorsally.

Gulars and branchiostegal rays are visible in lateral view (Figs. 5–6). The proximal portion of the median gular closest to the lower jaw is missing so that only the distal tip of this bone can be commented upon. The distal portion of the median gular bears short ridges of ganoine and a few tubercles. Posterior to the median gular lies the first of two lateral gulars. Both lateral gulars are teardrop shaped and bear short ridges of ganoine. When seen in lateral view, these ridges are diagonal on the first lateral gular but more horizontally

oriented on the second lateral gular. The second lateral gular bears a prominent pit line. Posterior to the lateral gulars follows a series of branchiostegal rays (Figs. 5–6). The branchiostegals are obscured just anterior to the posteroventral corner of the lower jaw, making determinations of their number and shape difficult. Anterior to this point, there are two branchiostegal rays. Posterior to this point, there are seven rays. If the size of the branchiostegal rays anterior to the posteroventral corner of the lower jaw are consistent with those directly anterior and posterior to this area of ambiguity, the total number of branchiostegal rays is estimated to be around 12.

4.7 Pectoral girdle

The posttemporal is a large bone with a rounded posterior margin (Figs. 5–6). The posttemporal bears prominent ridges of ganoine that extend to the posterior border of the bone to form a serrated posterior margin. The posttemporal overlaps the dorsal border of the ventrally located supracleithrum.

A rounded presupracleithrum is situated near the posterodorsal corner of the operculum, ventral to the posttemporal and overlapping the anterior margin of the supracleithrum (Figs. 5–6). The presupracleithrum bears diagonal ridges of ganoine that extend to the posterior end of the bone, giving the presupracleithrum a serrated posterior margin. The supracleithrum lies posterior to the operculum, overlapped by the presupracleithrum and posttemporal. The supracleithrum is about the same depth as the operculum (Figs. 5–6). At about two-thirds down the depth of the bone, the posterior margin of the supracleithrum is concave. The posterodorsal and posteroventral margins of the supracleithrum are convex. The supracleithrum bears strong ridges of ganoine. The ridges in the posterodorsal portion of the bone are curved, whereas the ornamentation on the anterodorsal portion of the bone consists of straight diagonal ridges. These ridges are more vertically oriented near the anterior border of the bone. The ridges in the ventral portion of the supracleithrum are slightly diagonal to vertical in orientation.

Ventral to the supracleithrum is a tall but narrow crescent-shaped postcleithrum (Figs. 5–6). The postcleithrum bears short diagonal ridges on the dorsal half of the bone and vertical ridges down the ventral half. In the dorsal half of the bone, these ridges extend to the posterior margin, giving the bone a pectinated posterior margin. The smooth area anterior to the postcleithrum and posterior to the suboperculum is the cleithrum, but the shape of this bone cannot be determined.

4.8 Squamation

There is a series of large dorsal ridge scales anterior to the origin of the dorsal fin (Figs. 4, 7). The dorsal ridge scales are not continuous to the occiput; rather, they begin at scale row 20. The dorsal ridge scale series consists of six large scales. The posterior border of the preceding scale overlaps the an-

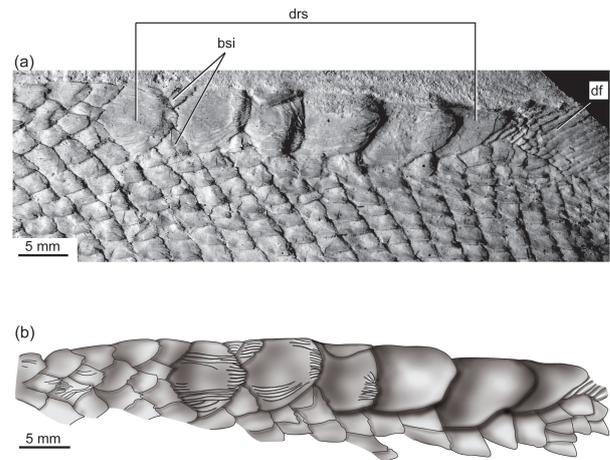


Figure 7. Dorsal ridge scales of †*Lambeia pectinatus*. (a) Photograph of dorsal ridge scales in type and only specimen (YPM 8664). (b) Illustration of dorsal ridge scales in YPM 8664. Abbreviations: bsi, inserted body scales; df, dorsal fin; drs, dorsal ridge scales. Scale bars equal 5 mm.

terior margin of the subsequent scale. The first dorsal ridge scale has more of an acuminate posterior margin compared to the subsequent scales with blunt and rounded posterior borders (Fig. 7). The first three dorsal ridge scales have serrated posterior margins (Fig. 7). These pectinations are formed by ridges of ganoine that run down the center of the ridge scales. The ganoine ridges on the lateral margin of these ridge scales are curved to follow the convex lateral margin of the scale.

The first and second dorsal ridge scales correspond to two ventrally placed rows of body scales (Fig. 7). Because of the overlap of the dorsal ridge scales, the second body scale row that is ventral to the posteroventral margin of the first dorsal ridge scale also overlaps the posterior margin of the second dorsal ridge scale. This gives the appearance of the body scale rows being inserted between the dorsal ridge scales (Fig. 7). This pattern is seen between dorsal ridge scale one and two, as well as two and three. This may indicate that the two vertical scale rows correspond to one myomere rather than a 1 : 1 ratio of scale rows to myomeres. The third dorsal ridge scale is unique in that it is the only one of the six to correspond to just one body scale row. Dorsal ridge scales four through six all correspond to two body scale rows (Fig. 7). There are no pectinations on the posterior edges of dorsal ridge scales four through six. These ridge scales also differ in shape from the anterior three ridge scales. Ridge scales four through six do not have the same rounded appearance as the first three, and they have more pronounced convex posterior margins (Fig. 7).

