Paleoichthyology and Sedimentology of the Paleocene Ravenscrag Formation, Saskatchewan, Canada

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Systematics and Evolution

Department of Biological Sciences

University of Alberta

ABSTRACT

The Paleocene Ravenscrag Formation of southern Saskatchewan preserves one of the best non-marine micro vertebrate assemblages in Canada. Because of their diffused nature, microfossils are quite frequently preserved and recovered from the flood plain deposits of rivers. Previous paleontological studies have examined the terrestrial vertebrates as well as the flora of the formation but not the non-terrestrial fossils. Hence, in this study, the focus is on the taxonomic diversity of the ichthyofauna recovered from this region from two different localities, namely- the Roche Percée (UAR2A site) locality from southeastern Saskatchewan and the Croc Pot locality from southwestern Saskatchewan. Seven known taxa, namely lepisosteids, holostean A, amiids, acanthomorphs, osteoglossomophs, esocids, and gonorhynchids are reported from the UAR2A site of the Roche Percée locality. Apart from these seven taxa, one unidentified teleost and 12 other unknown taxa have been reported. The morphology of these 12 taxa reported does not match with any other taxa reported before, hence they could belong to new species. The Croc Pot locality on the other hand, represents diverse taxa, of which six are known and one is an unidentified taxon. The identified taxa include lepisosteids, holostean A, amiids, acanthomorphs, osteoglossomophs, and gonorhynchids. In addition to the ichthyofauna, the stratigraphy of the Croc Pot locality has been studied, and specifically four different lithological sections have been constructed to study the characteristics of the beds. The extensive studies on the ichthyofauna from the two localities along with the sedimentology of the Croc Pot locality allows for paleoenvironmental reconstructions at the time of deposition of the strata with better confidence. The spatial and temporal diversity of the reported ichthyofauna from the region was assessed by comparing the fauna of southeastern and southwestern Saskatchewan. Also, the variation of morphology along the vertebral column of *Esox lucius* has been documented to better aid in identification of isolated centra in micro fossil localities. Lastly, the ichthyofauna from the Ravenscrag Formation has been compared to the formations lying above and below it to reconstruct the diversity and evolution of fishes in the region from Late Cretaceous to early Eocene.

ACKNOWLEDGEMENTS

I owe profound gratitude to my supervisor Dr. Alison M. Murray, Department of Biological Sciences, who has been a source of inspiration and a guiding light for me throughout my dissertation. I am very grateful to her for being patient with me throughout my degree, for providing me with feedback every time I presented my work to her and for teaching me things that I would have never found in textbooks. She has been a constant source of motivation and without her, it would not have been possible to finish the project and compile the work into the thesis. Her academic ideas, approaches, mentoring skills amazed me for the past two years and I consider myself fortunate to be her student.

I am extremely grateful to my committee members, Dr. Donald Brinkman, Royal Tyrell Museum of Palaeontology and Prof. Murray Gingras, Department of Earth and Atmospheric Sciences, University of Alberta. Dr. Brinkman's guidance on micro fossils was indispensable to my project's advancement. I am thankful to Prof. Gingras for providing me with the necessary software facilities, field work tools and guidance on sedimentology, without whom the work would not have been a successful one.

I gratefully acknowledge John Acorn, Department of Renewable Resources, for serving as my arm's length examiner. I deeply thank Dr. Lien Luong, University of Alberta for agreeing to be the chair for my defence. I would also like to extend my sincere thanks to Dr. Emily Bamforth, *T. Rex* Discovery Centre, Eastend, Saskatchewan for showing me the field sites during the field work in July 2017 and John Bruner for his help in cataloguing the several fossil specimen that I have used in my thesis and for the purpose of the project.

No assignment is an individual endeavour. I am grateful to the graduate scholars and technicians of the University of Alberta Laboratory for Vertebrate Paleontology, Dr. Hallie Street, Dr. Michelle Campbell Mekarski, Dr. Aaron Leblanc, Dr. Ilaria Paparella, Dr. Tiago

Simoes, Oksana Vernygora, Katherine Bramble, Meghan Dueck, Jasdeep Kaur, Luthfur Rahman, Gregory Funston, Mark Powers, Mathew Rhodes, Allan Lindoe and many others for helping me in various ways during my research work and for sharing with me various academic problems to make this work a success. I must mention Oksana was a great support right from the beginning of my degree. Apart from immensely helping me in the field, she made sure I settled in conveniently in Canada. The bonds I made with these peers would go a long way. Last, but not the least, I would like to thank my parents and brother for their constant support, encouragement, and motivation.

Funding for this research was provided by the Department of Biological Sciences of the University of Alberta and the Natural Sciences and Engineering Research Council of Canada Discovery Grant 327448 to Dr. Alison M. Murray.

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Chapter 1: General Introduction

The northern part of the mid-Late Cretaceous Western Interior seaway covered the area now found in the modern provinces of Alberta and Saskatchewan, and the Northwest Territories, in Canada (for example, Murray and Cook, 2016). The closure of the Western Interior Seaway by the end of the Late Cretaceous time period, led to the rise of numerous freshwater bodies in the area represented by the Paskapoo and Ravenscrag formations in Alberta and Saskatchewan respectively (for example, Murray and Cook, 2016). The fauna of the Paskapoo Formation has been well studied (for example, Wilson, 1996 and Grande, et al. 2000); in contrast, the geology as well as the ichthyofauna of the Paleocene Ravenscrag Formation have not been investigated elaborately. The Ravenscrag Formation, representing freshwater riverine environments, is exposed in several localities near the towns of Eastend, Evans, and Ravenscrag in southwestern Saskatchewan and around the town of Roche Percée in southeastern Saskatchewan. The Ravenscrag Formation is conformable with the underlying Late Cretaceous Frenchman Formation and it lies unconformably below the Eocene-Oligocene Cypress Hills Formation (Storer, 1975, 1993, 1996; Skwara, 1988). The Ferris (No. 1) coal seam occurs between the Frenchman and Ravenscrag formations and demarcates the K/Pg boundary. The Frenchman Formation is correlated to the Paleocene formations of Paskapoo and Scollard in Southern central Alberta, the Fort Union Group of southern Montana, and the Fort Union Formation of northern Wyoming (Mossop and Shetsen, 1994).

Extensive field work conducted by teams led by David Krause during the years 1972-1974, led to the discovery of diverse fossil groups in the area, including mammals, turtles, crocodiles, champsosaurs, birds, and fishes. Despite the formation being studied for the geology and fossils since the 1970s, not much information is present (Redman, et al., 2015) correlating the ichthyofauna with the sedimentological and paleoenvironmental aspects. To investigate this, two different sites, namely the Roche Percée (UAR2A locality) from southeastern Saskatchewan and the Croc Pot locality from southwestern Saskatchewan, have been studied in the first two chapters respectively. The Paleocene ichthyofauna described here is similar to that which is present in some modern-day fresh waters. Studies on these fishes will lead to an accurate description of the paleoenvironment present in the localities at the time of deposition of the strata.

The strata in southeastern Saskatchewan (Roche Percée locality) are composed of interbedded fine sandstones, clays, and shales, and coal seams are frequently documented (Russell, 1950; Krause, 1976). Several workers (e.g., Fraser et al., 1935; Broughton, 1972; Russell, 1974), including the department of Mineral Resources, Saskatchewan led by P.L. Broughton, have revised the stratigraphy of the Ravenscrag Formation. The provenance of the sediments from the Ravenscrag Formation is debated, with some suggesting it to be derived from the Upper Cretaceous and Lower tertiary rocks and older metamorphic rocks and carbonates to the south west in Montana (Byers 1969); while others suggesting that the Paleocene sediments entered the Williston Basin from the west and northwest (Royse 1971). Although the origin has still not been confirmed, the Williston Basin holds the Roche Percée strata and fauna (Fraser et al., 1935; Lerbekmo, 1985). Based on the mammals reported, the age of the locality is decided as Tiffanian (Fig. 1-1). The time interval between the first appearance of the primate *Plesiadapis* and the first appearance of rodents defines the Tiffanian North American Land Mammal Assemblage (Lofgren et. al., 2004; Krause, 1978, Fox, 2002).

The strata in southwestern Saskatchewan (Croc Pot locality) are composed mainly of sandstone with interbedded clays and siltstones. The strata are speculated to be deposited under floodplain conditions. Lithological sections have been prepared to discuss the sedimentology of the locality (Chapter 3). The strata are Puercan 2 (Fig.1-1) in age of the North American Land Mammal Assemblage.

Fishes in the Ravenscrag Formation are represented by disarticulated elements while articulated fishes have been reported from the equivalent units in Alberta (for example, Wilson, 1996). This raises the question why there are so many articulated fossil fishes coming from mass death layers from the Paleocene Paskapoo Formation in Alberta while the Ravenscrag Formation in Saskatchewan in comparison has so many microfossil sites. In addition, this study would also address whether this difference in articulation versus disarticulation of fossils is based on the changes in paleoenvironment or regional changes.

The closure of the Western Interior Seaway by the end of the Late Cretaceous and the rise of the isolated freshwater bodies are indicative of tectonic disturbances in the area. Thus, another aspect of the project is to investigate if sedimentology or stratigraphic data can aid in filtering taphonomic changes out of climate or tectonic changes between the two Ravenscrag sites.

In addition, fishes in the microfossil localities are often represented by robust and rounded centra as compared to other delicate fish bones. However, these centra are different in morphology and are often found with associated matrix. Thus, identifying them poses a challenge. To address this issue, the vertebral column of an extant pike has been studied (Chapter 4) to document the variation in morphology of centra along the column.

Overall this project involves assessing both taxonomic and morphological diversity of fishes in the Paleocene Ravenscrag Formation. It will expand this data temporally and spatially by incorporating data from underlying formations in order to test the presence of latitudinal diversity gradients in fishes and to reconstruct their diversity through time.

The University of Alberta Laboratory for Vertebrate Paleontology holds many Croc Pot microfossils which were bulk sampled in the years 1979, 1980, 1996, and 1997 and later by the Royal Tyrrell Museum of Paleontology in 2008 (Redman, et al., 2015). These microfossils have been used for the purpose of the study. The fossils from the Roche Percée locality have been collected by teams led by Dr. David Krause from 1972-1974 (Rankin, 2009) and are curated at the University of Alberta Laboratory for Vertebrate Paleontology. The fossils are identified based on literature and personal communications with Dr. Alison M. Murray and Dr. Donald Brinkman. Nelson's (2006) taxonomic system is followed throughout the work. A map showing the locations of the two localities has also been included (Fig. 1-2).

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FIGURES

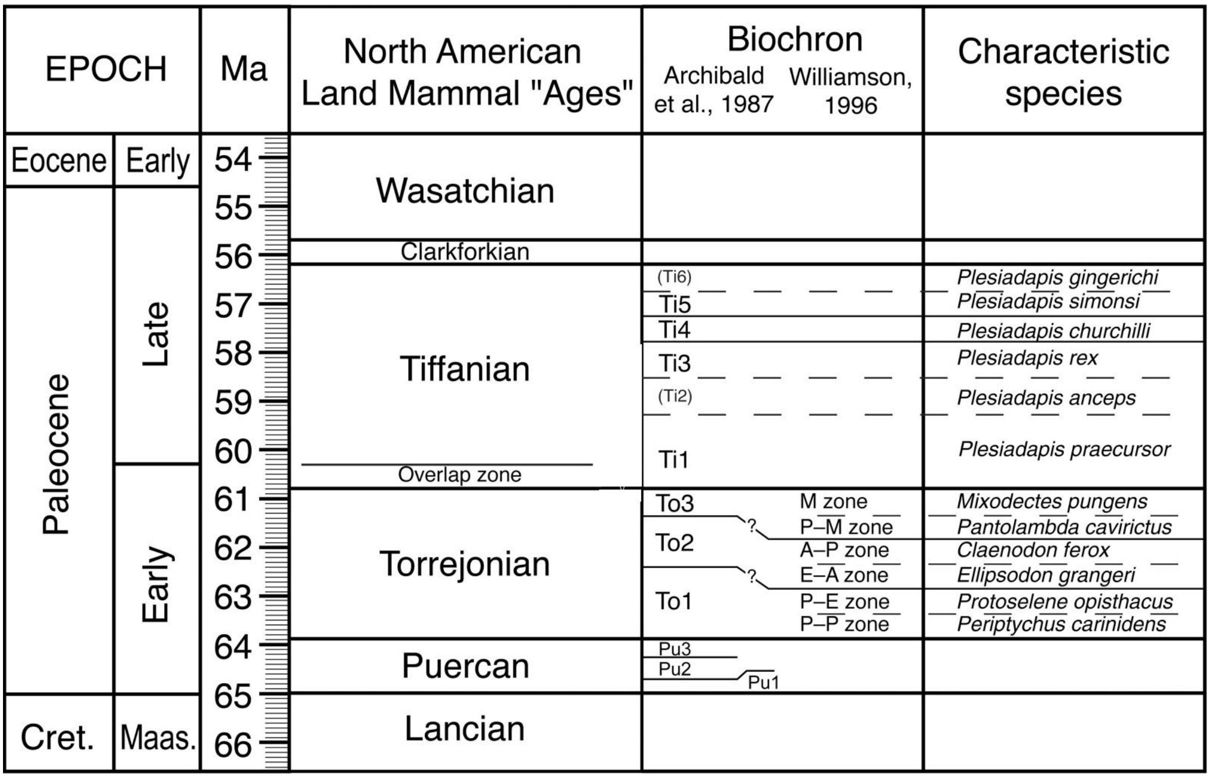

FIGURE 1-1. A geological time scale showing the ages of the Roche Percée (Tiffanian) and Croc Pot (Puercan) localities. The figure is modified from Higgins (2003) and Woodburne and Swisher (1995). The figure includes the divisions of Torrejonian and Tiffanian NALMAs and species that mark beginning of each division. Divisions of Tiffanian are those of Gingerich (1976) and Archibald et al. (1987). Divisions of Torrejonian are those of Archibald et al. (1987) and Williamson (1996). Abbreviations: Cret. = Cretaceous; Maas. = Maastrichtian.

FIGURE 1-2. A map showing the locations of the Roche Percée and the Croc Pot localities. The map is not to scale.

Chapter 2: Paleoichthyology of the late Paleocene Roche Percée locality; Ravenscrag Formation, southeastern Saskatchewan, Canada

INTRODUCTION

The Roche Percée locality was discovered in 1971 by Roxanne Young, a young girl from Winnipeg, Manitoba (Krause, 1977). Occurring within artificial and natural exposures of an abandoned lignite coal mine, the locality was discovered in overburden from the coal mine (Krause, 1977, 1978). Out of the eight additional sites discovered, the site UAR2A has been considered productive in terms of yielding different groups of fossils. Based on the mammals discovered from this locality, the age corresponds to the late middle Tiffanian, specifically Ti4 (Krause, 1976). Thus, the locality does not rest directly above the Cretaceous-Paleogene boundary.

The occurrence of abundant aquatic and semi-aquatic fossils indicate the environment of deposition to be tending towards lower velocity distal fluvial deposits (Fraser et al., 1935; Lerbekmo, 1985) with meandering streams, ponds, swamps, and lowland forests dominating the region (McIver and Basinger, 1993), while paleobotanical studies suggest the paleoclimate was most likely mild and humid with no dry season (McIver and Basinger, 1993; Postnikoff, 2009; Köppen and Geiger, 1936).

Following the discovery of the locality (Fig. 2-1), over 5000 specimens were collected by teams led by D.W. Krause, University of Alberta from 1972-1974 (Rankin, 2009). The different groups of isolated fossils that were collected included mammals (Krause, 1977, 1978), fishes (Wilson, 1980), salamanders (Naylor and Krause, 1981; Naylor, 1987), champsosaurs, crocodiles, and birds. Here, I describe the diverse fish fauna collected from the UAR2A site of the Roche Percée locality.

MATERIALS AND METHODS

The fossil material reported in this chapter is curated at the University of Alberta Laboratory for Vertebrate Paleontology (UALVP). The specimens were coated with ammonium chloride before photography to enhance the detail. Photographs were taken with a Nikon DCM1200C camera mounted on a Zeiss Discovery V8 stereo microscope.

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII Cope, 1887

Subclass NEOPTERYGII Regan, 1923 (sensu Rosen et al., 1981)

Order LEPISOSTEIFORMES Hay, 1929

Family LEPISOSTEIDAE Cuvier, 1825

(Fig. 2-2 A-B)

Material- Over 6635 complete scales (UALVP58691; Fig. 2-2 A) of one type and over 475 complete scales (UALVP58692; Fig. 2-2 B) of another type.

Description- The external surfaces of the scales are covered in ganoin. They lack a well- defined peg and socket joint. One of the types (Fig. 2-2 B) has a serrated dorsal edge while the other type (Fig. 2-2 A) does not have serrated edge(s).

Remarks- Grande (2010) regarded the scales with serrations to be *Atractosteus* and the scales without serrations to be *Lepisosteus.* Thus, the two different types of scales reported here could belong to these genera but are not distinct enough to attribute them to these genera with confidence.

Class ACTINOPTERYGII Cope, 1887

Order SEMIONOTIFORMES Arambourg and Bertini, 1958

HOLOSTEAN A (Brinkman, 1990)

(Fig. 2-2 C)

Material- Over 115 complete scales (UALVP58693; Fig. 2-2 C).

Description- The scales are nearly rectangular in shape with a well- defined peg and socket joint. The external surfaces of the scales are covered in ganoin. There is a distinct ridge present on the medial side.

Remarks- The scales are relatively thinner than scales of lepisosteids. The presence of a distinct peg and socket joint and the absence of a tab-like extension at the corner of the scales makes them different from lepisosteid scales. These types of scales were first mentioned by Russell (1974). They were suggested to belong to Semionotiformes (Neuman and Brinkman, 2005) and were later referred to as holostean A (Brinkman et al., 2014).

Order AMIIFORMES Hay, 1929 (sensu Grande and Bemis, 1998)

Suborder AMIOIDEA Bonaparte, 1832 (sensu Grande and Bemis, 1998)

Family AMIIDAE Bonaparte, 1832

(Fig. 2-2 D- I)

Material- Over 900 *Cyclurus* sp. teeth of one type (UALVP58694; Fig. 2-2 D), over 200 *Cyclurus* sp. teeth of another type (UALVP58695; Fig. 2-2 E), over 72 *Amia* sp. teeth (UALVP58696; Fig. 2-2 F), one Amiidae basioccipital (UALVP58697; Fig. 2-2 G), three Amiidae abdominal centra of one type (UALVP58698; Fig. 2-2 H) and 44 Amiidae abdominal centra of another type (UALVP58699; Fig. 2-2 I). The two different types are from different body positions.

Description- The *Cyclurus* sp. teeth (Fig. 2-2 D-E) are elongated with blunt tips and hollow bases, while the *Amia* sp. (Fig. 2-2 F) teeth are slightly curved and conical in shape. The bases of these teeth are oval and they possess shiny acrotin tips. The Amiidae basioccipital (Fig. 2-2 G) is broken and not distinct enough to be identified to lower taxonomic levels. It has an oval posterior facet and the notochordal foramen is centrally located. The bone is porous in texture and has a spongy appearance.

The anterior and posterior facets of the centra (Fig. 2-2 H-I) are nearly circular with a distinct central notochordal foramen. It is rectangular in dorsal, ventral, and lateral views and is wider than high. The relatively shallow neural arch pits cover almost the entire dorsal surface. The shapes of the two types of reported centra are different because they belong to different positions in the abdominal region.