It is questionable whether ridge scales are present between the pectoral and pelvic fins. Between the pectoral and pelvic fins there is an area of ambiguity caused by the body of a smaller palaeoniscoid overlapping the ventral margin of the larger specimen in YPM 8664. Partially visible are two

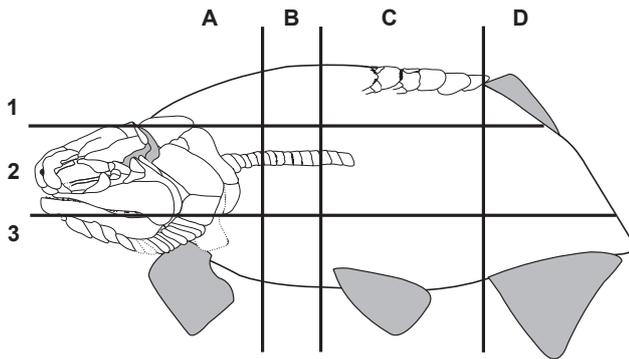


Figure 8. Schematic drawing detailing the scale regions described in the text for †*Lambeia pectinatus* (YPM 8664). A1, A2, A3: dorsal-most, mid-body, and ventral-most scales posterior to the pectoral girdle; B1, B2, B3: dorsal-most, mid-body, and ventral-most scales from scale rows 6–12; C1, C2, C3: dorsal-most, mid-body, and ventral-most scales from scale row 13–origin of dorsal fin; D1, D2, D3: dorsal-most, mid-body, and ventral-most scales from origin of dorsal fin to preserved end of specimen.

rounded structures that do not bear pectinated posterior margins or ganoine ornamentation. These could potentially be ventral ridge scales between the pectoral and pelvic fins. There are enlarged scales anterior to the anal fin and potentially the vent of the fish.

In order to describe the body scales, the body has been broken down into different regions. These regions are detailed and illustrated in Fig. 8. In YPM 8664, scales in region A1 (dorsally placed scales posterior to the skull roof) are heavily ornamented with ridges of ganoine and have strongly pectinated posterior margins. Posterior to the posttemporal, the posteroventral margins of the scales have four to five serrations, but at the level of the supracleithrum, there is a change so that the entire posterior margin is pectinated. In region A2 (mid-body scales posterior to the pectoral girdle), scales are generally pectinated and bear diagonal ridges of closely set ganoine. These scales are rhombic at the level of the supracleithrum. At the level of the supracleithrum, at scale rows 1 through 3, there are diagonal ridges of ganoine dorsally and curved ridges of ganoine near the ventral border of the scale. Scales ventral to the supracleithrum at about the level of the postcleithrum are taller, rectangular, and narrower. These scales only bear diagonal ridges of ganoine. The scales bearing the lateral line are notched posteriorly. The notch is more superiorly placed in this region than in regions B2 or B3. The lateral-line-bearing scales are pectinated.

In region A3 (ventrally placed scales posterior to the pectoral girdle), the scales are rhombic, but there is a trend of the scales being narrower and more rectangular in shape the more ventral they are on the body. Regardless of their placement, all of the scales in the A3 region bear close-set diagonal ridges of ganoine.

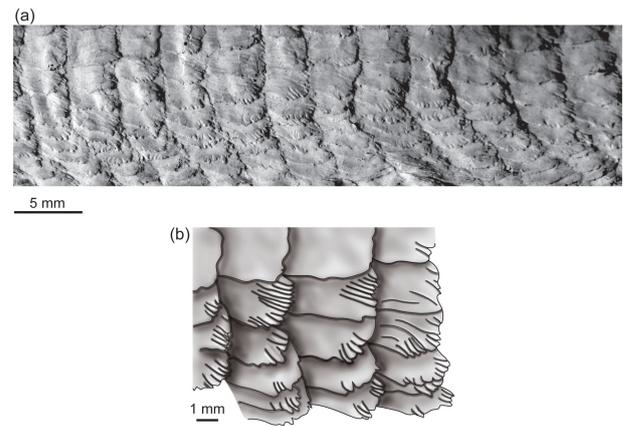


Figure 9. Scales from †*Lambeia pectinatus* (YPM 8664). Scales are from region B3 (see Fig. 8) and have pectinated posterior and ventral margins. (a) Photograph of scales from latex peel; (b) illustration of scales.

Scales in region B commence at scale row 6. Scales in region B2 (mid-body scales from scale rows 6–12) are tall, narrow, and rectangular in shape. The posterior margins are pectinated; the pectinations are formed by the closely set diagonal ridges of ganoine that ornament the scales. The lateral-line-bearing scales are notched posteriorly.

Scales in region B3 (ventrally placed scales from scale rows 6–12) are very unique. Here, the ventral margins of the scales, as well as the posterior margins, are pectinated (Fig. 9). These scales also bear ridges of ganoine.

Scale region C starts at scale row 13. Scales in region C1 (dorsally placed scales from scale row 13 to origin of dorsal fin) are more teardrop shaped in appearance as compared to the anteriorly placed rhombic and rectangular scales. These scales bear diagonal ridges of ganoine. The posterior edges are sometimes pectinated with five to six serrations.

The posterior borders of scales in region C2 (mid-body scales from scale row 13 to origin of dorsal fin) are pectinated with closely packed fine serrations. The exact number is hard to determine because of how close the serrations are, but there are at least a dozen serrations per scale. The scales that are located at the level of the ventral portion of the supracleithrum are more rectangular in shape than the rhombic scales above and below this point. The lateral-line-bearing scales are noticeably notched posteriorly. This notch is located mid-scale.

Like the scales in region B3, the scales in region C3 (ventrally placed scales from row 13 to origin of dorsal fin) are serrated on both the posterior and ventral borders. These scales are ornamented with fine diagonal ridges of ganoine. The more ventrally placed scales are shorter and more rectangular in shape than the more dorsally placed rhombic scales in this region.

Scale region D begins at the origin of the dorsal fin. The scales in region D1 (dorsally placed scales from origin of

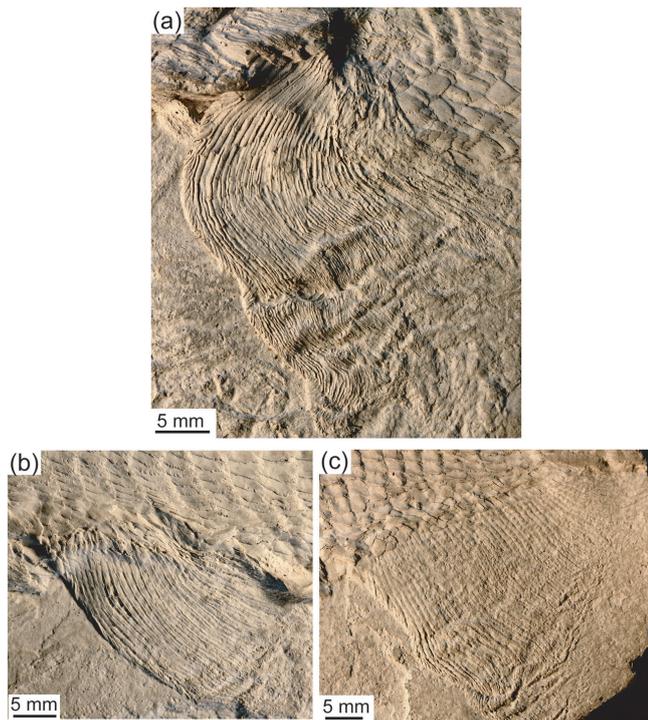


Figure 10. Photographs of the fins of †*Lambeia pectinatus* (YPM 8664). (a) Pectoral fin; (b) pelvic fin; (c) anal fin. All photographs depict the latex peel of YPM 8664. Scale bars equal 5 mm.

dorsal fin to preserved end of specimen), are short but rectangular in shape. They are closely packed and overlapping. There are faint signs of horizontal ridges of ganoine. The first four scales ventral to the dorsal fin are slightly different – these scales are about 2 times the depth of the others and rhombic in shape.

Scales in region D2 (mid-body scales from origin of dorsal fin to preserved end of specimen) are rhombic and not as tall as the more anteriorly placed scales. The posterior edges of scales in region D2 are pectinated with six to seven serrations. The ganoine ornamentation is not as dramatic as that of the more anteriorly placed scales but there are faint horizontal to diagonal ridges. Scales in the region D3 (ventrally placed scales from origin of dorsal fin to preserved end of specimen) are similar to those described for region C3, but the scales in D3 lack the serrations on the ventral margin. There are a few scales in D3 that have serrations on the posterior margin.

4.9 Fins

The pectoral fin is large, fan-shaped, and formed by highly bifurcated and closely packed fin rays (Fig. 10). Fringing fulcra line the leading edge of the pectoral fin. The fulcra are thicker and longer proximally and decrease in size down the height of the fin so that the distal-most fringing fulcra are fine and short. Proximally, the fringing fulcra from the opposite

side of the fin are seen. The two sides of the fulcra meet in midline to form a V-shaped unit.

All of the fin rays that make up the pectoral fin are segmented. The fin rays are bifurcated numerous times. The first bifurcation occurs in the proximal quarter of the fin. The fin rays bifurcate at least one more time distally so that the distal-most portion of the fin is made up of fine delicate fin rays. This makes determining how many times the fin rays bifurcate and detailed illustrations of the distal portion of the fin difficult. The first two fin rays do not extend down the entire depth of the fin to contribute to the distal margin, instead, the highly bifurcated fin rays posterior to the first two fin rays fill in and form the distal margin of the fin.

There is a large triangular pelvic fin that spans four scale rows and contains 25 fin rays (Fig. 10). The pelvic fin originates at scale row 12. Like the pectoral fin, the fin rays that form the pelvic fin are highly bifurcated. The first bifurcation occurs close to the proximal margin of the fin at about the second or third segment. At about mid-depth of the pelvic fin, the fin rays bifurcate again. Because of all the bifurcations, the distal region of the pelvic fin is made of very fine closely packed fin rays. There are fringing fulcra along the leading edge of the pelvic fin, but the fulcra are not as large or dramatic as that of the pectoral fin. The most proximal structure on the leading edge of the pelvic fin is different from the distal fringing fulcra – it is a single median structure that looks more like a ridge scale than the start of the fringing fulcra series.

The triangular anal fin originates posterior to the origin of the dorsal. The anal fin is large – spanning about 12 scale rows and containing 42 fin rays (Fig. 10). Like the other fins, the anal fin has highly bifurcated fin rays and fringing fulcra. The fringing fulcra are clearest on the leading edge of the distal portion of the fin, though it is presumed to be continuous along the entire anterior margin. The caudal fin is not preserved.