Division TELEOSTEI Müller, 1846

Subdivision OSTEOGLOSSOMORPHA Greenwood, Rosen, Weitzman, and Myers, 1966

Order HIODONTIFORMES McAllister, 1968

Family indet.

CORIOPS Estes, 1969

(Fig. 2-3A- C)

Materials- 50 *Coriops* caudal centra (UALVP58700- UALVP58701; Fig. 2-3 A-B), three posterior precaudal centrum (UALVP58702; Fig. 2-3 C).

Description- The anterior and posterior articular facets of the *Coriops* caudal centra (Fig. 2-3 A-B) are nearly oval in shape with a distinct centrally located notochordal foramen. The centra are wider than high and are rectangular in dorsal, ventral, and lateral views. The centra have prominent deep mid-dorsal and mid-ventral pits. They have prominent pits for the articulation of ribs, which is a distinct feature of this type of centra. A finer complex of bony laminae covers the entire lateral surface.

The anterior and posterior facets of the *Coriops* precaudal centra (Fig. 2-3 C) are bordered with parapophyses and pleural ribs along the lateral margin. The ribs are located posterior to the parapophyses. There is a distinct mid-dorsal and mid-ventral pit.

Remarks- Distinctive components of the centra are broken, hence they could not be attributed to lower taxonomic levels. The precaudal centrum is similar in morphology to those of hiodontids.

Order ?HIODONTIFORMES McAllister, 1968

(Fig. 2-3 D)

Material- Five anterior abdominal centra (UALVP58703; Fig. 2-3D).

Description- The anterior and posterior facets of the centra are nearly circular in shape with a distinct notochordal foramen. The centra are wider than high. The neural arch pits are separated by a triangular pit widening posteriorly. These three pits protrude out of the centra and are visible at the dorsal end on the anterior and posterior views. A shallow, wide, matrix-filled depressed area covers the entire ventral surface. The pits for the articulation of ribs are circular in shape. A porous bony texture with no distinct pattern covers the lateral surface.

Remarks- Attempts have been made to compare this specimen to extant hiodontids to confirm its identification. The presence of anteriorly located neural arch pits are indicative of these centra belonging to hiodontiforms, however, extant hiodontids do not possess the wide ventral pit. Due to these differing features, identification at lower taxonomic levels could not be confirmed.

Order HIODONTIFORMES McAllister, 1968

(Fig. 2-3 E)

Material- One centrum (UALVP58704; Fig. 2-3 E).

Description- The anterior and posterior facets of the centrum are almost circular. The notochordal foramen is centrally located, but is matrix filled. The parapophyses are articulated along the lateral margin of the centrum. The neural arch pits are circular in shape and separated by a triangular pit located posteriorly. The pit for articulation of ribs is distinct and circular in shape.

Remarks- The anteriorly located neural arch pits are a distinctive feature of this centrum. This centrum is also the first report of a hiodontiform in the Paleocene (Brinkman, 2017, Personal Communication).

Class ACTINOPTERYGII Cope, 1887

Superorder OSTARIOPHYSI Sagemehl, 1885

Order GONORYNCHIFORMES Berg, 1940

Family GONORYNCHIDAE Bonaparte, 1850

(Fig. 2- 4 A-B)

Material- Three anterior abdominal centra (UALVP58712; Fig. 2-4 A) of one type and one centrum (UALVP58713; Fig. 2-4 B) of another type.

Description- The anterior and posterior articular facets of the abdominal centra (Fig. 2-4 A) are circular with broader ventral edges than dorsal edges and possess a centrally located notochordal foramen. There is a distinct bony ridge in the deep mid-dorsal pit in between the neural arch pits. A deep mid-ventral pit covers the surface in between the two parapophyseal pits. The ridges on the lateral sides are thick and robust and cover the entire length of the centrum.

The anterior and posterior facets of the other type of centrum (Fig. 2-4 B) are circular to pentagonal in shape with flattened margins. The notochordal foramen is centrally located. The centrum is higher than wide in morphology with curved lateral sides. The neural arch pits are slender and nearly circular in shape. The bony ridges forming a complex are robust and give rise to several ornamented pits. There is a thick bony mid-ventral ridge.

Remarks- The presence of a raised ridge in the deep mid-dorsal pit in between the neural arch pits is a distinctive feature of these centra (Fig. 2-4 A). The other type of centrum (Fig. 2-4 B) forms a part of the weberian apparatus and hence the shape of the anterior and posterior facets could range from being circular to rectangular and have flattened margins. The mid-ventral ridge is a distinctive feature that is absent in other centra.

Subdivision EUTELEOSTEI Greenwood, Rosen, Weitzman, and Myers, 1966

Superorder PROTACANTHOPTERYGII Greenwood, Rosen, Weitzman, and Myers, 1966

Order ESOCIFORMES Berg, 1940

Family ESOCIDAE Cuvier, 1817

ESOX Linnaeus, 1758

ESOX (*ESOX*) Linnaeus, 1758

(Fig. 2-4 C-E)

Materials- Three centra (UALVP58711; Fig.2-4 C), four teeth (UALVP58709; Fig.2-4 D), and one partial jaw (UALVP58710; Fig.2-4 E).

Description- The anterior and posterior articular facets of the centra (Fig.2-4 C) are circular with a central notochordal foramen. The centra are as high as wide, hence appear square shaped in dorsal and ventral views. The neural arch pits and the parapophyseal pits are deep and extend along the full length of the centra. The neural arch pits are separated by a complex of closely spaced longitudinal bony laminae. The teeth (Fig. 2-4 D) are conical, unstriated, with pointed tips and oval bases. The jawbone (Fig. 2-4 E) is flat and lamellar and possesses several teeth sockets, which are circular in shape.

Remarks- The morphology of the teeth and the centra are similar to that of extant esocids, *Esox* sp. but the reported centra cannot be attributed to a species without looking at other species of the same family.

Superorder ACANTHOMORPHA Rosen, 1973 (sensu Stiassny, 1986)

(Fig. 2-5 A-B)

Material- Three basioccipitals (UALVP58705; Fig. 2-5 A) and over 30 acanthomorph first vertebra HC-2 type (Brinkman et al., 2014) centra (UALVP58706; Fig. 2-5 B).

Description- The basioccipitals (Fig. 2-5 A) are broken, hence the components are not distinctive. The posterior facet is nearly circular with the dorsal end being broken. The notochordal foramen is dorsally located. Parallel bony ridges are present on the dorsal surface and the deep circular pits on the dorsal side are possibly for the articulation of the exoccipitals.

The anterior articular facet of the HC- 2 (Brinkman et al., 2014) first vertebral centra type is tripartite and is a distinctive feature of this type of centrum (Fig. 2-5 B). The neural arch is not fused to the centrum. The antero-dorsal articular surfaces of the centrum contact one another above the basioccipital articular surface. The centrum has a deep mid-dorsal pit bordered by a complex lamina of bone.

Remarks- Pits for zygopophyseal articulations and pits for articulation of ribs in lateral surface of neural arch, rather than low on the centrum, are distinctive features of acanthomorph centra (Rosen and Patterson, 1969; Grande, 1988).

Unidentified (Fig. 2-5 C)

Material- Over 32 anterior abdominal centra (UALVP58707; Fig. 2-5 C).

Description- The anterior and posterior facets of the centra are nearly circular. The centrum is as high as wide. The median region of the dorsal surface has longitudinally arranged bony fibres, while the mid-ventral region possesses a deep pit. The lateral surface has a complex of bony laminae giving the centrum a spongy texture. The neural arch bases flare out postero-laterally and become attached to the dorsal postzygapophyses.

unidentified centra (Fig. 2-5 D)

Material- Over ten centra (UALVP58708; Fig. 2-5 D).

Description- The anterior and posterior facets of the centra are nearly circular. The bases of the neural arch project out and connect to the dorsal postzygapophysis. However, the deep mid-ventral pit or the dorsal longitudinal bony fibre like structures are missing.

Remarks- Some of the features of these centra are similar to that of perciforms. Hence, the centra could belong to Perciformes but cannot be attributed with confidence. In addition, although the morphological features of these centra looks like Acanthomorpha, they are matrix filled, hence the identity could not be confirmed.

Division TELEOSTEI Müller, 1846

Unidentified teleost (Fig. 2-6 A-E)

Material- One teleost caudal centrum (UALVP58714; Fig. 2-6 A).

Description- The anterior and posterior facets of the centrum are circular with a central notochordal foramen. The centrum is as high as wide and appears rectangular in dorsal and ventral views. The parapophyses protrude out of the dorsal end. The neural arch pits are slender in shape and separated by a thick bony ridge. The centrum is conical in shape in lateral views. A complex of interconnected bony robust laminae covers the entire lateral surface.

Remarks- The features of the caudal centrum are not distinct enough to be identified to a particular taxon.

Unidentified teleost (Fig. 2-6 B)

Material- Five caudal centra (UALVP58715; Fig. 2-6 B).

Description- The anterior and posterior facets of the centra are nearly circular in shape. There is a central notochordal foramen, which is filled with matrix. The centra are as high as wide with curved lateral ends. The deep mid dorsal and mid ventral pits are similar to *Coriops* caudal centra. The pits on the left lateral side is separated by a thick bony ridge. The complex of bony ridges is generated as a result of interconnected robust bony laminae. There is a distinct ornamentation of bony ridges on the lateral sides of the centra.

Remarks- The morphology of the centra looks similar to *Coriops* in anterior, posterior, dorsal, and ventral views, however, the ornamentation of bony ridges on the lateral side is distinct and not similar to any other *Coriops* centra reported. Hence, these centra could not be identified as *Coriops*.

Unidentified teleost (Fig. 2-6 C)

Materials- One centrum (UALVP58716; Fig. 2-6 C).

Description- The anterior and posterior facets of the centra are irregular. The notochordal foramen is matrix filled. The centrum is rectangular in dorsal, ventral, and lateral views.

Remarks- The morphology of the centrum is similar in anterior, posterior, dorsal, and ventral views to that of a *Coriops* mid-precaudal centrum. However, the centrum lacks the distinct lateral pits for the articulation of ribs on the lateral side. Also, the centrum is partially obscured by matrix, hence it could be possible that the pit for the articulation of ribs is present but is not observable.

Unidentified teleost (Fig. 2-6 D)

Material- Three centra (UALVP58717; Fig. 2-6 D).

Description- The anterior and posterior facets of the centra are circular with the notochordal foramen being matrix filled. The centra are wider than high and appear rectangular in dorsal, ventral, and lateral views. The other components of the centra could not be clearly identified because of the associated matrix.

Remarks- The morphology of the centra is similar to amiid caudal centra but is not distinct due to presence of matrix to be regarded as Amiidae.

Unidentified teleost (Fig. 2-6 E)

Material- One centrum (UALVP58718; Fig. 2-6 E).

Description- The anterior and posterior facets of the centrum are circular with the notochordal foramen being matrix filled. The centrum is as high as wide with curved lateral ends. The mid-dorsal pit is bordered by longitudinal bony ridges. A complex of interconnected bony laminae covers the entire lateral surface, giving a spongy texture to the centra.

Remarks- The overall morphology of the centrum looks like that of extant esocids, but the components of the centrum are not distinct enough to be attributed to esocids.

Unidentified specimens (Fig. 2-7 A-D)

Material- One centrum (UALVP58719; Fig. 2-7 A).

Description- The anterior and posterior articular facets of the centrum are nearly circular to being irregular at the dorsal ends. The notochordal foramen is distinct and centrally located. The centrum is wider than high and appears to be flattened. The area near the neural arch pits are broken and hence the morphology of the neural arch pits could not be defined. A complex of interconnected bony ridges covers the entire ventral and lateral surfaces. The pit for the articulation of ribs is circular in shape and located dorsally on the left lateral surface.

Remarks- This type of centrum with a complex of interconnected bony ridges covering the entire ventral and lateral surfaces has not been reported before, hence this could belong to a previously undescribed taxon.

Unidentified (Fig. 2-7 B)

Material- One centrum (UALVP58720; Fig. 2-7 B)

Description- The anterior and posterior facets of the centrum are nearly circular with irregular and rough edges. The centrum is wider than high and has irregular edges. The neural arch pits are circular in shape and are separated by a deep mid-dorsal pit. However, the ventral and lateral surfaces are not entirely free of matrix, which gives the surfaces a rough texture.

Remarks- An irregular edged centrum with a mid-dorsal pit in between the neural arch pits is distinct has not been reported before. Thus, there is a possibility that this centrum could belong to a new species.

Unidentified (Fig. 2-7 C)

Material- One centrum (UALVP58721; Fig. 2-7 C)

Description - The anterior and posterior articular facets of the centrum are nearly circular with irregular edges. The morphology of this centrum is similar to that of the centrum described above (Fig. 2-7 A) except for the ornamentation on the dorsal surface. The neural arch pits include finer longitudinal bony laminae, which are separated by a mid-dorsal pit. The parapophyseal pits are located laterally and are separated by a complex of interconnected fine bony ridges. A complex of interconnected bony ridges covers the entire lateral surface.

Remarks- The centrum could belong to a new species as well as could be similar to the centrum described above (Fig. 2-7 A).

Unidentified (Fig. 2-7 D)

Material- One centrum (UALVP58722; Fig. 2-7 D)

Description- The anterior and posterior facets of the centrum are nearly circular in shape. The notochordal foramen is not distinct as it filled with matrix. The centrum is as high as wide and appears almost square shaped in dorsal and ventral views. The neural arch pits are circular with being broader dorsally and are separated by a thick bony ridge. The ventral and lateral surfaces include smaller accessory pits with several closely spaced longitudinal finer bony laminae surrounding them.

Unidentified specimen (Fig. 2-8 A-D)

Material- Four centra (UALVP58723- UALVP58724; Fig. 2-8 A-B).

Description- The anterior articular facet is circular and has a concave edge, while the posterior articular facet, though circular, has a convex edge. The notochordal foramen is centrally located. The centra are wider than high with concave anterior end and convex posterior ends. The parapophyses flare out from the ventro-lateral end. A complex of finer interconnected bony laminae covers the entire dorsal, ventral, and lateral sides. This centrum (Fig. 2-8 A) is nearly complete, while the other centrum (Fig. 2-8 B) is broken, thus the centra apparently looks different.

Remarks- Both the centra (Fig 2-8 A and B) are the same. They have been photographed twice to better understand the morphology. The centra are opistocoelus much like the centra of lepisosteids, but the morphology of the other components is not similar to that of lepisosteids.

Unidentified specimen (Fig. 2-8 C)

Material- One centrum (UALVP58725; Fig. 2-8 C).

Description- The anterior and posterior articular facets of the centrum are nearly oval in shape with a distinct centrally located notochordal foramen. The notochordal foramen could not be seen in the centrum because it is filled with matrix. The centrum is wider than high and is broken at the edges. The parapophyseal pits are separated by a prominent mid-ventral pit. The dorsal and lateral surfaces are covered with a complex of interconnected bony laminae, which gives a spongy texture.

Remarks- The morphology of the centrum is similar to that of *Coriops* mid-precaudal centra, but is broken, hence it could not be attributed with confidence.

Unidentified specimen (Fig. 2-8 D)

Material- One centrum (UALVP58726; Fig. 2-8 D).

Description- The anterior and posterior facets of the centrum are circular with a central notochordal foramen. The centrum is as high as wide and has a spongy texture on the dorsal, ventral, and lateral sides. There is a prominent mid-dorsal and mid-ventral pit in between the neural arch pits and parapophyseal pits respectively.

Remarks- The centrum could be a *Coriops* precaudal centrum but is not distinct enough to be attributed to it.

DISCUSSIONS

The UAR2A site of the Roche Percée locality contains a diverse ichthyofauna. Here, I report seven known taxa, one unidentified teleost and 12 other unidentified taxa which could belong to new species. These 12 unidentified taxa have been described in this study, but I could not attribute them to any level of classification of actinopterygians based on the morphological descriptions. The identified taxa (attributed to a particular family, at the very least) include lepisosteids, holostean A, amiids, acanthomorphs, osteoglossomophs, esocids, and gonorhynchiformes.

All the fish taxa described from this locality have been reported from the Late Cretaceous (Brinkman et al., 2013, 2014). Thus, the K/Pg mass extinction did not have a drastic effect on the diversity of fauna across the boundary. The holostean A and the hiodontids are the first reported in the Paleocene. On comparing the Paleocene assemblage to that of the Eocene assemblage, it is found that the Holostean A are absent in the Eocene assemblages, while the siluriformes and cypriniformes are absent in the late Paleocene assemblages, implying that the Eocene assemblage is similar in composition to that of the modern day fresh water fish faunas.

The presence of fishes such as lepisosteids (Scott and Crossman, 1973), amiids, (Welcomme, 1979) indicate that the local environment could be hypoxic, since these fishes are capable of surviving in hypoxic conditions (Scott and Crossman, 1973). The fossils are relatively small in size which is common in shallow depositional settings. The presence of lepisosteids, esocids, and amiids is also indicative of aquatic macrophytes, since these fishes required macrophytes for hiding, hunting or spawning (Scott and Crossman, 1973). Esocids are ambush predators and can thrive in various oxygen levels of waters. Thus, presence of esocids also supports the fact that the water level was relatively shallow, clear, had low water current, and abundant macrophytes. They can survive in a wide range of alkalinity (for example, Margenau et al. 1998, Scott and Crossman 1973, Inskip 1982) and salinity (for example, Mann, 1996). However, the acanthomorphs thrive in well-oxygenated waters, which indicate that the water in the depositional basin was not stagnant. The shallow water may have had a slow current, which led to the deposition and preservation of the microfossils. There could be a possibility that the locality represents different parts of a fluvial system comprising of a hypoxic part connected to a well oxygenated and active flowing component. The small size of the individual elements and the large size of foramen of centra indicate that the fishes in the locality were smaller in sizes or juveniles.