5 Discussion

5.1 Comparison to other Albert Formation fishes

The new Albert Formation fish differs from the other actinopterygians described from this site in regard to scale, cranial, and fin characteristics. The scales with pectinated posterior and ventral margins are unique and set †*Lambeia pectinatus* apart from all other Albert Formation fishes, as well as Carboniferous fishes from other localities. The ganoine ornamentation on the nasal bones is also different from the other previously described Albert Formation fishes, which all show vertical continuous ridges of ganoine. The presence of multiple suborbital bones, a large tuberculated rostro-premaxilla, a single supraorbital bone, the size and shape of the dermopterotic, the presence of accessory opercular bones, and the body shape also distinguish †*Lambeia*

pectinatus from the other Albert Formation fishes. Other Albert Formation fishes have a series of dorsal ridge scales beginning at or just behind the occiput, whereas †*Lambeia pectinatus* has six dorsal ridge scales that start at about mid-body at scale row 20.

†*Elonichthys brownii* is of a similar size as the new fish. Though specimens of †*E. brownii* do not preserve much cranial information, there are enough characteristics regarding scales and fins to support separating †*Lambeia pectinatus* from †*E. brownii*. These include the placement of the dorsal fin relative to the anal fin, with the dorsal fin originating slightly anterior to the anal fin in †*Lambeia pectinatus* and far in advance of the anal fin in †*E. brownii*, and the presence of scales with serrated posterior and ventral margins in †*Lambeia pectinatus* and the absence of this scale type in †*E. brownii*.

5.2 Characters of note

While describing †*Lambeia pectinatus*, certain characters were uncovered that deserve more discussion. These characters include dorsal ridge scales, suborbital bones, and supraorbital bones.

5.2.1 Dorsal ridge scales

An interesting characteristic of †*Lambeia pectinatus* involves the dorsal ridge scales. In †*Lambeia pectinatus*, the dorsal ridge scales occupy the space of two body scale rows. A review of the literature shows that dorsal ridge scales that correspond to more than one body scale row are often overlooked. For example, this detail may have been overlooked in †*Mansfieldiscus* – at least it is not mentioned in the description of the dorsal ridge scales that they span more than one body scale row; nevertheless, the figure of this fish shows that the dorsal ridge scales occupy two body scale rows (Woodward, 1906, Plate XI, fig. 1B; Long, 1988, p. 43, fig. 41C). The same appears to be the case in †*Howqualepis rostridens*, which has dorsal ridge scales that span at least three body scale rows (Long, 1988, p. 34–35, figs. 32C, 33F). Gardiner (1984) figured †*Mimipiscis toombsi* as having dorsal ridge scales that correspond to three or four body scale rows (fig. 145) but does not mention this in the description. The reconstructions of †*Cycloptychius concentricus*, †*Elonichthys serratus*, †*E. pulcherrimus*, and others, show dorsal ridge scales corresponding to more than one body scale row (Moy-Thomas and Bradley Dyne, 1938, figs. 21, 24, 25).

Poplin and Lund (2002) described the dorsal ridge scales in †*Kalops monophrys* as spanning two to three body scale rows and figured the dorsal ridge scales in †*K. diophrys* as spanning two body row scales (Poplin and Lund, 2002, fig. 6). Choo et al. (2009) commented that the dorsal ridge scales in †*Gogosardinia* are 20 times larger than the adjacent flank scales, so it is not surprising that the dorsal ridge scales appear to correspond to multiple body scale rows in the fig-

ures (Choo et al., 2009, fig. 14, p. 205). Lastly, another fish from the Albert Formation, the type specimen of †*R. cairnsii*, also has dorsal ridges scales corresponding to more than one body row (Fig. 3b).

As Arratia (2008) pointed out, the diversity of fulcra, fin rays, and ridges scales is often ignored and may provide phylogenetically informative characters. Dorsal ridge scales are not uncommon in lower actinopterygians and are often described in figures and text. These structures now need to be described in depth rather than comments on their presence or absence in certain taxa. Specific features of dorsal ridge scales should be included in phylogenetic analyses to see if these characters have any phylogenetic signal.

5.2.2 Suborbital bones

Numerous suborbital bones are present in †*Lambeia pectinatus*. There are other Carboniferous fishes with multiple suborbital bones, including †*Kalops monophrys*; †*K. diophrys* (Poplin and Lund, 2002); †*Beagiascus pulcherrimus* and †*Lineagruan snowyi* (Mickle et al., 2009); and †*Namaichthys schroederi* (Gardiner, 1962). Fishes with one to two large suborbital bones are much more common in the Carboniferous and are found in †*Cyranorhis bergeraci* and †*Wendyichthys dicksoni* (Lund and Poplin, 1997); †*Mansfieldiscus sweeti* (Woodward, 1906; Long, 1988); †*Novogonatodus kasantsevae* (Long, 1988); †*Canobius ramsayi*, †*Cycloptychius concentricus*, †*Rhadinichthys canobiensis*, †*Mesopoma pulchellum*, and †*Elonichthys serratus* (Moy-Thomas and Bradley Dyne, 1938); †*Mesopoma carricki* (Coates, 1993); †*M. planti* (Coates, 1999); †*Cosmoptychius striatus* (Gardiner, 1963); and †*Nozamichthys*, “†*Elonichthys peltigerus*”, and “†*E. hypsilepis*” (Schultze and Bardack, 1987).

Suborbital bones are uncommon in Devonian fishes. The majority of Devonian fishes have a series of circumorbital bones that are anterior to the preoperculum with no intervening suborbital bones. This is the case for †*Cheirolepis canadensis* (Pearson and Westoll, 1979; Arratia and Cloutier, 1996), †*C. trailli* (Pearson and Westoll, 1979; Pearson, 1982), †*Moythomasia durgaringa* (Gardiner, 1984), †*Mimipiscis toombsi* (Gardiner, 1984), †*Gogosardinia coatesi* (Choo et al., 2009), †*Limnomis delaneyi* (Daeschler, 2000), †*Howqualepis rostridens* (Long, 1988), †*Stegotrachelus finlayi* (Swartz, 2009), and †*Tegeolepis clarki* (Dunkle and Schaeffer, 1973). The only exceptions to this are †*Osorioichthys marginis* (Taverne, 1997) and †*Moythomasia nitida* (Gross, 1953; Jessen, 1968). †*Osorioichthys* is described as having one suborbital bone and †*Moythomasia nitida* as having either one or two (Gross, 1953; Jessen, 1968).

The presence or absence of suborbital bones in †*Kentuckia deani* is considered to be questionable. Rayner (1951) describes †*Kentuckia* with no suborbital bones. Though the cheek is not well preserved, Rayner (1951) states that the cir-

cumorbital bones are so close to the preoperculum that there is no room for suborbital bones. Dunkle (1964) describes a suborbital bone in a †*Kentuckia* specimen preserved in dorsal view. In a reconstruction of a lateral view of this fish, Dunkle (1964, fig. 4) illustrates two suborbital bones anterior to the preoperculum with dashed lines and question marks. Gardiner and Schaeffer (1989, fig. 8D) figure †*Kentuckia* with a single suborbital bone with no dashed lines or question marks. The presence of suborbital bones in †*Kentuckia* is not accepted here.

What can be said is that suborbital bones are commonly seen in Carboniferous fish and are rare if not absent in Devonian fishes. Carboniferous fishes can have one or two large suborbital bones or numerous bones arranged in numerous rows. This is at odds with Gardiner et al. (2005), who state that suborbitals are first noticed in the Triassic †*Pteronisculus* and are present in varying numbers in primitive neopterygians. This result was reached on the basis of their parsimony tree – which included few Carboniferous fishes in an investigation into the relationships of lower actinopterygians (Gardiner et al., 2005).

5.2.3 Supraorbital bones

Gardiner and Schaeffer (1989) described the presence of supraorbitals as being a character found in advanced lower actinopterygians and some neopterygians. The presence of multiple anamestic supraorbital bones is the only stem-neopterygian apomorphy that resulted from their phylogenetic analyses (Gardiner and Schaeffer, 1989; Coates, 1999). Gardiner and Schaeffer (1989) described the presence of these bones in the Permian †*Palaeoniscum freieslebeni* and the Triassic fishes †*Birgeria* and †*Perleidus*. Though Gardiner and Schaeffer (1989) concentrated on advanced lower actinopterygians, there are Carboniferous fishes with supraorbital bones. These include palaeoniscoids such as †*Elonichthys serratus* (Moy-Thomas and Bradley Dyne, 1938) and †*Kalops monophrys* and †*K. diophrys* (Poplin and Lund, 2002). These three named fishes have multiple supraorbital bones in a series dorsal to the orbit. †*Lambeia pectinatus* can be added to the list of Carboniferous fishes with supraorbital bones. †*Lambeia pectinatus* differs from the other Carboniferous fishes in that it possesses a single rectangular supraorbital bone in a more anterodorsal position than the supraorbital bones in other Carboniferous fishes.

The shape and placement of the supraorbital bone in †*Lambeia pectinatus* differs from other Carboniferous fishes but is similar to what is seen in the only Devonian fish with supraorbital bones. The Devonian †*Cheirolepis trailli* has a single rectangular supraorbital bone located in the anterodorsal corner of the orbit (Pearson and Westoll, 1979; Pearson, 1982), similar to the placement of the bone in †*L. pectinatus*. In both fishes, the ventral margin of the supraorbital bone approaches mid-orbit. Though the size and extent of the nasal bones that border the supraorbital bones in †*Cheirolepis*

trailli and †*Lambeia pectinatus* differ, both fish possess a single bone that is not fragmented into multiple supraorbitals. Gardiner and Schaeffer's (1989) statement that supraorbital bones are only found in advanced lower actinopterygians and neopterygians is not supported, nor is the stem-neopterygian apomorphy of the presence of multiple anamestic supraorbital bones. Supraorbital bones have been found in a handful of Carboniferous fishes and a Devonian fish and should be considered common in lower actinopterygians in general.

5.2.4 Separate and distinct antorbital bones

†*Lambeia pectinatus* has an antorbital bone that is separate and distinct from the other bones of the snout. This antorbital bone helps to form the anteroventral corner of the orbit. As pointed out by Mickle (2015), separate antorbital bones are commonly seen in Carboniferous fishes, with only one potential example of a Devonian fish with a separate antorbital bone, †*Tegeolepis clarki*. In Devonian forms, the antorbital is typically part of a bone complex associated with other bones of the snout (Mickle, 2015).

5.3 Conclusions

The Albert Formation of New Brunswick, Canada, preserves an array of palaeoniscoid fishes from the Lower Carboniferous. Much of this diversity is not understood because of the need for redescrptions. Albert Formation taxa have been assigned and reassigned to numerous paraphyletic taxa. Attempts at redescrbing the previously described taxa from the Albert Formation will not be successful until the genera these taxa have been described as belonging to are redescrbed. The taxonomic review of the Albert shale formation fishes has brought attention to the fundamental need for descriptive and revisionary work. In order to form a stronger understanding of lower actinopterygian fishes, we must have a firm foundation when it comes to the taxonomy and systematics of this group of fishes.