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FIGURES

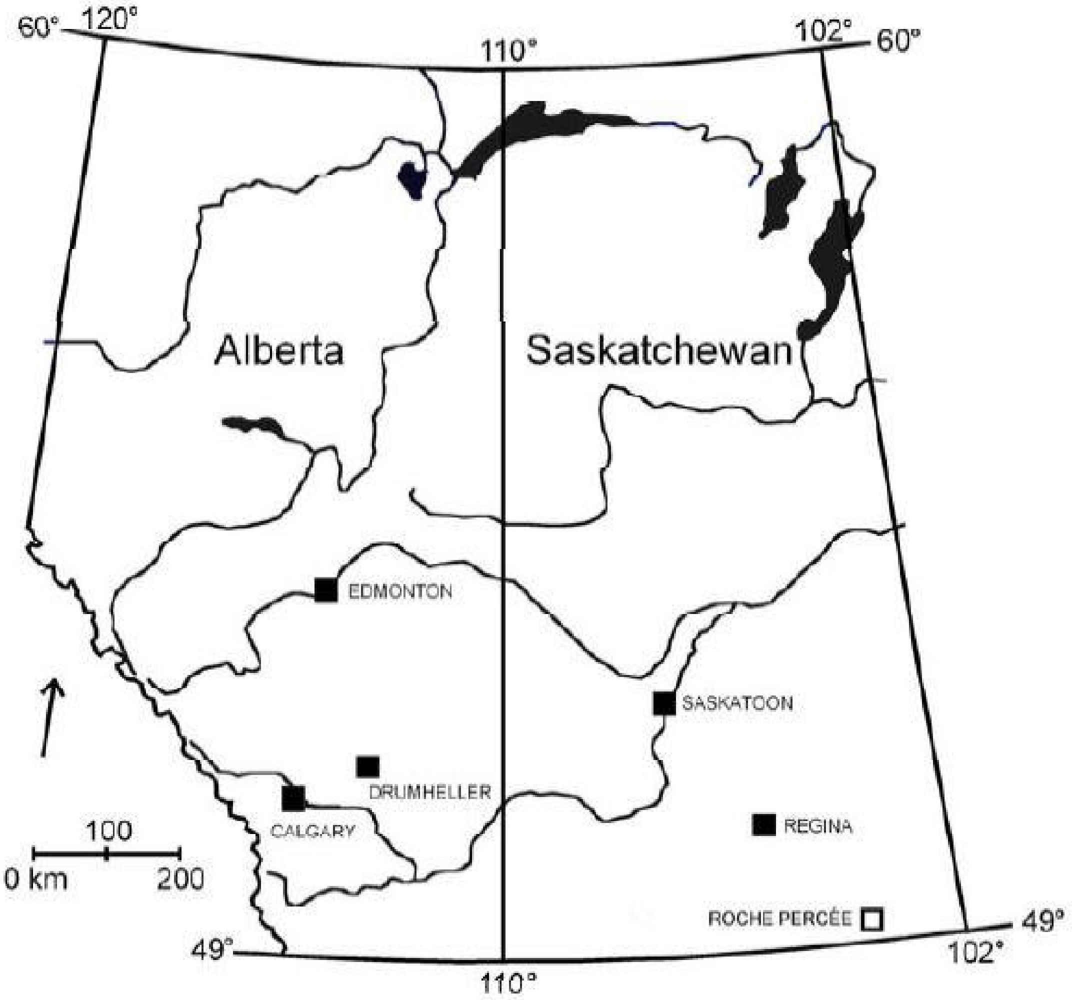

FIGURE. 2-1. Map of Alberta and Saskatchewan showing the position of the Roche Percée locality (Adapted from Scott 2006).

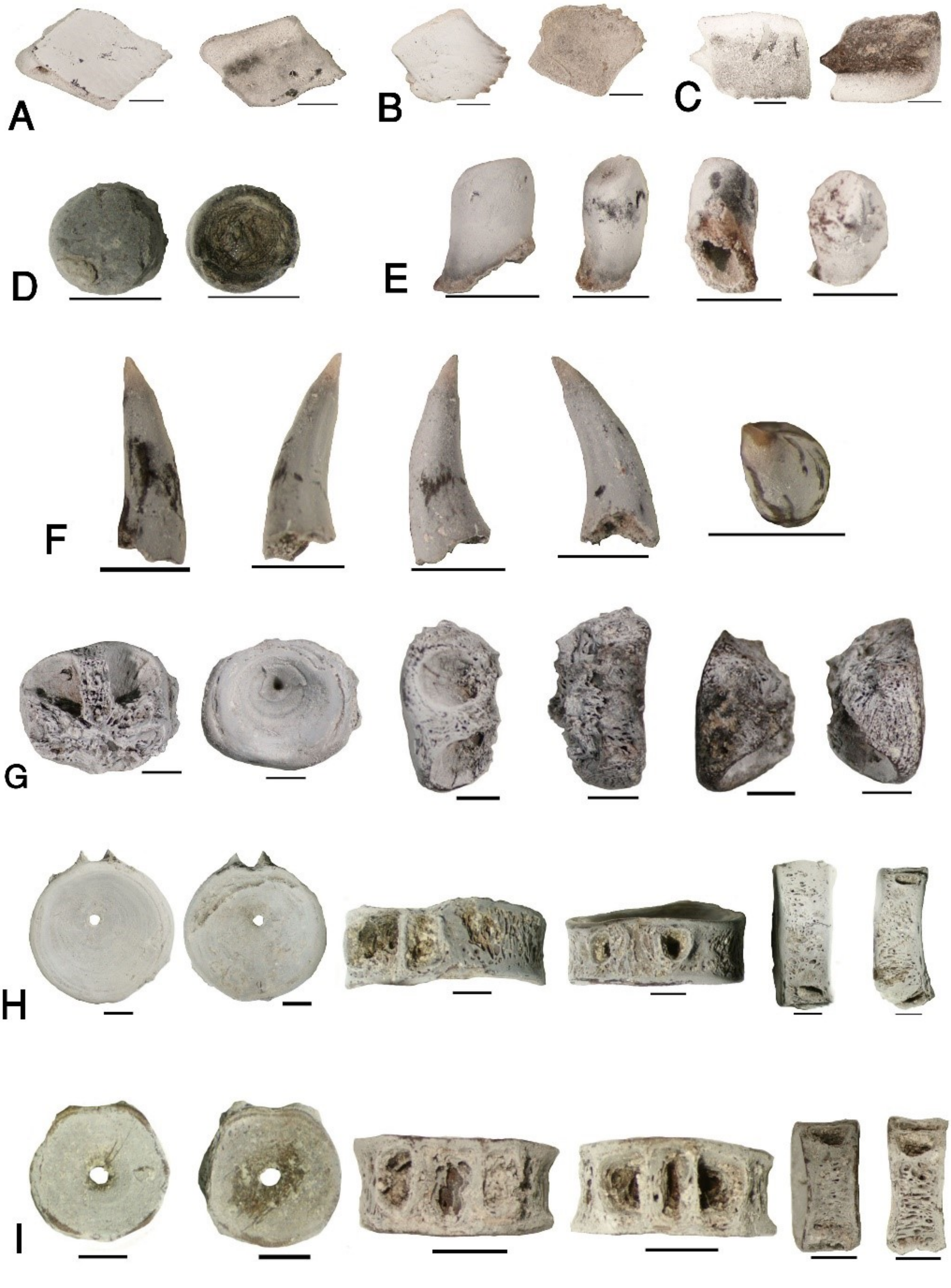
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FIGURE 2-2. Roche Percée lepisosteid, holostean A, and amiid material. A-B, Lepisosteidae scale in lateral and medial views (UALVP58691- UALVP58692); C, Holostean A scale in lateral and medial views (UALVP58693); D, *Cyclurus* sp. tooth in top and bottom views (UALVP58694); E, *Cyclurus* sp. tooth from left to right in three side views and top views (UALVP58695); F, *Amia* sp. tooth from left to right in side and top views (UALVP58696); G, Amiidae basioccipital (UALVP58697); H-I, Amiidae abdominal centra (UALVP58698-UALVP58699). Basioccipital and centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral, and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

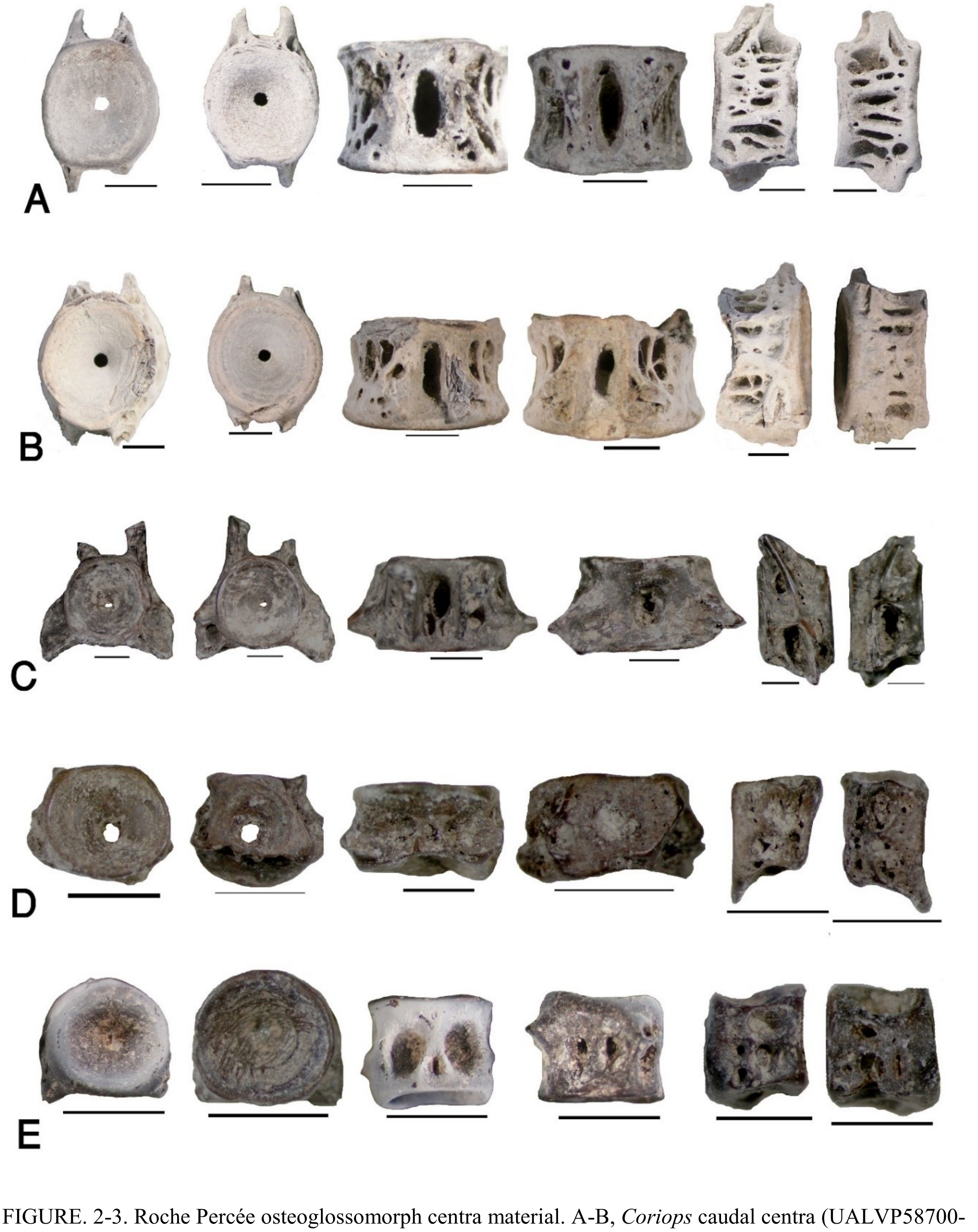

FIGURE. 2-3. Roche Percée osteoglossomorph centra material. A-B, *Coriops* caudal centra (UALVP58700-UALVP58701); C, Posterior pre caudal centrum of *Coriops* (UALVP58702); D, ?hiodontiformes abdominal centrum (UALVP58703); E, hiodontiformes centrum (UALVP58704). Centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral, and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

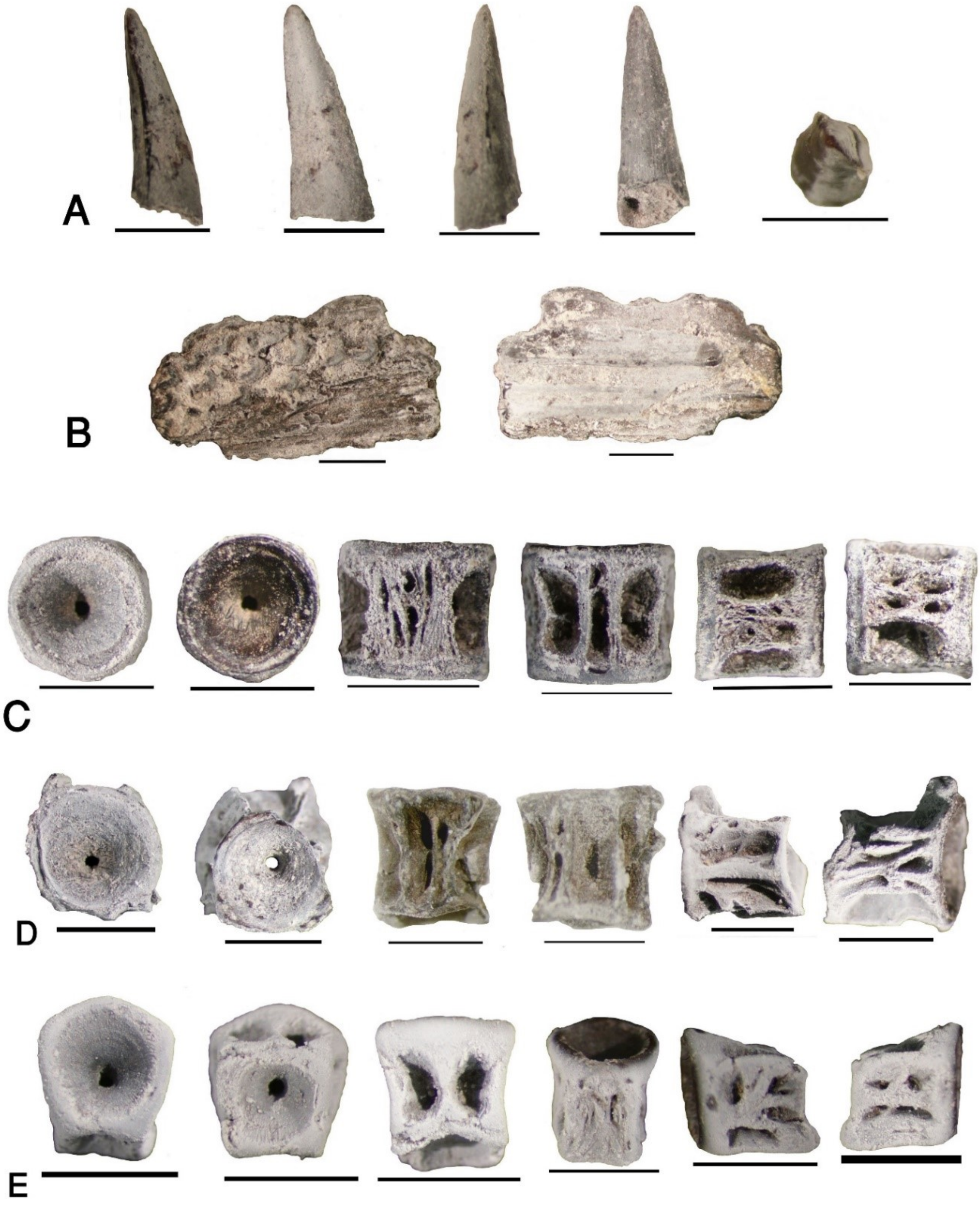

FIGURE 2-4. Roche Percée gonorhynchid and esocid centra, teeth, and jaw material. A-B, Gonorhynchiformes centra (UALVP58712- UALVP58713); C, *Esox*, sp. centra (UALVP58711); D, *Esox*. sp. teeth (UALVP58709); E, *Esox*. sp. partial jaw (UALVP58710); Centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral, and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

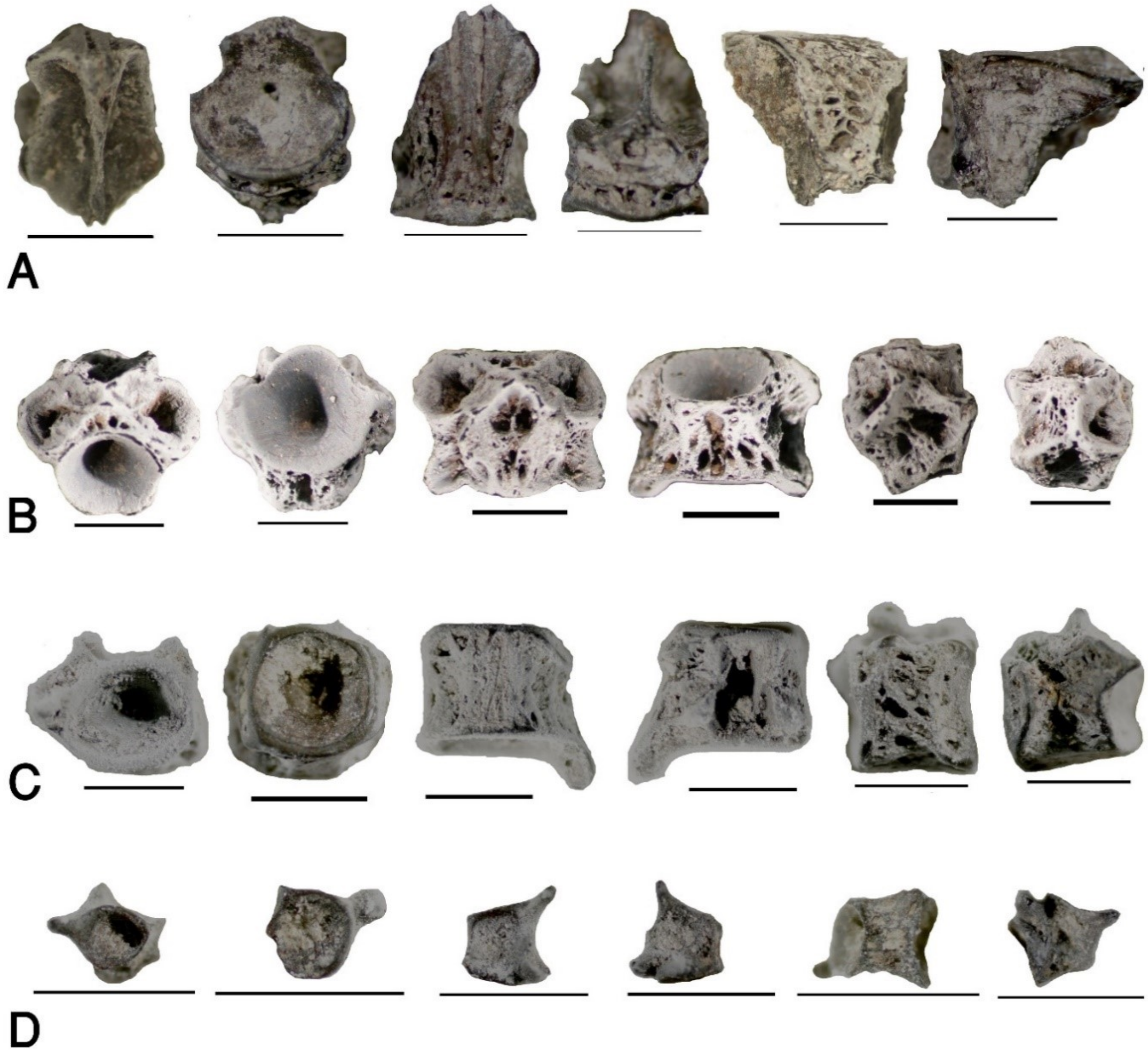

FIGURE 2-5. Roche Percée acanthomorph basioccipital and centra and indet. centra material. A, Acanthomorpha basioccipital (UALVP58705); B, Acanthomorpha centrum type HC-2 (UALVP58706); C, indeterminate perciformes anterior abdominal centrum (UALVP58707); D, unidet. perciformes centra (UALVP58708). Basioccipital and centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral, and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