On top of revisionary work, there is a need for descriptions of new taxa. Undescrbed diversity remains to be uncovered. Here, a new genus and species is described from the Albert shale formation. This new taxon shows affinities to Carboniferous fishes. Many of the morphological features of this new taxon are typically seen in Late Carboniferous forms, not Devonian forms. The presence of a separate antorbital bone and multiple suborbital bones arranged in many rows are two such features. This said, the presence of a single supraorbital bone is only seen in the Devonian †*Cheirolepis trailli* (Pearson and Westoll, 1979; Pearson, 1982). It was thought that fishes from the Albert Formation, which is right above the boundary between the Devonian and the Carboniferous, may preserve forms that help bridge morphological gaps between Devonian and Carboniferous lower actinopterygians. While there are features seen in Devonian fishes, most notably the single supraorbital bone, †*Lambeia pectinatus* does preserve

characters that are more commonly seen in later Carboniferous forms. †*Lambeia pectinatus* presents a mixture of Devonian and Carboniferous characters, suggesting these morphological features were present early in the Carboniferous.

Acknowledgements. I would like to thank the two reviewers, S. Stamberg and T. Schindler, for their helpful comments and suggestions. Their comments greatly improved this publication. I want to thank H.-P. Schultze for his discussions regarding palaeoniscoid taxonomy and his comments on this manuscript. This research was funded by a NSF Dissertation Improvement Grant (DEB-1010973) and formed part of Kathryn E. Mickle's dissertation at the University of Kansas, Lawrence, KS. Kathryn E. Mickle also received grant support from Philadelphia University, Philadelphia, PA, for this work.

Edited by: F. Witzmann

Reviewed by: S. Stamberg and T. Schindler

References

- Agassiz, J. L. R.: Recherches sur les Poissons Fossiles, Neuchâtel et Soleure, Petitpierre, 2, part 1:XII + 306 pp., 1833–43.
- Arratia, G.: Actinopterygian postcranial skeleton with special reference to the diversity of fin ray elements, and the problem of identifying homologies, in: Mesozoic Fishes 4 – Homology and Phylogeny, vol. 4, edited by: Arratia, G., Schultze, H.-P., and Wilson, M. V. H., Verlag Dr. Friedrich Pfeil, München, 49–101, 2008.
- Arratia, G. and Cloutier, R.: Reassessment of the morphology of *Cheirolepis canadensis* (Actinopterygii), in: Devonian Fishes and Plants of Miguasha, Quebec, Canada, edited by: Schultze, H.-P. and Cloutier, R., Verlag Dr. Friedrich Pfeil, München, 165–197, 1996.
- Bailey, L. W. and Ells, R. W.: Report on the Lower Carboniferous belt of Albert and Westmorland counties, N. B., including the Albert Shales, Geological Survey of Canada, Report of Progress for 1876–77, 1878.
- Bailey, L. W., Matthew, G. F., and Ells, R. W.: Report on the geology of southern New Brunswick, etc., Geological Survey of Canada, Report of Progress for 1878–1879, 1880.
- Choo, B., Long, J. A., and Trinajstić, K.: A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia, Acta Zool.-Stockholm, 90, 194–210, 2009.
- Coates, M. I.: New actinopterygian fish from the Namurian Manse Burn Formation of Bearsden, Scotland, Palaeontology, 36, 123–146, 1993.
- Coates, M. I.: Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians, Philos. T. R. Soc. Lon B, 354, 435–462, 1999.
- Cope, E. D.: Contribution to the ichthyology of the Lesser Antilles, T. Am. Philos. Soc., 14, 445–483, 1871.
- Daeschler, E. B.: An early actinopterygian fish from the Catskill Formation (Late Devonian, Famennian) in Pennsylvania, P. Acad. Nat. Sci. Phila., 150, 181–192, 2000.
- Dawson, J. W.: Carboniferous fishes of New Brunswick, Canadian Naturalist, 2nd series, 8, 337–340, 1877.
- Dawson, J. W.: Supplement to the Second Edition of Acadian Geology, containing additional facts as to the geological structure, fossil remains, and mineral resources of Nova Scotia, New Brunswick, and Prince Edward Island, MacMillan and Co., London, 1–103, 1878.
- Ducrotay de Blainville, H. M.: Poissons Fossils Nouveau Dictionnaire d'Historie Naturelle, Paris, XXVII, 1818.
- Dunkle, D. H.: Preliminary description of a palaeoniscoid fish from the Upper Devonian of Ohio, Scientific Publications of the Cleveland Museum of Natural History, 3, 1–24, 1964.
- Dunkle, D. H. and Schaeffer, B.: *Tegeolepis clarki* (Newberry), a palaeonisciform from the Upper Devonian Ohio Shale, Palaeontogr. Abt. A, 143, 151–158, 1973.
- Eastman, C. R.: Devonian Fishes of Iowa, Iowa Geological Survey 18, 29–386, 1908.
- Ells, R. W.: The Albert Shale deposits of Albert and Westmorland Counties, N. B. Summary Report of the Geological Survey Department for 1902, Geological Survey of Canada, 1903.
- Gardiner, B. G.: *Namaichthys schroederi* Gürich and other Palaeozoic fishes from South Africa, Palaeontology 5, 9–21, 1962.
- Gardiner, B. G.: Certain palaeoniscoid fishes and the evolution of the actinopterygian snout, B. Brit. Mus. (Natur. Hist.) Geol., 8, 237–325, 1963.
- Gardiner, B. G.: Catalogue of Canadian fossil fishes, Royal Ontario Museum, Life Sciences Contribution no. 68, University of Toronto Press, Toronto, 154 pp., 1966.
- Gardiner, B. G.: The relationships of the palaeoniscoid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia, B. Brit. Mus. (Natur. Hist.) Geol., 37, 173–428, 1984.
- Gardiner, B. G. and Schaeffer, B.: Interrelationships of lower actinopterygian fishes, Zool. J. Linn. Soc.-Lond., 97, 135–187, 1989.
- Gardiner, B. G., Schaeffer, B., and Masserie, J. A.: A review of the lower actinopterygian phylogeny, Zool. J. Linn. Soc.-Lond., 144, 511–525, 2005.
- Giebel, C. G.: Fauna der Vorwelt, mit steter Berücksichtigung der lebenden Tiere, Vol. 1: Wirbeltiere, Dritte Abteilung: Fische, Brockhaus, Leipzig, 1–467, 1848.
- Greiner, H.: Facies and sedimentary environments of Albert Shale, New Brunswick, B. Am. Assoc. Petrol. Geologists, 45, 219–234, 1962.
- Greiner, H.: The Albert Formation of New Brunswick: a Paleozoic lacustrine model, Geol. Rundsch., 63, 1102–1113, 1974.
- Greiner, H.: Crossopterygian fauna from the Albert Formation, New Brunswick, Canada, and its stratigraphic–paleoecologic significance, J. Paleontol., 51, 44–56, 1977.
- Gross, W.: Devonische Palaeonisciden-Reste in Mittel und Osteuropa, Palaeont. Z., 27, 85–112, 1953.
- Gussow, W. C.: Carboniferous stratigraphy and structural geology of New Brunswick, Canada, Am. Assoc. Petr. Geol. B, 37, 1713–1816, 1953.
- Hay, O. P.: Bibliography and catalogue of the fossil Vertebrata of North America, Bulletin of the United States Geological Survey, 179, 1–868, 1902.

- Hay, O. P.: Second bibliography and catalogue of the fossil Vertebrata of North America, Carnegie Institution of Washington Publication 390, Vol. 1, vii + 916 pp. 1929.
- Huxley, T. H.: On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia, P. Zool. Soc. Lond., 1880, 649–662, 1880.
- Jackson, C. T.: Report on the Albert Coal Mine, in: Reports on the geological relations, chemical analysis and microscopic examination of the Albert Coal Mining Company situated in Albert County, New Brunswick, New York, C. Vinten, 48 pp., 1851a.
- Jackson, C. T.: Description of five new species of fossil fishes, Boston Society of Natural History, 4, 138–142, 1851b.
- Jessen, H.: *Moythomasia nitida* GROSS und *M. cf. striata* GROSS, devonische Palaeonisciden aus dem Oberen Plattenkalk der Bergisch-Gladbach-Paffrather Mulde, Palaeontogr. Abt. A, 128, 87–114, 1968.
- Jollie, M.: Chordate Morphology, Reinhold Publishing Company, New York, XIV + 498 pp., 1962.
- Jordan, D. S.: The Genera of Fishes: From Linnaeus to Cuvier, 1758–1833, Seventy-five years, with the accepted type of each: a contribution to the stability of scientific nomenclature, Leland Stanford University Publications, University Series, 161 pp., 1917.
- Lambe, L. M.: The fish fauna of the Albert Shales of New Brunswick, Am. J. Sci., 28, 165–174, 1909.
- Lambe, L. M.: Palaeoniscid fishes from the Albert Shales of New Brunswick, Contributions to Canadian Palaeontology, Geological Survey of Canada, Memoir 3, Vol. III, Part V, 1910.
- Long, J. A.: New palaeoniscoid fishes from the Late Devonian and Early Carboniferous of Victoria, in Devonian and Carboniferous Fish Studies, edited by: Jell, P. A., Association of Australian Palaeontologists Memoir, 7, 1–64, 1988.
- Lund R. and Poplin, C.: The Rhadinichthyids (palaeoniscoid Actinopterygians) from the Bear Gulch Limestone of Montana (USA, Lower Carboniferous), J. Vertebr. Paleontol., 17, 466–486, 1997.
- Malabarba, M. C. L.: A new genus and species of stem group actinopteran fish from the Lower Permian of Santa Catarina State, Brazil, Zool. J. Linn. Soc-Lond., 94, 287–299, 1988.
- Mickle, K. E.: Identification of the Bones of the Snout in Fossil Lower Actinopterygians – A New Nomenclature Scheme Based on Characters, Copeia, 103, 838–857, 2015.
- Mickle, K. E., Lund, R., and Grogan, E. D.: Three new palaeoniscoid fishes from the Bear Gulch Limestone (Serpukhovian, Mississippian) of Montana (USA) and the relationships of lower actinopterygians, Geodiversitas, 31, 623–668, 2009.
- Miller, R. F. and Brazeau, M. D.: A Late Devonian Porolepiform fish (*Holoptychius*) and the age of the Kennebecasis Formation, southern New Brunswick, Canada, Atlantic Geol., 43, 187–196, 2007.
- Miller, R. F. and McGovern, J. H.: Preliminary report of fossil fish (Actinopterygii: Palaeonisciformes) from the Lower Carboniferous Albert Formation at Norton, New Brunswick (NTS 21/H/12), in: Current Research, edited by: Carroll, B. M. W., New Brunswick Department of Natural Resources and Energy, Minerals and Energy Division, Mineral Resource Report 97-4, 191–200, 1996.
- Moy-Thomas, J. A.: A revision of the fishes referred to the genus *Canobius* from the Lower Carboniferous localities other than Glencartholm, Annals and Magazine of Natural History, London, 2, 291–299, 1938.
- Moy-Thomas, J. A. and Bradley Dyne, M.: The actinopterygian fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire, T. Roy. Soc. Edin., 59, 437–480, 1938.
- Newberry, J. S.: The Palaeozoic fishes of North America, United States Geological Survey Monograph 16, 1–340, 1889.
- Pearson, D. M.: Primitive bony fishes, with especial reference to *Cheirolepis* and palaeonisciform actinopterygians, Zool. J. Linn. Soc-Lond., 74, 35–67, 1982.
- Pearson, D. M. and Westoll, T. S.: The Devonian actinopterygian *Cheirolepis* Agassiz, T. Roy. Soc. Edin., 70, 337–399, 1979.
- Poplin, C.: The dermosphenotic in early actinopterygians, a nomenclatural problem, in: Mesozoic Fishes 3 – Systematics, Palaeoenvironments and Biodiversity, edited by: Arratia, G. and Tintori, A., Verlag Dr. Friedrich Pfeil, München, 165–178, 2004.
- Poplin, C. and Lund, R.: Two Carboniferous fine-eyed palaeoniscoids (Pisces, Actinopterygii) from Bear Gulch (USA), J. Paleontol., 76, 1014–1028, 2002.
- Poschmann, M. and Schindler, T.: Sitters and Grügelborn, two important Fossil-Lagerstätten in the Rotliegend (Late Carboniferous-Early Permian) of the Saar-Nahe Basin (SW-Germany), with the description of a new palaeoniscoid (Osteichthyes, Actinopterygii), Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 232, 283–314, 2004.
- Rayner, D. H.: On the cranial structure of an early palaeoniscoid, *Kentuckia* gen. nov., T. Roy. Soc. Edin.-Earth, 62, 53–83, 1951.
- Romer, A. S.: Vertebrate Paleontology, 2nd Edition, University of Chicago Press, Chicago, 687 pp., 1945.
- Schindler, T.: “*Elonichthys palatinus* n. sp., a new species of actinopterygians from the Lower Permian of the Saar-Nahe Basin (SW-Germany), in: New Research on Permo-Carboniferous Faunas, 29, edited by: Heidtke, U., Pollichia-Buch, Bad Durkheim, 67–88, 1993.
- Schindler, T.: Tierisches aus dem Oberkarbon: Wettin ist auch für Fische gut, Fossilien, 6, 363–366, 2009.
- Schultze, H.-P.: Nomenclature and homologization of cranial bones in actinopterygians, in: Mesozoic Fishes 4 – Homology and Phylogeny, edited by: Arratia, G., Schultze, H.-P., and Wilson, M. V. H., Verlag Dr. Friedrich Pfeil, München, 23–48, 2008.
- Schultze, H.-P. and Bardack, D.: Diversity and size changes in palaeonisciform fishes (Actinopterygii, Pisces) from the Pennsylvanian Mazon Creek Fauna, Illinois, USA, J. Vertebra. Paleontol., 7, 1–23, 1987.
- St. Peter, C.: Maritimes Basin evolution: key geologic and seismic evidence from the Moncton Subbasin of New Brunswick, Atlantic Geol., 29, 233–270, 1993.
- Sternberg, R. M.: Fossil fishes from the Albert Shales of New Brunswick, T. Roy. Soc. Can., 33, 111–117, 1939.
- Swartz, B.: Devonian actinopterygian phylogeny and evolution based on a redescription of *Stegotrachelus finlayi*, Zool. J. Linn. Soc-Lond., 156, 750–784, 2009.
- Taverne, L.: *Osorioichthys marginis*, “Palaeonisciforme” du Famennien de Belgique, et la phylogénie des Actinoptérygiens dévoniens (Pisces), Bulletin de l’Institut Royal des Sciences Naturelles de Belgique, 67, 57–78, 1997.
- Traquair, R. H.: On the Agassizian genera *Amblypterus*, *Palaeoniscum*, *Gyrolepis*, and *Pygopterus*, Q. J. Geological Society, 33, 548–578, 1877.