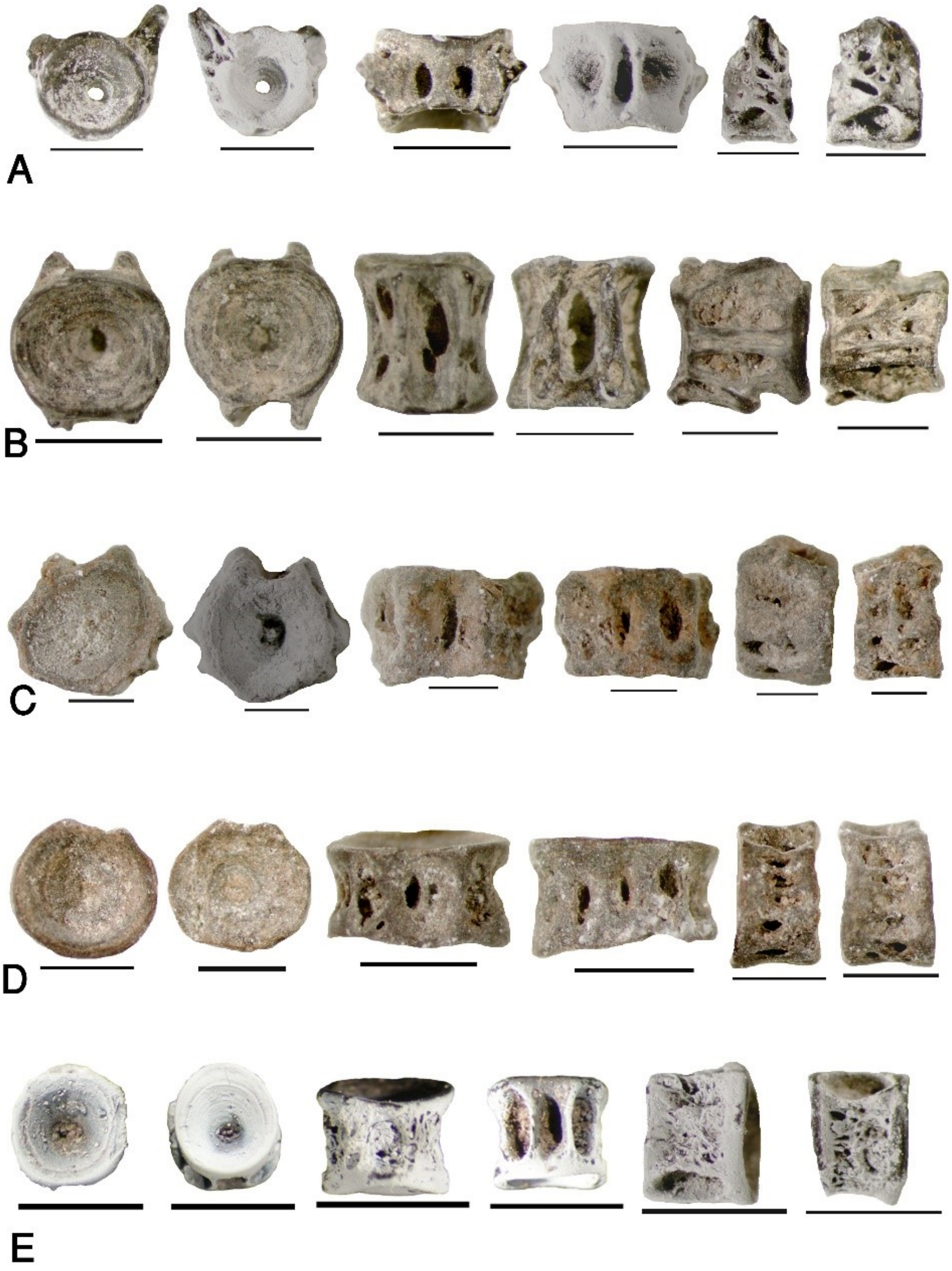

FIGURE 2-6. Roche Percée teleost centra material. A, indet. teleost caudal centrum (UALVP58714); B, unidentified caudal centra (UALVP58715); C, unidentified teleost centra (UALVP58716); D, unidentified centra (UALVP58717); E, unidentified centrum (UALVP58718). Centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral, and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

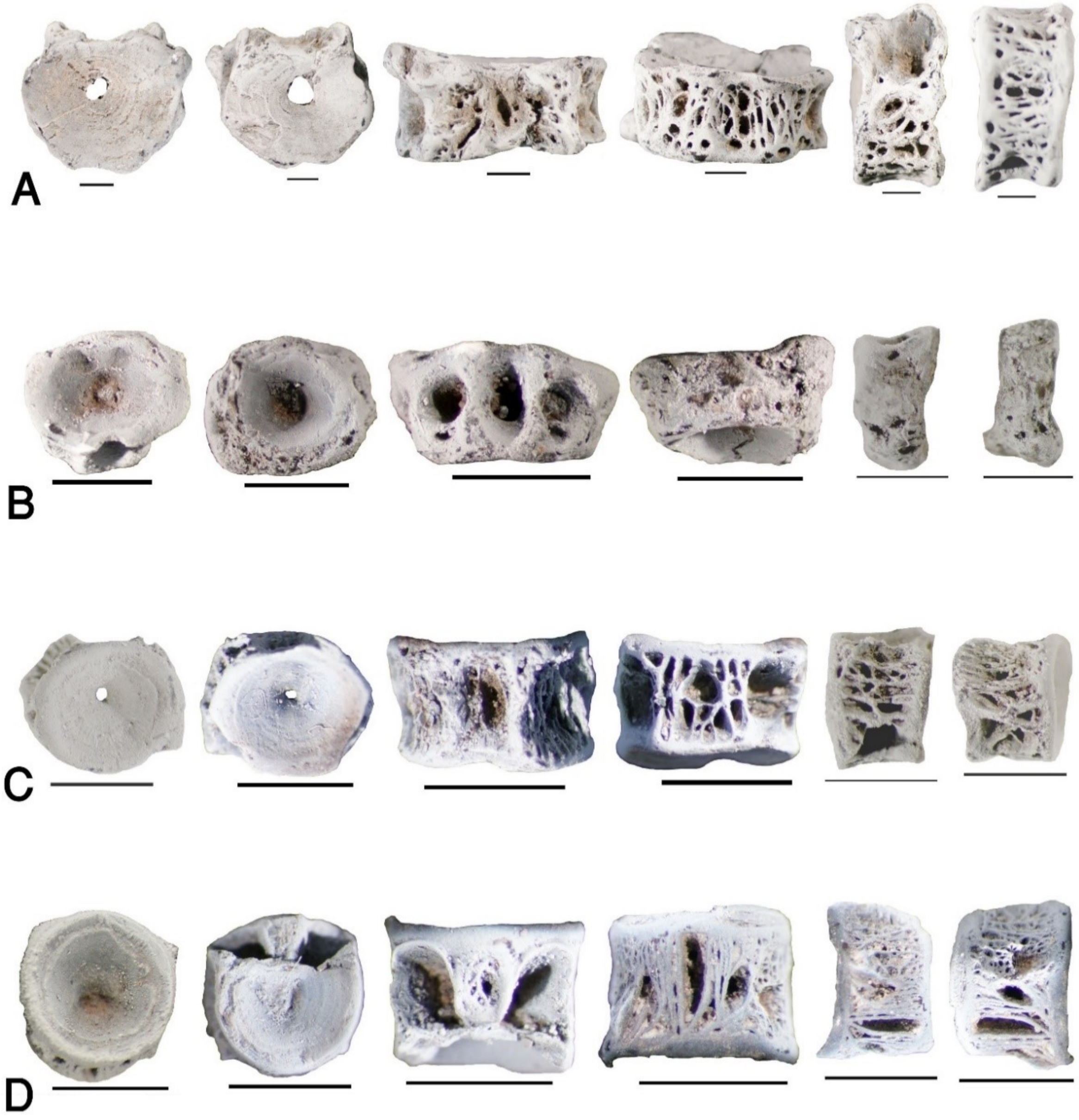

FIGURE 2-7. Roche Percée unidentified centra material (UALVP58719-UALVP58722; A-D). Centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral, and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

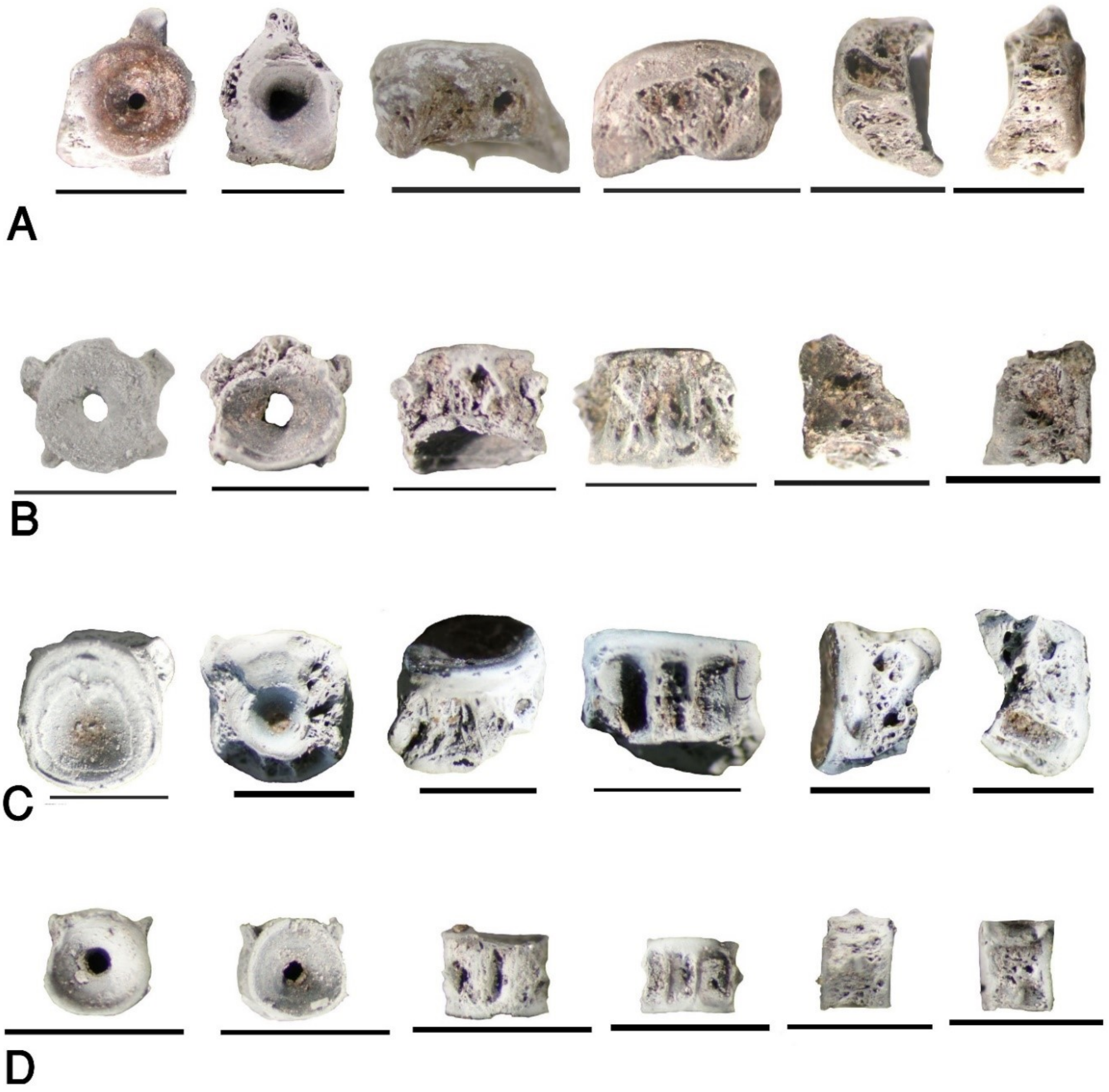

FIGURE 2-8. Roche Percée unidentified centra material (UALVP58723-UALVP58726; A-D). Centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral, and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

Chapter 3: Paleoichthyology and sedimentology of the early Paleocene Croc Pot locality; Ravenscrag Formation, southwestern Saskatchewan, Canada

INTRODUCTION

The Paleocene Ravenscrag Formation crops out in smaller localities near the towns of Eastend and Ravenscrag in western Saskatchewan. In particular, four fossil localities of Puercan age of the first NALMA Paleogene period, namely Croc Pot, French Fry, RAV W1, and Pine Cree, are known from this area (Redman et al., 2015). In this chapter, I describe the geology of the Croc Pot locality as well as the ichthyofauna recovered from it. The Croc Pot locality comprises well-exposed, cross-bedded sandstone outcrops located at the top of a small hill, 5 km west of the town of Ravenscrag (Redman et al., 2015). Previously from these strata, sections have been prepared, studied, and sampled for fossils and palynomorphs (Redman et al., 2015). Studies have also been conducted to determine the structural and geographical position of the Croc Pot locality relative to the K/Pg boundary (Johnston, 1980a) but detailed investigations are yet to be done (Redman, et.al., 2015). Since the discovery of the site in 1979, all vertebrate fossil groups (fishes, amphibians, reptiles, birds, and mammals) have been reported (Spivak, 1997), however, only the mammalian fauna has been extensively documented (Fox, 1990; Fox and Scott, 2011; Johnston 1980b). In this chapter, first the fish fossils from this locality are described and second, the composition and structure of the strata are analyzed. These two areas will allow us to have a complete record of the spatial diversity of fishes in the locality as well as aid in paleoenvironmental studies and deciphering ancient river deposits in the area.

MATERIALS AND METHODS

The fossils reported here were collected during field work in the 1970s. The fossil material is curated in the University of Alberta Laboratory for Vertebrate Paleontology (UALVP). The specimens were coated with ammonium chloride before photography to enhance the detail. Photographs were taken with a Nikon DCM1200C camera mounted on a Zeiss Discovery V8 stereo microscope.

For sedimentological studies, four stratigraphic sections within the locality were prepared by scraping off the surface sediments and macrophytes to gain a clear view of the sediments. Each bed of each of the sections was thoroughly photographed, and lithological data including grain size, color of each bed, and presence of sedimentological structures were collected. The SciOptic grain size chart and Munsell color system was adopted to record the grain size and color for each bed respectively.

RESULTS

Outcrop descriptions

Field work was done in July 2017 in the Croc Pot locality during which time the four prepared sections, namely Croc Pot South Quarry, Croc Pot North Quarry, Don's Sandstone 4, and Croc Pot East (Fig. 3-1, 3-2, 3-3, and 3-4), were studied. GPS coordinates of the locality are N49°29'19.8'' W109°09'49.3'' and elevation is 1053 meters. The overlying Eocene-Miocene Cypress Hills Conglomerates are exposed at this locality and is distinct in the Don's Sandstone 4 section (Fig 3-5). However, the Cretaceous/Paleogene boundary and the underlying Late Cretaceous Frenchman Formation are not exposed at this locality. The locality is highly faulted and offset beds could be observed in the exposures. A table (Table 3-1) comprising of sedimentary structures from the locality has also been included.

Croc Pot South Quarry (Fig.3-1) **-** The Quarry is 109 centimeters thick and is well exposed in between two covered sections on a hill-top. A minor normal fault runs through the middle of the exposure offsetting the beds in the section (Fig. 3-6). A pebbly bed is present at the base and again at 82 cm above the base of the section. The beds are gently dipping and are cross-bedded from 30 cm to 67 cm from the base (Fig.3-6). The grain size varies from fine (lower) to fine (upper). The colour of the majority of the sandstone beds is 2.5Y/8/4, and of the shale beds is 2.5Y/7/1, and the iron leached bed is 7.5YR/5/6. During field work an amiid centrum was collected from this section (Fig. 3-13 A).

Croc Pot North Quarry (Fig. 3-2) **-** The quarry is 154 centimeters thick and is adjacent to the Croc Pot South Quarry. The exposure is composed of fine (upper) grained sandstones with two pebble beds, one at 40 cm to 42 cm and the other at 112 cm to 114 cm from the base of the section. The pebble bed at 40 cm from the base correlates with the basal pebble layer of the Croc Pot South Quarry. The exposure comprises gently dipping cross beds. There is trough cross stratification (Fig. 3-7) present from 82 cm to 112 cm from the base. The GPS location at the top of the strata is N 49º29’23.2’’ W109 º09’45.7.’’ The majority of the sandstone beds in this section belong to colour 2.5Y/7/3 of the Munsell colour system.

Croc Pot Don’s Sandstone 4 (Fig. 3-3) **-** The strata lie at the top of a hill and are capped by the Cypress Hill conglomerates (Fig.3-5). Don’s Sandstone 4 is essentially correlated with the North and South Quarry. It also correlates with the sandstone beds in the East section at 2588 cm. The thickness of the strata is 358 cm. The base of the strata is a massive sandy shale overlain by flaky sandy shale upto 25 cm. These shales are overlain by sandstone (Fig. 3-8). The grain size varies from very fine (lower) for the sandy shales to very fine (upper) for the sandstones. The colour of the sandstones varies from 2.5Y/8/2 at the bottom of the section to 2.5Y/8/4 at the top. The sandy-shale belongs to colour 2.5Y/7/1 while the iron leached sandstone beds are 7.5YR/5/6. Planar lamination is present throughout this exposure and is very distinct in the beds from 69 cm to 130 cm (Fig. 3-9). There are two calcitic beds of 1 cm, one at 165 cm and another at 211 cm. Distinct cross bedding is present from 288 cm to 338 cm upto the base of the Cypress Hill conglomerates (Fig. 3-10). Traces of roots are present in the section from 313 to 338 cm (Fig.3-10). There are several minor faults running across the strata. The GPS location is N49 º 29'20.4'' W109 º09'47.7''.

Croc Pot East section (Fig. 3-4) **-** The section was cleaned, and a trench was made to expose the bedrock. The thickness of the section is 3008 centimeters and is mainly composed of sandstone along with siltstone and claystone. The grain size of the beds varies from very fine (lower) to very fine (upper). The colour codes of the mudstone, siltstone, claystone and sandstone beds are 10YR/6/3. Occasionally the colour of the beds are 10YR/8/4. The base of the exposure and beds from 313 cm to 408 cm are pedogenically altered with potential root traces. Organic detritus has been observed at 160 cm to 175 cm in the section. The sandstone beds are consolidated from 643 cm to 663 cm. The bedsets from 1243 cm to 1333 cm are cross-bedded and are intercalated with mud lenses (Fig. 3-11). The top of the section is covered, and a lot of overburden would have to be removed to expose the bed rock. The section is capped with the Cypress Hills conglomerates. Approximately 2588 cm from the base of the section correlated with the Croc Pot North and South Quarry on the other side of the same hill. The GPS location of this section is N49 º29'21.1'' W109º09'44.0''.

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII Cope, 1887

Subclass NEOPTERYGII Regan, 1923 (sensu Rosen et al., 1981)

Order LEPISOSTEIFORMES Hay, 1929

Family LEPISOSTEIDAE Cuvier, 1825

Lepisosteus Lacépède, 1803

(Fig. 3-12 A-K)

Material- Over 5000 scales (UALVP58727- UALVP58736; Fig. 3-12 A-J) of different shapes and over 900 teeth (UALVP58754).

Description- The scales are covered in ganoin. The peg and socket joint is distinct in some of the scales (Fig. 3-12 A, B, G, and I) while not prominent in the others (Fig. 3-12 C, D, E, F, H, J). These scales have a tab-like extension at the anterior end on the medial side. The teeth (Fig. 3-12 K) are conical in shape with a thick and shiny acrutin cap like structure. The teeth are faceted.