- Traquair, R. H.: The ganoid fishes of the British Carboniferous Formations, Part I – Palaeoniscidae, Monographs of the Palaeontographical Society, 123–158, 1911.
- Troschel, F. H.: Beobachtungen über die Fische in den Eisenminen des Saarbrücker Steinkohlengebirges, Verhandlungen des Naturhistorischen Vereins preussischen Rheinland und Westphalen, 14, 1–19, 1857.
- Utting, J.: Palynostratigraphic investigation of the Albert Formation (Lower Carboniferous) of New Brunswick, Canada, Palynology, 11, 73–96, 1987.
- Wiley, E. O.: Phylogenetics: The Theory and Practice of Phylogenetic Systematics, Wiley-Intersciences, New York, 439 pp., 1981.
- Wiley, E. O.: Homology, identity and transformation, in Mesozoic Fishes 4 – Homology and Phylogeny, edited by: Arratia, G., Schultze, H.-P., and Wilson, M. V. H., Verlag Dr. Friedrich Pfeil, München, 9–21, 2008.
- Woodward, A. S.: Catalogue of Fossil Fishes, Part 2, British Museum (Natural History), London, 567 pp., 1891.
- Woodward, A. S.: On a Carboniferous fish fauna from the Mansfield District, Victoria, Memoirs of the National Museum, Melbourne, 1, 1–32, 1906.