Remarks- The shapes of the scales are different because the scales are from different positions of the body. These scales dominate the entire fish fauna recovered from this locality. The scales lack serrations, hence, have been regarded as *Lepisosteus* (Grande 2010). *Atractosteus*, is characterized by scales with a serrated margin but *Lepisosteus*, do not have the serrated margins on their scales (Grande, 2010). Since the scales reported here do not possess the serrated margins, they have been regarded as *Lepisosteus*.

Class ACTINOPTERYGII Cope, 1887

Order SEMIONOTIFORMES Arambourg and Bertini, 1958

Family indet.

Genus and species indet. (Holostean A) Brinkman, 1990

(Fig. 3-12 L)

Material- Over 300 scales (UALVP58737; Fig. 3-12 L).

Description- The scales are ganoid, relatively thinner than *Lepisosteus* scales (Fig.3-12 A-J) and have a well-developed peg and socket joint connected by a ridge on the medial side. The absence of a tab-like extension at the corner of the scale makes it different from the scales of *Lepisosteus* (Brinkman et al., 2014).

Remarks- These types of scales were first mentioned by Russell (1974). They were suggested to belong to Semionotiformes (Neuman and Brinkman, 2005) and were later referred to as Holostean A (Brinkman et al., 2014).

Order AMIIFORMES Hay, 1929 (sensu Grande and Bemis, 1998)

Suborder AMIOIDEA Bonaparte, 1832 (sensu Grande and Bemis, 1998)

Family AMIIDAE Bonaparte, 1832

(Fig. 3-13 A-C)

Material- 17 Amiidae caudal centra (UALVP58745- UALVP58744; Fig. 3-13 A-B) and one Amiidae dentary fragment (UALVP58739; Fig. 3-13 C).

Description- The anterior and posteriors facets of the Amiidae caudal centra are rounded with a prominent notochordal foramen located centrally. The centra are rectangular in dorsal, ventral, and lateral views. They are wider than high. The other components of the centra are not clearly visible because of the associated matrix. The neural arch pits are centrally located while the haemal arch pits are located laterally (Fig. 3-13 A). The centra (Fig. 3-13 A-B) are very fragile, hence not much effort was made to clean the matrix. As a result, the components of the centra are not clearly observable. The Amiidae dentary (Fig. 3-13 C) is in fragments (broken) with rounded teeth sockets on it. This bone is flat and lamellar.

Cyclurus sp. (Fig. 3-13 D – G)

Material- 30 *Cyclurus* sp. tooth plate fragments (UALVP58738; Fig. 3-13 D), three coronoid *Cyclurus* sp. teeth attached to the jaw (UALVP58741; Fig. 3-13 E), over 1000 isolated *Cyclurus* sp. teeth (UALVP58742; Fig. 3-13 F), nine blunt styliform sections of isolated *Cyclurus* sp. teeth (UALVP58743; Fig. 3-13 G)

Description- The *Cyclurus* sp. tooth plate fragment (Fig. 3-13 D) is small and comprises five teeth which are relatively higher than wide. The tooth plate (Fig. 3-13 D) is similar to a coronoid plate but is not very well preserved so that it could be assigned to the maxilla, dentary or pharyngeal bone.

The teeth (Fig. 3-13 E-F) are not striated and hollow with blunt tips. The morphology of the bone of the tooth plate is flat and lamellar. These teeth (Fig. 3-13 E-F) are not distinct enough to be attributed to any species but are morphologically similar to those of *Cyclurus* (Grande and Bemis, 1998). They are cylindrical in shape with blunt tops, hollow from within and are oval in cross sectional view (Fig. 3-13 G).

Amia sp. (Fig. 3-13 H)

Material- Six isolated *Amia* sp. teeth (UALVP58740; Fig. 3-13 H),

Description- These teeth are slender and conical in shape with a transparent shiny acrotin cap. The teeth (Fig.3-13 H) are similar in morphology to that of *Amia* (Grande and Bemis, 1998), but they are not distinct so they cannot be attributed to a particular species.

Division TELEOSTEI Müller, 1846

Subdivision OSTEOGLOSSOMORPHA Greenwood, Rosen, Weitzman, and Myers, 1966

Order HIODONTIFORMES Taverne, 1979

Family indet.

CORIOPS Estes, 1969

(Fig. 3-14 A- D)

Material- Ten caudal centra (UALVP58747; Fig. 3-14 A), four precaudal centra of *Coriops* (Brinkman, personal communications).
(UALVP58748 - UALVP58749; Fig. 3-14 B-C).

Description- The anterior and posterior articular facets of the *Coriops* centra are nearly oval in shape with a distinct centrally located notochordal foramen. The notochordal foramen could not be seen in the precaudal centra (Fig. 3-14 B and Fig. 3-14 C) because they are filled with matrix. The centra have prominent deep mid-dorsal and mid-ventral pits. They have prominent pits for the rib articulation, which is a distinct feature of these type of centra (Fig. 3-14 B and Fig. 3-14 C).

Remarks- The centra are broken from the edges and filled with matrix. Hence, they could not be attributed to any species and thus just referred to the genus *Coriops*.

Lopadichthyes sp. Murray, Zelenitsky, Brinkman, and Neuman, 2018

(Fig. 3-14 D)

Material- One caudal centrum (UALVP58750; Fig. 3-14 D).

Description- The anterior and posterior facets of the centrum are nearly circular. The notochordal foramen is filled with matrix. There is a shallow mid-dorsal pit bordered by the neural arch pits on either side. The mid-ventral portion is raised and pits for ribs articulation is prominent on the lateral side.

Remarks- The specimen is assigned to *Lopadichthyes* on the basis of the dorsal and ventral facets. Based on Murray et al. 2018, the centra of *Lopadichthyes* sp. and *Coriops* sp. may be indistinguishable and so this specimen may be better referred to as *Coriops sp*.

Order GONORYNCHIFORMES Berg, 1940

Family GONORYNCHIDAE Bonaparte, 1850

(Fig. 3-15 A and 3-15 B)

Material- 20 centra (UALVP58752; Fig. 3-15 A).

Description- The anterior and posterior facets of the centrum are nearly circular in shape with a central notochordal foramen. The centrum appears rhomboid in shape in dorsal and ventral views. The mid-dorsal ridge is a distinctive feature of these centra. A complex of interconnected laminae covers most of the ventral and the lateral sides.

Remarks- The centra are much more robust compared to the other centra. The presence of the distinct mid-dorsal ridge allows the attribution of these centra to this family.

NOTOGONEUS Cope, 1885 (Fig. 3-15 B)

Material- Two basioccipitals (UALVP58753; Fig. 3-15 B).

Description- The basioccipitals have oval posterior facets, which are broken at the edges. They are higher than wide and are conical in shape, which is prominent in the lateral views. The notochordal foramen is centrally located on the posterior surface. A pair of thin bony ridges runs longitudinally along the basioccipital. A pair of mid-ventral ridges forms a depressed area in between them and tapers anteriorly. The pits on either side of the mid-dorsal ridges are most likely for the articulation of exoccipitals and are a distinct feature for the family.

Superorder ACANTHOMORPHA Rosen, 1973 (sensu Stiassny, 1986)

(Fig. 3-15 C)

Material- Two abdominal centra (UALVP58746; Fig. 3-15 C).

Description- The abdominal centra are amphicoelus with a central notochordal foramen. The anterior and posterior facets of the centra are nearly circular with rough edges and finer bony laminae protrude out of the edges. The centra are equal in height and width and nearly hourglass in shape in the dorsal and ventral views. There is a relatively large mid-dorsal pit along the midline of the centrum. The neural arch pits are laterally located. The dorsal half of the lateral surface has a deep accessory pit and several other pits, which have been generated as a result of the interconnected bony laminae.

Remarks- Due to lack of distinct features, the centra could not be classified into lower taxonomic levels and have been referred to as Acanthomorpha.

Division TELEOSTEI Müller, 1846

Unidentified teleost (Fig. 3-15 D)

Material– Teleost centrum (UALVP58751; Fig. 3-15 D).

Description- The anterior and posterior articular facets of the centrum are nearly circular with rough edges. The notochordal foramen is distinct and is centrally located. There are several longitudinal bony ridges throughout the centrum.

Remarks- The centrum is broken from the edges and is not preserved well, hence it could not be attributed to lower taxonomic levels.

DISCUSSIONS

The ichthyofauna from this locality is composed of diverse taxa, of which six are known and one is an unidentified taxon. This implies that the diversity of fishes in this locality is lower compared to the Roche Percée locality, where seven identified taxa of fishes, two unidentified teleost caudal and 12 unidentified specimens of fishes are reported. The position of this locality with respect to the Cretaceous-Paleogene boundary is not confirmed (Redman et al. 2015) due to the locality being highly faulted. According to palynological data (Redman et al.2015), and as observed during field work, the Frenchman, the Battle, and the Whitemud formations are all absent in the Croc Pot locality, and the Ravenscrag Formation unconformably lies over the Eastend Formation. The locality belongs to Puercan 2 age of the NALMA and the Ferris coal seam demarcating the Paleocene strata from the Cretaceous are not exposed at this locality. In contrast, the late Paleocene Roche Percée locality of Tiffanian age of the NALMA represents comparatively more diverse taxa. All the taxa reported from this locality have been reported from the Roche Percée locality as well. Some taxa are missing as compared to the Roche Percée locality which may be because the local environment was not suitable for certain taxa.

The presence of holostean A is particularly interesting. Holostean A has not been reported in Cenozoic formations prior to this study. Lepisosteids (Scott and Crossman, 1973) and amiids (Scott and Crossman, 1973), are capable of surviving in hypoxic waters. Hypoxic conditions in water also indicates that there was limited photosynthetic activity in the water. Limited photosynthetic activity is usually due to higher water temperatures, turbid or stagnant waters (Davenport and Sayer, 1993). Also, lepisosteids and amiids depend on macrophytes for hiding and ambushing prey, hiding themselves from predators and for spawning (Scott and Crossman, 1973). Therefore, there is a high chance that the locality had aquatic macrophytes. However, since the locality preserves both hypoxic (lepisosteids and amiids) and normoxic (acanthomorph, gonorhynchids) fishes, it could be speculated that the hypoxic part of the river basin was in connection to a well-oxygenated portion as well. Only scales and teeth were collected for lepisosteids. This is not believed to be a collection bias because centra of lepisosteids are robust and difficult to miss. It could be possible that the robust centra remained in the upstream portion of the rivers, while the ganoid scales and teeth because of their better preservation potential travelled to the depositional basins along with other isolated taxa. Thus, indicating that there was flow of water.

In addition, based on the occurrence in this locality of a cross-bedded sandstone with mudstone clasts and iron concretions and wood fragments, it was suggested that the site may represent different parts of a fluvial system (Redman et al., 2015). The fine grain size of the sediments is indicative of flood plain deposits, which may have settled out of suspension from flood waters. The finer grain size of the sediments intercalated with siltstones and shales are indicative of shallow water levels and slower velocity water currents.

Thus, based on the ichthyofauna reported and the lithology of the strata, the Croc Pot locality may represent a shallow flood plain deposit with slower current. The basin is made up of several parts of a fluvial system including both hypoxic as well as normoxic components.

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Table 3-1. A table of sedimentary structure from the Croc Pot locality

Section name	Observed Structure	Inference
Croc Pot South Quarry	Trough Cross-stratification	Low velocity water current
Croc Pot North Quarry	Trough Cross-stratification	Low velocity water current
Don's Sandstone 4	Trough Cross-stratification	Low velocity water current
Don's Sandstone 4	Planar Bedding	Varying velocity of water current
Croc Pot East section	Trough Cross-stratification	Low velocity water current

FIGURES

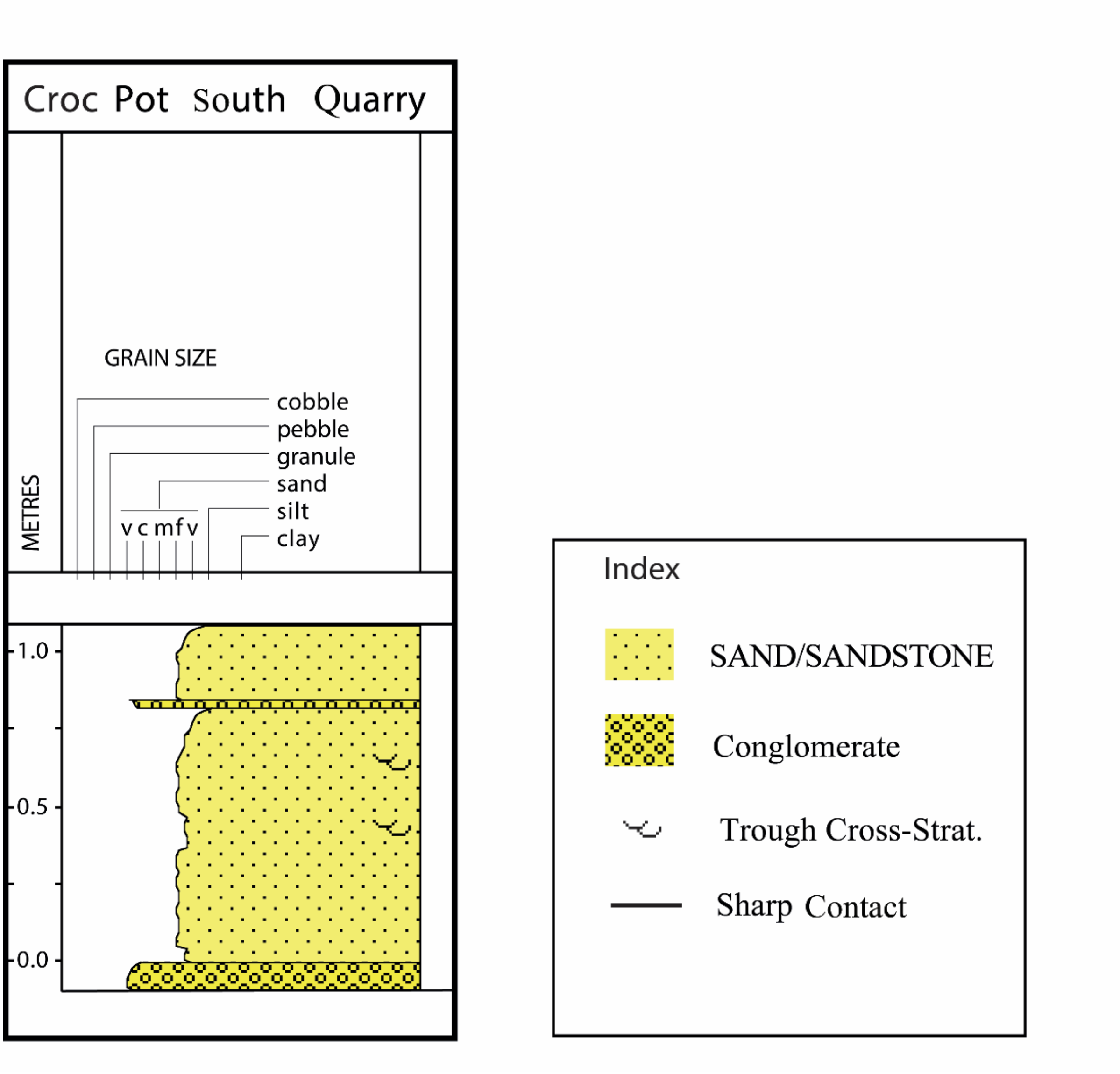

FIGURE. 3-1. Croc Pot South Quarry section.

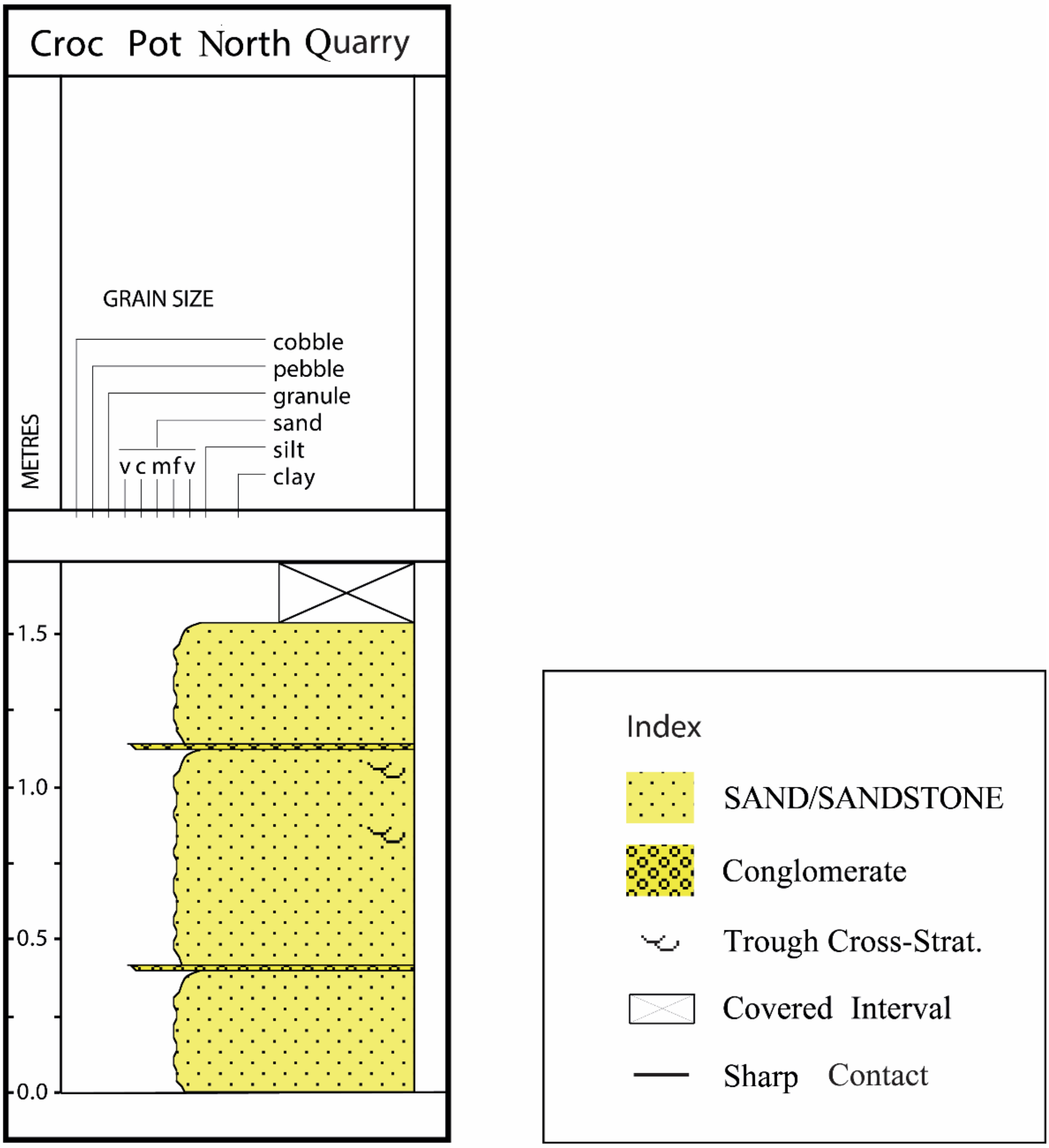

FIGURE 3-2. Croc Pot North Quarry section.

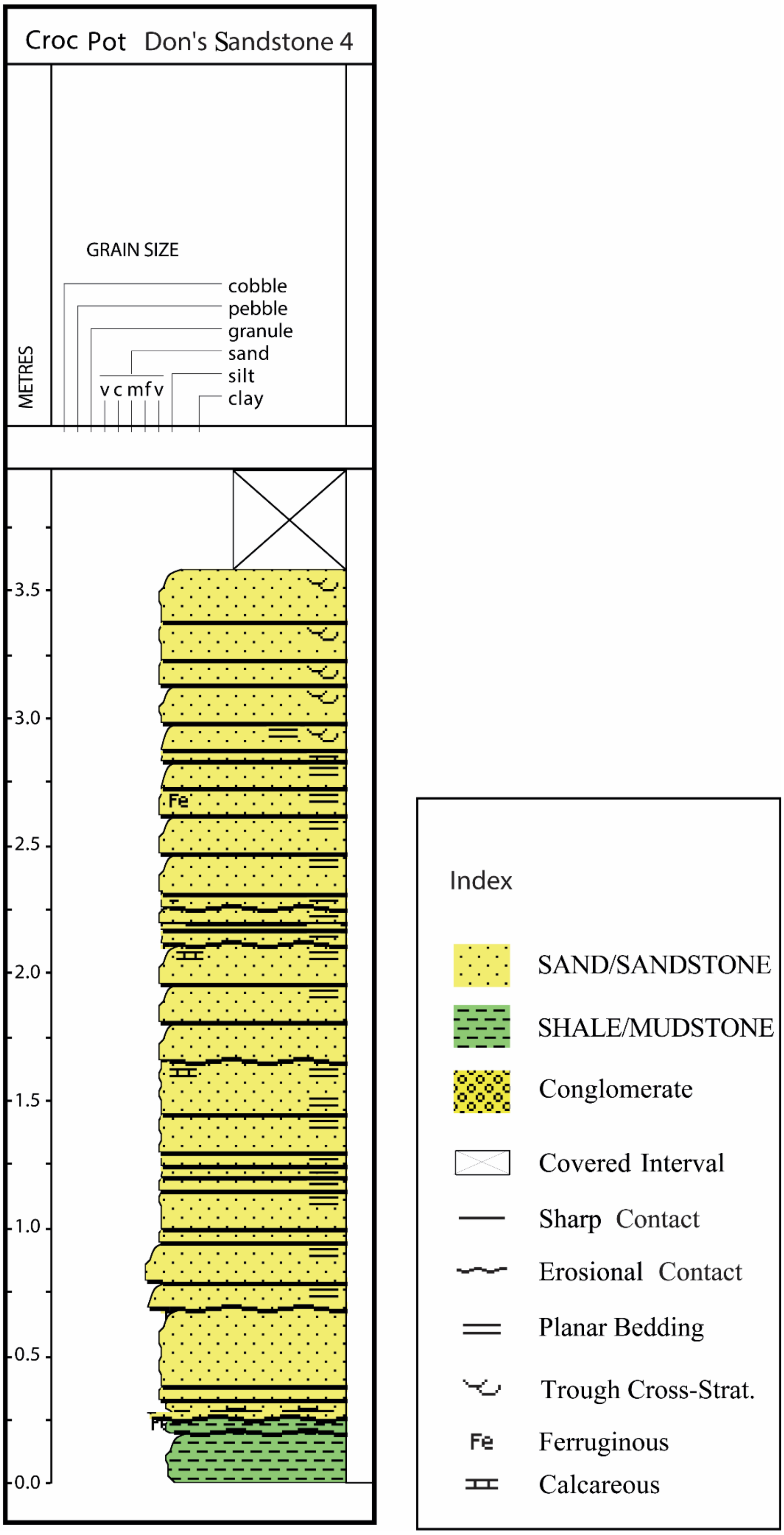

FIGURE 3-3. Croc Pot Don’s Sandstone 4 section.

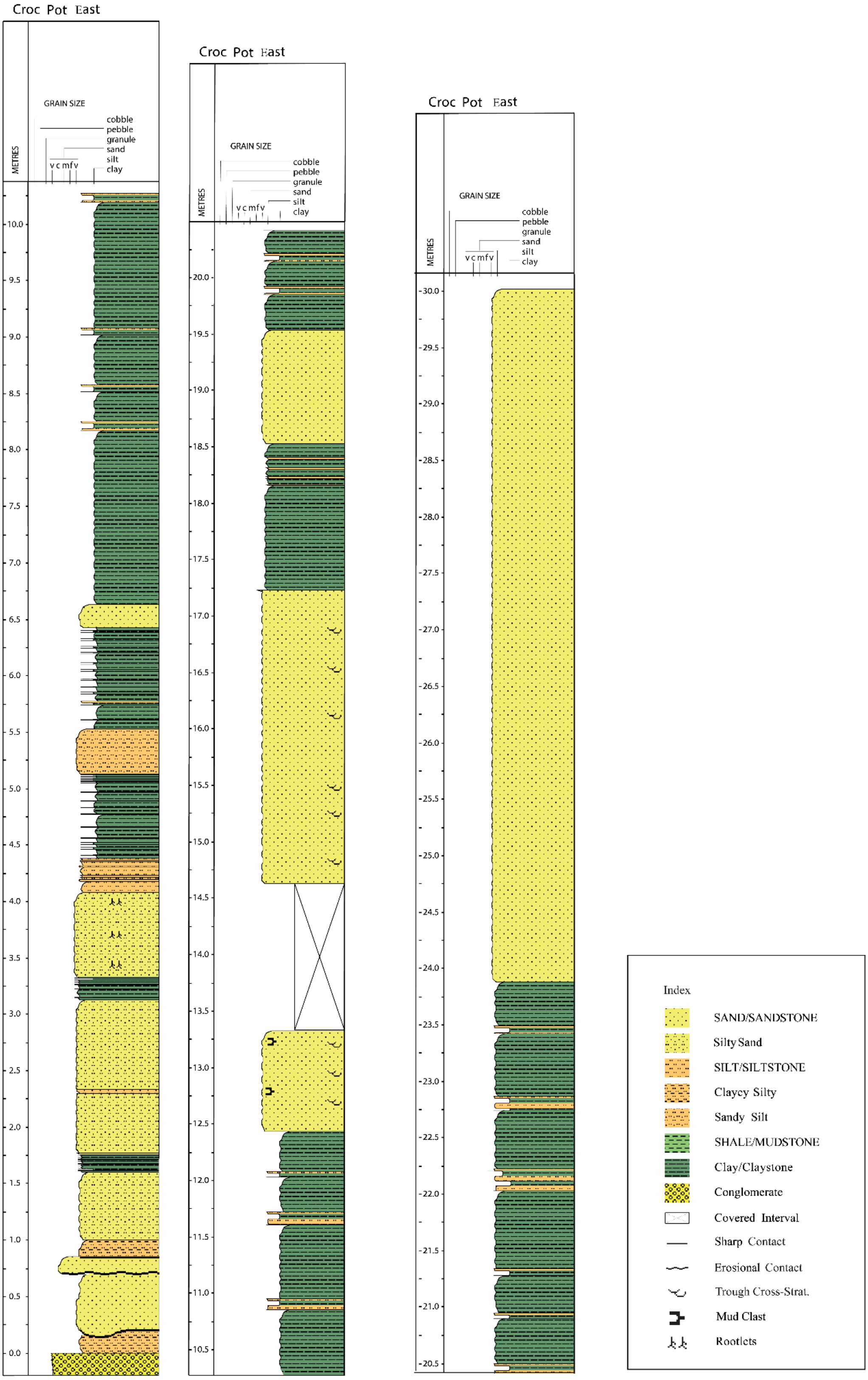

FIGURE 3-4. Croc Pot East section.

FIGURE 3-5. Don’s Sandstone 4 outcrop showing the early Eocene-Miocene Cypress Hills conglomerates at the top.

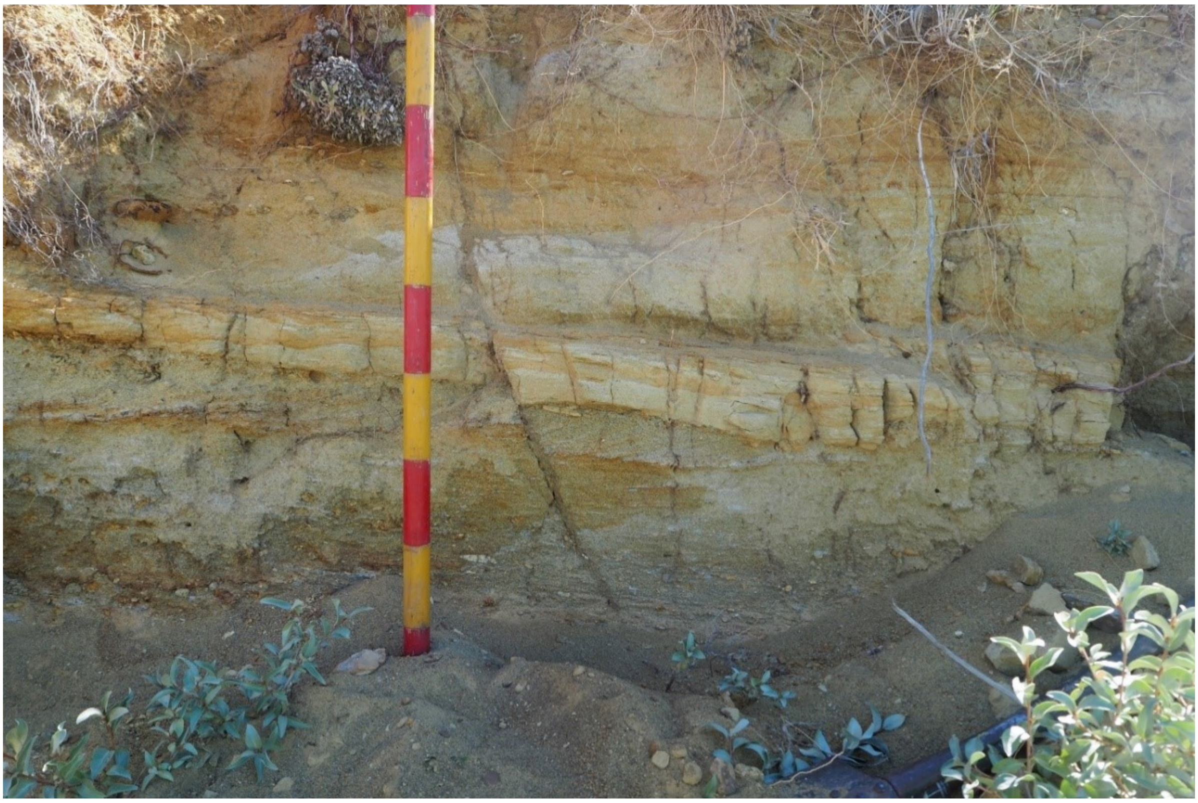

FIGURE 3-6. Croc Pot South Quarry outcrop photograph showing the minor fault.

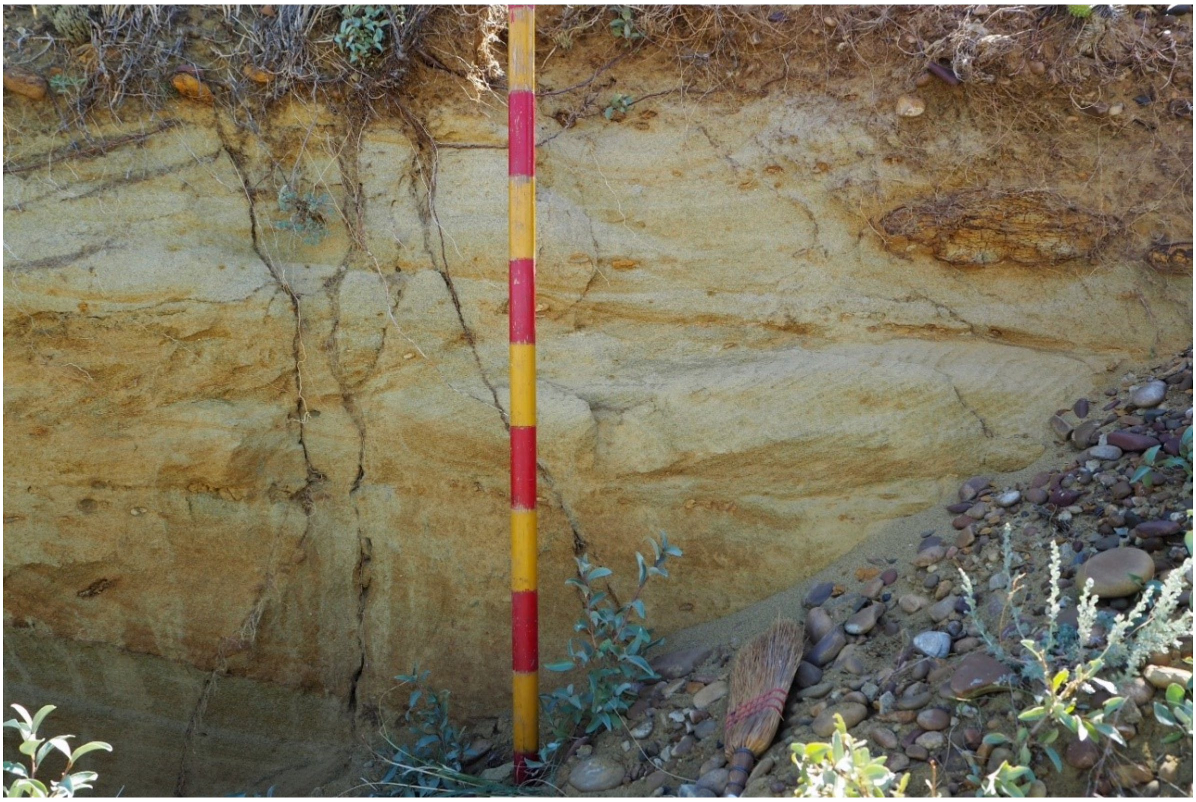

FIGURE 3-7. Croc pot North Quarry outcrop showing trough cross stratification.

FIGURE 3- 8. Base of Don’s Sandstone 4 outcrop.

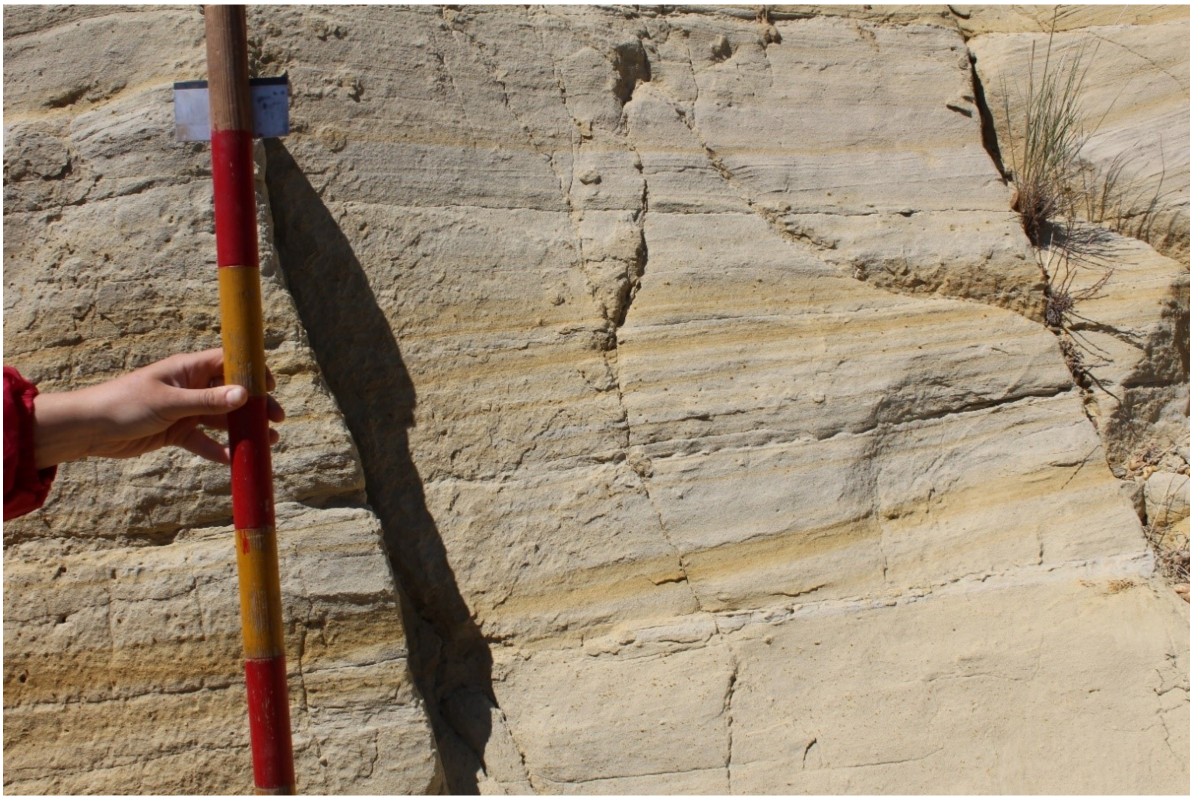

FIGURE 3-9. Don’s Sandstone 4 outcrop showing planar laminations.

FIGURE 3-10. Don’s Sandstone 4 outcrop showing cross bedding and root traces.

FIGURE 3-11. Cross-bedded sandstone intercalated with mud lenses in the Croc Pot East section.

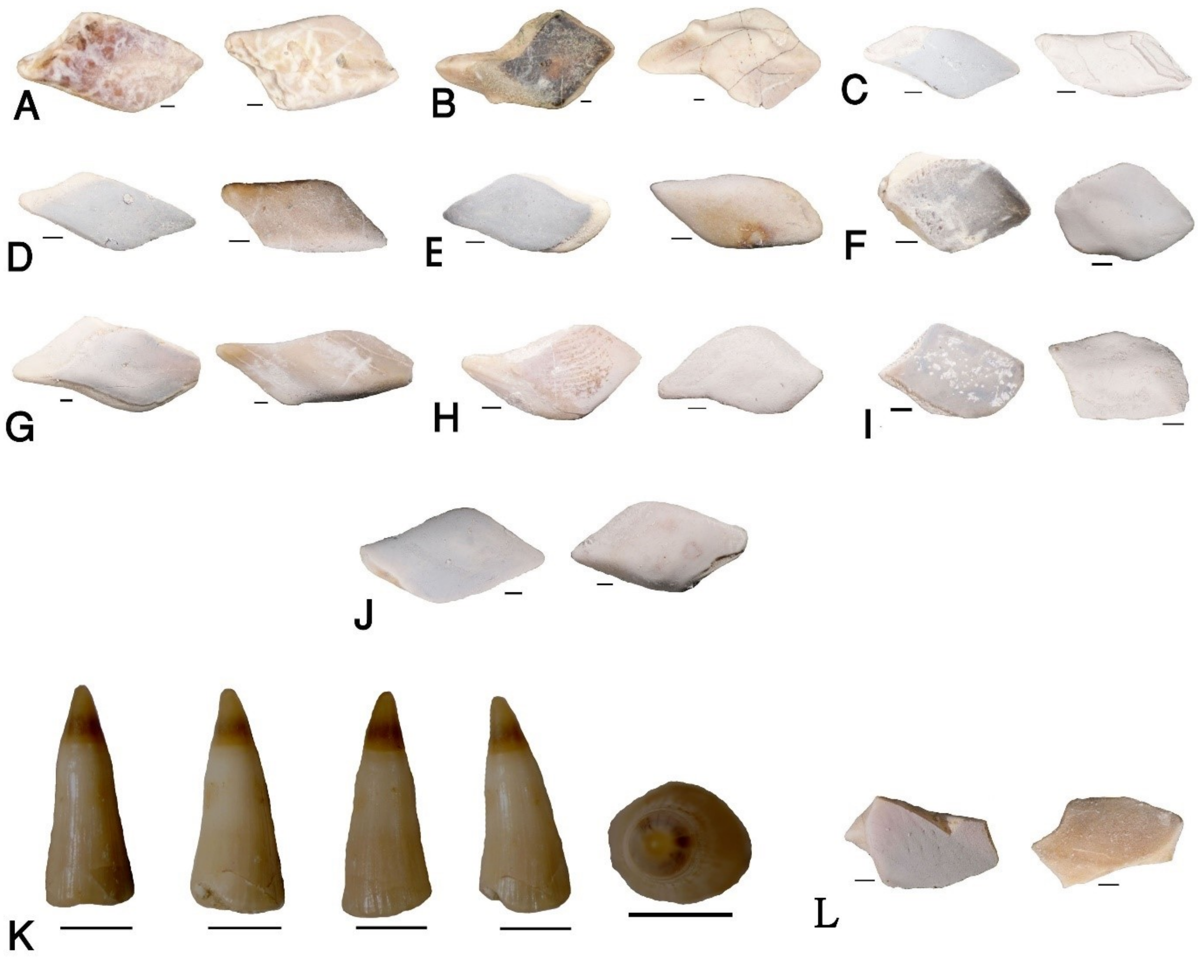

FIGURE 3-12. Croc Pot lepisosteid and holostean A scales in lateral and medial views. A, *Lepisosteus* scale (UALVP58727); B, *Lepisosteus* scale (UALVP58728); C, *Lepisosteus* scale (UALVP58729); D, *Lepisosteus* scale (UALVP58730); E, *Lepisosteus* scale (UALVP58731); F, *Lepisosteus* scale (UALVP58732), G, *Lepisosteus* scale (UALVP58733); H, *Lepisosteus* scale (UALVP58734); I, *Lepisosteus* scale (UALVP58735); J, *Lepisosteus* scale (UALVP58736); K, *Lepisosteus* teeth; L, unident. holostean A scale (UALVP58737). Scale bar equals to 2 mm.

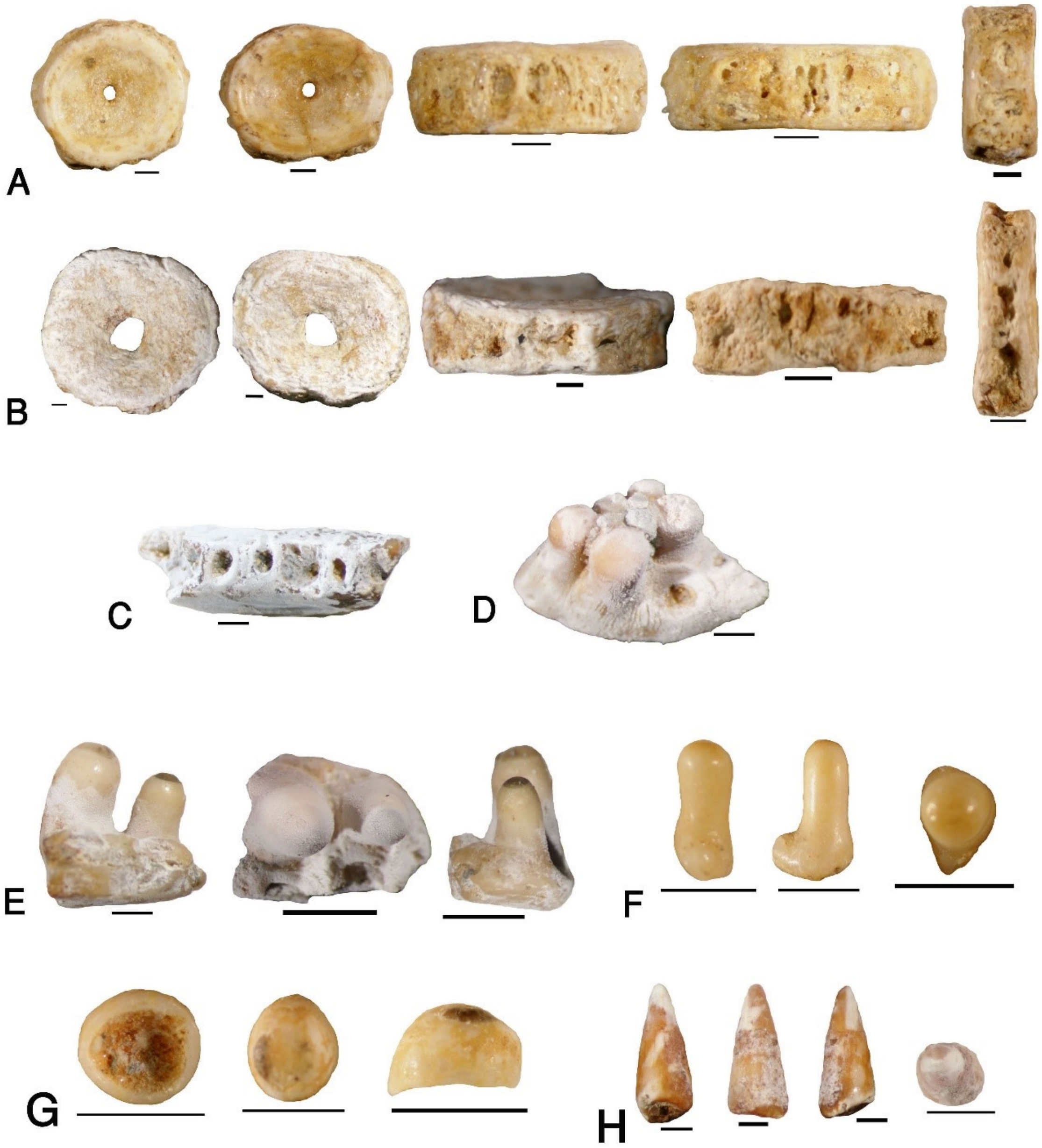

FIGURE 3-13. Croc Pot amiid centra, dentary, and teeth material. A-B, Amiidae caudal centra (UALVP58745-UALVP58744); C, Amiidae dentary in occlusal view (UALVP58739); D, *Cyclurus* sp. tooth plate fragment in anterior view UALVP58738); E-F, *Cyclurus* sp. anterior coronoid teeth from left to right in side and top views (UALVP58741- UALVP58742); G, *Cyclurus* sp. anterior coronoid teeth from left to right in bottom, top, and side views (UALVP58743); H, *Amia* sp. coronoid tooth from left to right in side and top views (UALVP58740). Centra are presented from left to right, in anterior, posterior, dorsal, ventral, and left lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

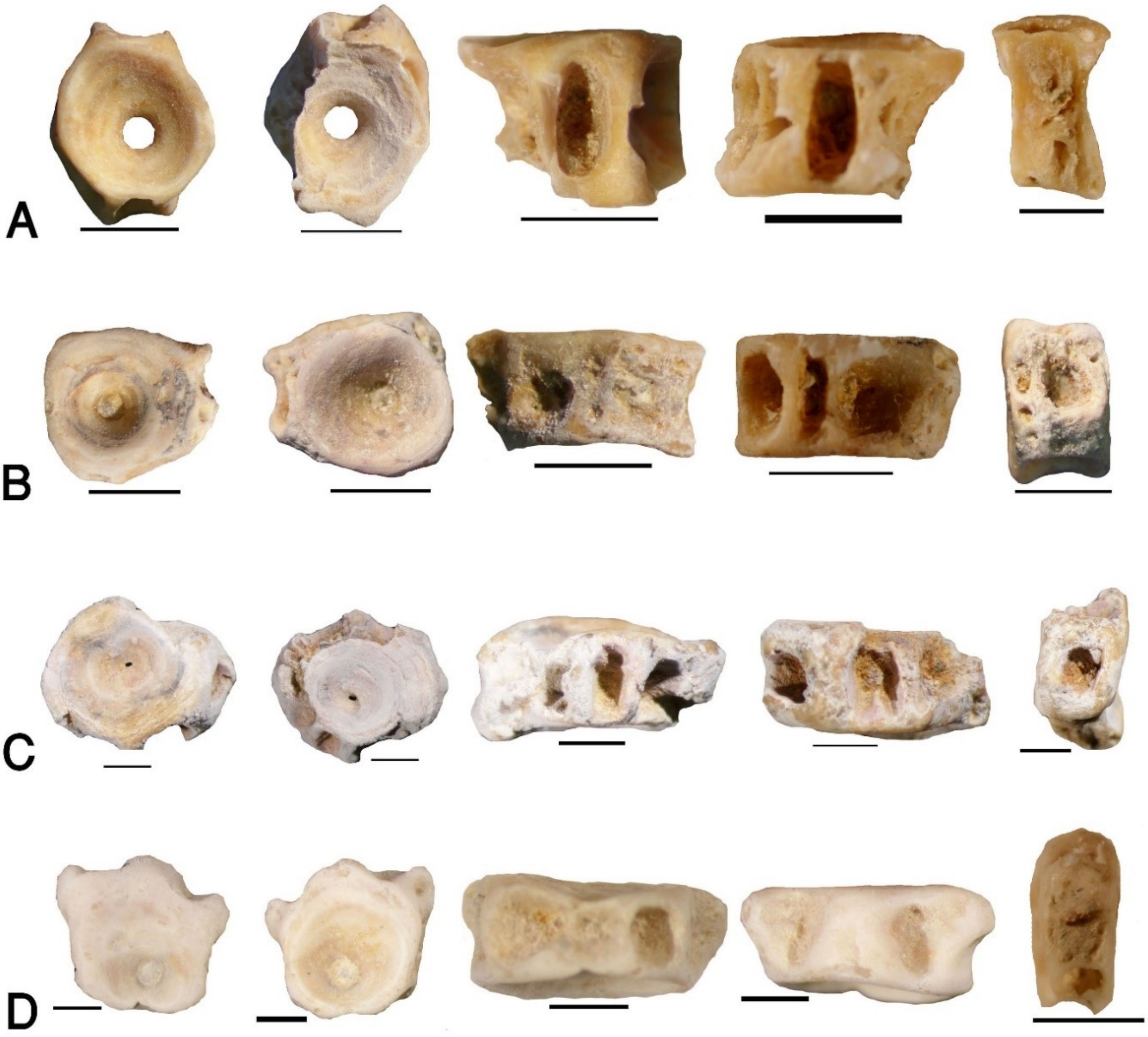

FIGURE 3-14. Croc Pot osteoglossomorph centra material. A, *Coriops* caudal centrum UALVP58747); B-C, *Coriops* centra (UALVP58748- UALVP58749); D, *Lopadichthyes* sp. centrum (UALVP58750). Centra are presented from left to right, in anterior, posterior, dorsal, ventral, and left lateral, views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

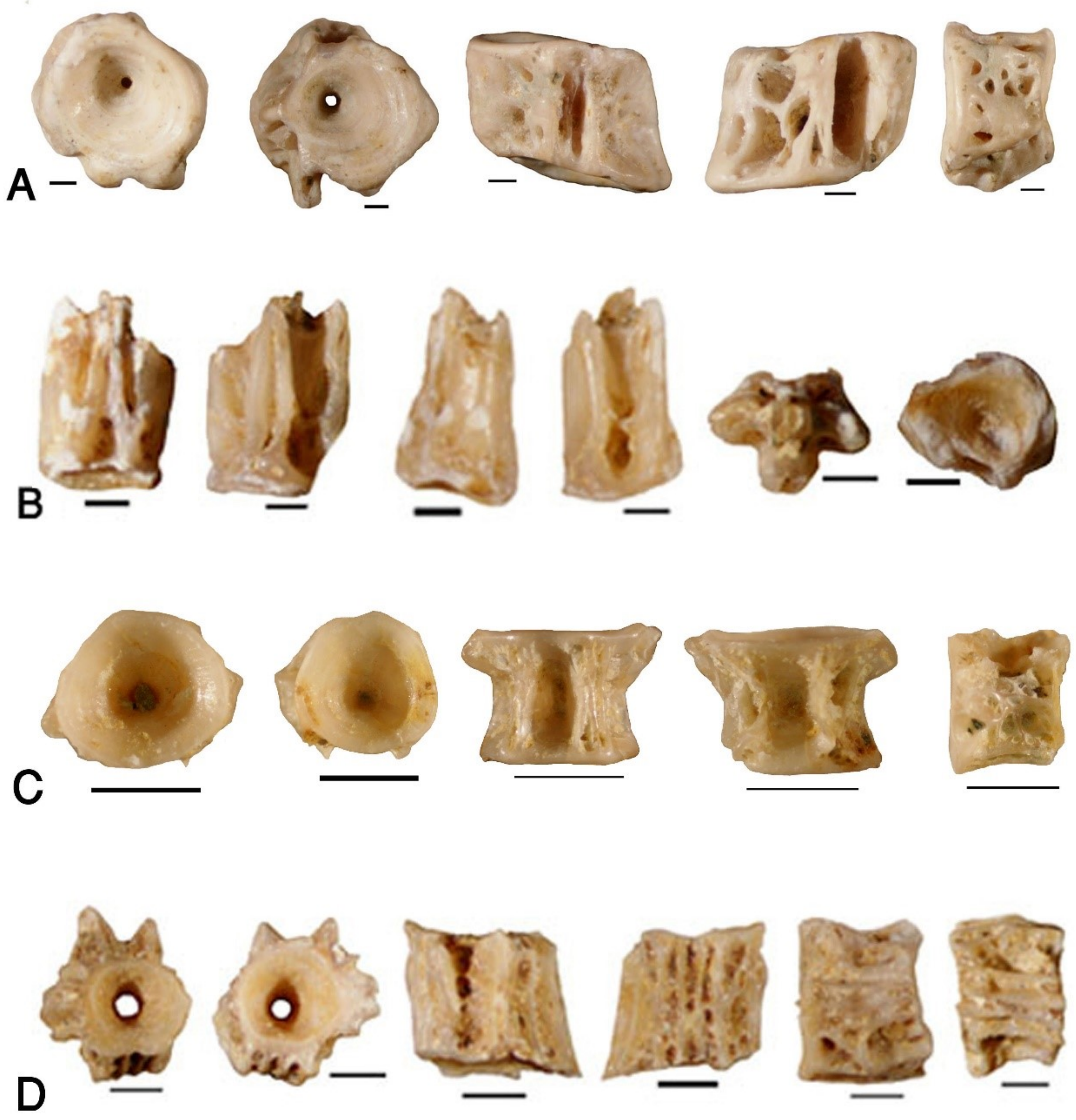

FIGURE 3-15. Croc Pot gonorhynchid centrum and basioccipital, acanthomorph, centra and unidentified teleost centra material A, Unidentified Gonorhynchidae centrum (UALVP58752); B, *Notogoneus* basioccipital (UALVP58753); C, Acanthomorph abdominal centrum (UALVP58746); D, unidentified teleost centrum (UALVP58751). The basioccipital is presented from left to right in ventral, dorsal, right lateral, left lateral, anterior, and posterior views. Centra are presented from left to right, in anterior, posterior, dorsal, ventral, and left lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

Chapter 4: Morphology of vertebral centra in the extant northern pike (*Esox lucius*)

INTRODUCTION

One of the most frequently documented micro vertebrate fish fossils are vertebral centra. They are quite robust, subcircular in shape, and are greater in quantity as compared to other delicate fish bones. Proper identification of these centra can greatly contribute to faunal analyses. However, they may differ in their morphology along the column even in the same species, which makes it difficult to assign them to a particular taxon. In addition to this, detailed study of the morphological variation of centra along the column has only been conducted on two orders of fishes, namely the Lepisosteiformes (Grande, 2010) and Amiiformes (Grande and Bemis, 1998). Because of this limited information, it becomes very challenging to study other commonly found fishes in microvertebrate localities. For example, the Northern pike, *Esox lucius* belonging to the order Esociformes is very common in Holoarctic fresh water, but a complete study on its vertebral column has never been done. Centra that are thought to belong to *Esox* sp. have been recovered from the late Paleocene Roche Percée locality of the Ravenscrag Formation (chapter 2) and apart from the ural caudal centra, the rest have been identified by referring to published literature (Divay and Murray, 2013) and consultation (Brinkman, 2018, personal communication). Probably there is no description of the two ural caudal centra of *Esox lucius* in the literature because they tend to look alike and have never been distinctly identified. According to Wilson (1984), Paleocene pikes do not differ much in structure from the extant pikes, hence, instead of consulting the literature, another approach towards the better identification of centra of *Esox lucius* would be to compare the fossil material to the extant material. Appropriate identification would allow the highly varied centra of *E. lucius* to be recognized and better incorporated in faunal analyses such as deciphering relative abundance, diversity, and distribution patterns. The ural caudal centra, being smaller in size than the other centra, could be preserved completely and also be transported for longer distances, thereby potentially aiding in better species recognition and depositional setting of adjacent basins. Hence, this study includes an examination of the complete vertebral column of an individual specimen of the extant *Esox lucius* (Specimen number UAMZ F8552) to document the changes in morphology of vertebrae along the column.

MATERIALS AND METHODS

The specimens are curated in the fish collections of the University of Alberta Museum of Zoology (UAMZ F). The studied specimen (UAMZ F8552) was compared to seven other specimens, namely UAMZ 4877, UAMZ 4879, UAMZ F9077, UAMZ F9078, UAMZ F9079, UAMZ F9080, and UAMZ F9102 of the same species to determine the consistency of morphological changes.

Every 5th centrum was studied and photographed. If a change was encountered on any particular 5th centrum, an attempt was made to discover the first centrum from the anterior end to undergo the change in morphology. Any centrum which marked the beginning of a morphological change along the column was then also studied and photographed. The centra were coated with ammonium chloride before photography to enhance the detail. Photographs in six different views (anterior, posterior, dorsal, ventral, left lateral, and right lateral) were taken for each of the centra. Photographs were taken with a Nikon DCM1200C camera mounted on a Zeiss Discovery V8 stereo microscope.

RESULTS

The centra were numbered from 1 to 62 from anterior to posterior end (Fig. 4-1 A and B). The first 42 centra in the studied specimen form the abdominal region, while centra 43 to 62 form the caudal region of the vertebral column. The vertebral column was 37.7 cm long from the anterior tip of centrum 1 to the posterior tip of centrum 62. The average height to width ratio of each centrum is 1.14. The centra in the entire column are almost rounded in anterior and posterior views, flattened in dorsal and ventral views, and appear elongated in the lateral views. A table (Table 4-1) summarizing the morphological changes in the column has been included. A generalized diagram (Fig. 4-2) showing the different components of pike vertebra is also included.

Abdominal region:

The centra in the abdominal region (Fig. 4-2 A) do not preserve all the neural arches. However, the presence of prominent neural arch pits confirms the fact that *E. lucius* does possess neural arches in this region. In the region, centra 1, 2, 3, 4, 10, 16, 17, 20, 21, and 40 mark the beginning of each morphological change and they are described in detail in the following section:

Centrum 1 (Fig. 4-3 A) **-** The anterior and posterior facets of the centrum are subcircular with a central notochordal foramen. The centrum is rectangular in dorsal and ventral views with slightly concave sides. It is elongated in lateral views with a concave anterior end. In the right lateral view, it is slightly depressed in the center. The neural arch pits are nearly oval in shape, centrally located, and are separated by a thick bony ridge.

Centrum 2 (Fig. 4-3 B) **-** The shape of centrum 2 is similar to that of centrum 1, except in the dorsal and ventral views, where the shape is rectangular with straighter sides as compared to concave sides of centrum 1. The neural arch pits are bigger and more rectangular in shape as compared to centrum 1. The parapophyseal pit is nearly circular in shape. The centrum is slightly depressed in the center and finer laminae run from left to right on both lateral sides.

Centrum 3 (Fig. 4-3 C) **-** The anterior and posterior facets of the centrum are almost circular in shape; but rectangular in dorsal, ventral and lateral views. The neural arch pits are nearly rectangular in shape and extend almost completely across the centrum. The two parapophyseal pits are separated by numerous closely spaced bony laminae running longitudinally.

Centrum 4 (Fig. 4-3 D) **-** The centrum has circular anterior and posterior facets; it is rectangular in dorsal, ventral and lateral views. The neural arch pits are oval to rectangular in shape and extend almost completely across the centrum. The evident change in centrum 4 from centrum 3 is on the ventral surface, where the network of finer bony laminae in the center is depressed. The parapophyseal pits are at the lateral ends.

Centrum 5 (Fig. 4-3 E) **-** This centrum was photographed, but no significant morphological change is observed from the previous centrum.

Centrum 10 (Fig. 4-4 A) **-** This centrum has almost rounded anterior and posterior facets and the circular notochordal passage is clearly seen. The centrum is nearly hourglass in shape in dorsal and ventral views in contrast to the rectangular shape of the preceding centrum. The lateral views of the centrum are rectangular with a concave dorsal end in the left lateral view. The neural arch pits are elongated. A thin bony lamina protrudes out towards the separating ridge from each of the neural arch pit walls. The network of thin bony laminae on the ventral surface is depressed in the center.

Centrum 15 (Fig. 4-4 B) **-** Centrum 15 was photographed, but no significant morphological change is observed.

Centrum 16 (Fig. 4-4 C) **-** The anterior and posterior facets of the centrum are subcircular but slightly flattened dorsally with a distinct centrally located notochordal foramen. The centrum is rectangular in other views with the exception of concavely curved at the posterior end in ventral view. The neural arch pits are slender, centrally located, and are separated by a thick bony ridge. A thin bony lamina protrudes out towards the separating ridge from each of the neural arch pit walls.

Centrum 17 (Fig. 4-4 D) **-** The anterior and posterior facets of the centrum are oval shaped and is slightly flattened dorsally. It is rectangular in both the lateral views and nearly hourglass shaped in dorsal and ventral views. A narrow thin bony lamina divides the left neural pit in half. The arrangement of bony laminae in ventral view is different from the preceding centra. It is depressed in the center and is bordered by longitudinally closely spaced thin bony ridges. The left and right parapophyseal pits are nearly circular in shape and centrally located.

Centrum 20 (Fig. 4-5 A) **-** The centrum has circular anterior and posterior facets and is nearly hourglass shaped in dorsal and ventral views. It is rectangular with concave dorsal and ventral ends in lateral views. The neural arch pits are slender. The distinct difference from the preceding centrum is observed in the ventral and lateral sides. There are no longitudinal thin bony ridges on the ventral side, instead the finer bony laminae are merged into one another surrounding the parapophyseal pits. In the lateral sides, the neural arch pits and one of the parapophyseal pits are irregularly shaped and are separated by a thick complex of bony laminae.

Centrum 21 (Fig. 4-5 B) **-** The anterior and posterior facets of the centrum are circular with a central notochordal foramen. The dorsal and ventral facets are hourglass, and the lateral facets are rectangular. The bony lamina protruding out is a deformity in this specimen. The neural pit is irregular in shape and slightly narrower posteriorly. Both the neural arch and the parapophyseal pits in the lateral views are located dorsally and ventrally.

Centra 25 (Fig. 4-5 C), **30** (Fig. 4-5 D), and **35** (Fig. 4-5 E) were photographed but no significant morphological changes are observed in these centra. The morphology of centra 21 to 39 is the same.

Centrum 40 (Fig. 4-5 F) **-** The anterior and posterior facets of the centrum are circular. The dorsal and ventral facets are hourglass, and the lateral facets are nearly rectangular. The neural arch pits are separated by a narrow bony ridge with a slit on it. The neural arch pits are divided in half by a thin inwardly pointing lamina. The two irregularly shaped parapophyseal articular pits are located dorsally and ventrally and visible in the lateral views. One of the neural arch pits and one of the parapophyseal pits are separated by thick network of bony laminae.

Caudal region (Fig. 4-6)**-**

Centra 43 to 60 form the caudal region. All the centra in this region bear neural arches and neural spines as well as haemal arches and haemal spines. The spines of centra 56 to 60 are not present in the studied specimen because of lack of preservation. But these five centra do possess the spines which is confirmed from the prominent neural and haemal arch pits. Changes in morphology are observed in centra 43, 45, 47, 50, 54, 56, and 60. The changes are described below:

Vertebra 43 (Fig. 4-7 A) **-** The centrum of this vertebra has circular anterior and posterior facets with a central notochordal foramen. It is hourglass shaped in dorsal and ventral views and is rectangular in both the lateral views. The neural arch project dorsally and fuse to form the spine. The haemal arches project ventrally; however, in this specimen they are broken and the haemal spine is not preserved. The ventral facet of the centrum is formed of a complex of finer bony laminae in between the haemal arch. The dorsal anterior as well as posterior zygapophyses are visible dorsally in the left lateral view. A complex of bony laminae forms the centrum in both lateral views.

Vertebra 45 (Fig. 4-7 B) **-** The shape of the vertebra is similar to that of the preceding centrum, except for the characteristics mentioned hereafter. The haemal spine is nearly half the size of the neural spine. In the dorsal and ventral views, finer bony laminae cover (or forms) the depressed area between the neural and haemal spines. The bone on the lateral sides of the centrum is made up of a finer complex of laminae. The dorsal anterior and posterior zygapophyses are located dorsally in left lateral view.

Vertebra 47 (Fig. 4-7 C) **-** The centrum has circular anterior and posterior facets with a central notochordal foramen. Although the shape in dorsal and ventral view is almost hourglass, the length and breadth of the centrum is almost the same, hence, the centrum looks square in both the lateral views. The spines of this centrum are equal in length. Only the dorsal posterior zygapophysis is visible at dorsally in left lateral view. The sizes of the following centra become smaller.

Vertebra 50 (Fig. 4-7 D) **-** The shape of this vertebra is the same as the preceding vertebra, with no significant change in centrum morphology except for the following: The spines in this vertebra are equal in length but are thicker than the preceding one. The transverse processes are projecting out of the centrum and are very prominent in both the dorsal and ventral views. There is a complex of bony laminae in between the bases of the neural and haemal spines. Both the dorsal anterior as well as the dorsal posterior zygapophyses are visible on the dorsal end in the left lateral view. Only the ventral anterior zygapophysis is prominent at the ventral end in the left lateral view. The entire centrum comprises of a complex of finer bony laminae in both the lateral views.

Vertebra 54 (Fig. 4-7 E) **–** The anterior and posterior facets of the centrum are circular with a central notochordal foramen. The centrum is hourglass in shape in dorsal and ventral views and is rectangular in lateral views. The neural arch is longer and thinner than the haemal arch. There is no complex of bony laminae between the bases of the neural and haemal spines as is present in the preceding caudal centra. The entire centrum is formed of a complex of finer bony laminae in both the lateral views.

Vertebra 55 (Fig. 4-8 A) **-** No significant morphological changes are observed in this centrum compared to the previous one.

Centrum 56 (Fig. 4-8 B) - The centrum has sub circular anterior and posterior facets and is square shaped in dorsal, ventral and both the lateral views. The neural arch pits are separated by a narrow bony ridge which has perforations in it. The ridge separating the two haemal arch pits has a narrow slit on it. The neural arch pit and haemal arch pit are visible in both lateral views. These two pits and interconnected finer bony laminae make up the center of the centrum.

Centrum 60 (Fig. 4-8 C) **-** The centrum has oval anterior and posterior facets and has the notochordal foramen in the center. The neural arch pits and the haemal arch pits run from anterior to posterior edges of the centrum. The right haemal arch pit is slightly triangular in shape. The lateral facets of the centrum are formed of densely spaced interconnected bony laminae, giving a spongy appearance. The spongy texture is more prominent in the left lateral facet versus the right lateral facet of the centrum.

Ural region-

In the studied specimen, there are two ural centra (centra 61 and 62) and both of them differ morphologically. Only the centrum is preserved in these two caudal vertebrae.

Centrum 61 (Fig. 4-8 D) **-** The centrum has a nearly oval anterior facet and the notochordal foramen is slightly above the center. The centrum has an almost circular posterior facet and the notochordal foramen sits on a bulge in the center. It is hourglass shaped in the dorsal and ventral views. The uroneural articulating pit which looks like a circular depression covers the entire dorsal surface. A fine network of bony laminae covers the entire ventral surface, giving it a spongy texture. The centrum is trapezoid in shape in lateral views, with the center being depressed. It is irregular dorsally, and slightly depressed ventrally in left lateral view. The centrum is slightly depressed ventrally in the left lateral view. A complex of fine bony laminae covers the centrum in the right lateral view giving a spongy appearance.

Centrum 62 (Fig. 4-8 E) **-** The anterior facet of the centrum is circular in shape with irregular edges, posteriorly it is nearly trapezoid, and it is completely trapezoid in dorsal and ventral views. The uroneural articular pit is a circular depression and covers the entire dorsal view. The hypural articular pits on the ventral surface runs across the centrum. Both the lateral surfaces of the centrum have a spongy appearance due to the densely spaced network of bony laminae. The dorsal edge in both the lateral views is irregular.

DISCUSSIONS

There are 19 significant morphological changes documented along the entire length of the vertebral column. The first four centra are significantly different from one another and these changes were observed in all specimens examined (for example, Fig. 4-9).

The comparative specimen UAMZ F9102 (Fig. 4-10) showed morphological changes in the same centra positions to that of the studied specimen except for the 34th position (Fig. 4-11 and Fig.4-12). The type of morphological changes which are encountered in centrum 40 in the studied specimen UAMZ F8552 are observed in centrum 34 in the comparative specimen (UAMZ F9102). Thus, centra 40, 41 and 42 in the studied specimen UAMZ F8552 look similar to centra 34, 35,36, 37, 38, 39, and 40 in the comparative specimen UAMZ F9102. The shape, size, and morphological changes encountered in centrum 41 to 44 in specimen UAMZ F9102 are exactly the same as those of centrum 43 and 44 in the studied specimen and the same pattern continues.

The variation among specimens means that I cannot identify a single fossil vertebra to a particular position in the column, but I can identify them to which region of the vertebral column it belongs to.

The result of this study demonstrates the morphological changes in the vertebral column of *Esox lucius*. This is the first study which provides information and detailed descriptions about morphological changes in centra along the column in *E. lucius*. From this study, I have documented that two centra which look different from one another could in fact belong to the same species. Previous descriptions of the centra of *E. lucius* have focused on abdominal and non-ural caudal centra (for example, Divay and Murray, 2013) presumably because of lack of proper identification of ural centra. However, in this study ural centra of *E. lucius* have been described and henceforth, could be used in faunal analyses.

Micro vertebrate fossil concentrations are usually the result of deposition during the high velocity flooding phase of a river. Robust pike centra, including the ural centra, can better survive the high velocity depositional phase than more delicate fish bones. This better preservational potential ensures that centra are abundantly found and thus makes them excellent elements for potential identification. There is a high likelihood that these fossils could get transported to adjacent basins and so they may be important for resolving geographical and temporal biases. Additionally, faunal mixing is a common phenomenon in micro vertebrate localities; therefore, knowledge of the variable morphology of individual centra of *Esox lucius*, as provided in this chapter, will allow these elements to be confidently sorted from mixed and diverse micro vertebrate fossil assemblages.

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TABLE

Table 4-1. A table summarizing the morphological changes in the column.

Number	Anterior	Posterior	Dorsal	Ventral	Left Lateral	Right Lateral
1	Sub circular	Sub circular	Rectangular with concave sides; neural arch pits are oval and separated by thick bony ridge	Rectangular with concave sides	Elongated with concave anterior end	Elongated with concave anterior end; depressed in the centre
2	Sub circular	Sub circular	Rectangular with straight sides; neural arch pits relatively bigger and more rectangular	Rectangular with straight sides; parapophyseal pit is subcircular	Slightly depressed in the center and finer laminae run from left to right.	Slightly depressed in the center and finer laminae run from left to right.
3	Almost circular	Almost circular	Rectangular ; neural arch pits are nearly rectangular and extend almost completely across the centrum	Rectangular ; the two parapophyseal pits are separated by numerous closely spaced bony laminae running longitudinally	Rectangular	Rectangular
4	Circular	Circular	Rectangular ; neural arch pits are oval to rectangular in shape and extend almost completely	Rectangular ; the network of finer bony laminae in the center is depressed; parapophyseal pits are	Rectangular	Rectangular

			across the centrum	at the lateral ends		
10	Almost rounded	Almost rounded	Hourglass; neural arch pits are elongated; a thin bony lamina protrudes out towards the separating ridge from each of the neural arch pit walls	The network of thin bony laminae is depressed in the center	Rectangular with concave dorsal end	Rectangular
16	Sub circular with flattened dorsal end	Sub circular with flattened dorsal end	Rectangular; neural arch pits slender, centrally located, and separated by a thick bony ridge; a thin bony lamina protrudes out towards the separating ridge from each of the neural arch pit walls.	Rectangular with concave posterior end	Rectangular	Rectangular
17	Oval with flattened dorsal end	Oval with flattened dorsal end	Hourglass; a narrow thin bony lamina divides the left neural pit in half	Hourglass; arrangement of bony laminae is depressed in the center and bordered by longitudinally closely spaced thin bony ridges; the left and right parapophyseal pits are	Rectangular	Rectangular

				nearly circular in shape and centrally located		
20	Circular	Circular	Rectangular; neural arch pits are slender	Rectangular; there are no longitudinal thin bony ridges instead the finer bony laminae are merged into one another surrounding the parapophyseal pits	Rectangular with concave dorsal end; neural arch pits and one of the parapophyseal pits irregularly shaped and separated by a thick complex of bony laminae.	Rectangular with concave dorsal end; the neural arch pits and one of the parapophyseal pits irregularly shaped and separated by a thick complex of bony laminae.
21	Circular	Circular	Hourglass; neural pit is irregular in shape and slightly narrower posteriorly	Hourglass	Rectangular; neural arch and parapophyseal pits located dorsally and ventrally.	Rectangular; neural arch and the parapophyseal pits located dorsally and ventrally.
40	Circular	Circular	Hourglass; neural arch pits divided in half by a thin inwardly pointing lamina.	Hourglass	Rectangular; two irregularly shaped parapophyseal pits located dorsally and ventrally and visible; one of the neural arch pits and one of the parapophyseal pits are separated by thick network of	Rectangular; two irregularly shaped parapophyseal pits are located dorsally and ventrally and visible; one of the neural arch pits and one of the parapophyseal pits are separated by thick network of

					bony laminae.	bony laminae.
43	Circular	Circular	Hourglass	Hourglass; complex of finer bony laminae in between the haemal arch	Rectangular; dorsal anterior as well as posterior zygapophyses are visible dorsally; complex of bony laminae present	Rectangular; complex of bony laminae present
45	Circular	Circular	Hourglass; finer bony laminae covers the depressed area between the neural spines	Hourglass; finer bony laminae covers the depressed area between the haemal spines	Rectangular; a finer complex of laminae; dorsal anterior and posterior zygapophyses are located dorsally	Rectangular; a finer complex of laminae
47	Circular; spines of this centrum are equal in length	Circular; spines of this centrum are equal in length	Hourglass	Hourglass	Square; dorsal posterior zygapophysis is is visible at dorsally	Square
50	Circular; spines in this vertebra are equal in length but are thicker than the preceding vertebra	Circular; spines in this vertebra are equal in length but are thicker than the preceding vertebra	Hourglass; prominent transverse processes projecting out of the centrum; complex of finer laminae between the bases of the neural spines	Hourglass; prominent transverse processes projecting out of the centrum; complex of finer laminae between the bases of the haemal spines	Square; complex of finer bony laminae; dorsal anterior as well as the dorsal posterior zygapophyses are visible on the dorsal end; ventral anterior zygapophysis is prominent	Square; complex of finer bony laminae

					at the ventral end	
54	Circular; neural arch is longer and thinner than the haemal arch	Circular; neural arch is longer and thinner than the haemal arch	Hourglass; no complex of bony laminae between the bases of the neural spines	Hourglass; no complex of bony laminae between the bases of the haemal spines	Square; complex of finer bony laminae	Square; complex of finer bony laminae
56	Sub circular	Sub circular	Square; neural arch pits (covering the centrum) separated by a narrow bony ridge which has perforations in it	Square; haemal arch pits covers the centrum; ridge separating the two haemal arch pits has a narrow slit on it	Square; neural arch pit and haemal arch pit are visible	Square; neural arch pit and haemal arch pit are visible
60	Oval	Oval	Hourglass; neural arch pits run from anterior to posterior edges of the centrum	Hourglass; haemal arch pits run from anterior to posterior edges of the centrum; right haemal arch pit is slightly triangular in shape	Rectangular ;more densely spaced inter-connected bony laminae, giving a spongy appearance	Rectangular ; densely spaced inter-connected bony laminae, giving a spongy appearance
61	Oval	Oval	Hourglass; circular depressing uroneural pit	Hourglass; fine network of bony laminae giving a spongy texture	Trapezoid (depressed in the centre); irregular dorsally, and slightly depressed ventrally	Trapezoid (depressed in the centre); complex of fine bony laminae giving a spongy appearance

FIGURES

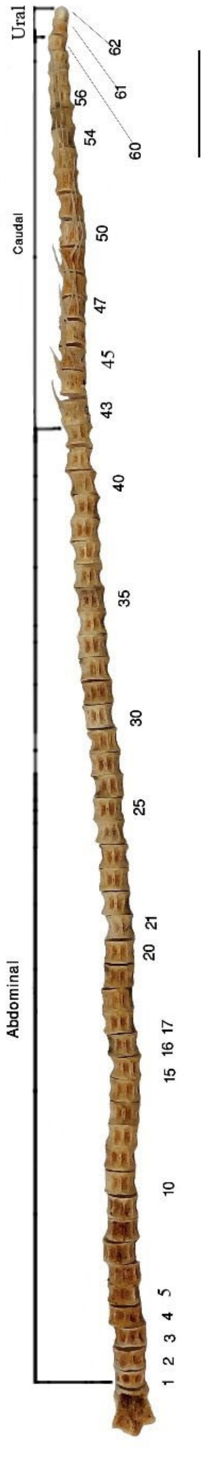


FIGURE 4-1 A. *Esox lucius* skeleton (UAMZ F8552) in dorsal view demarcating the different regions. The centra showing the morphological changes (centra number 1, 2, 3,4, 10, 16, 17, 20, 21, 40, 43, 45, 47, 50, 54, 56, 60, 61, and 62) are indicated. Scale bar equals 3 cm.

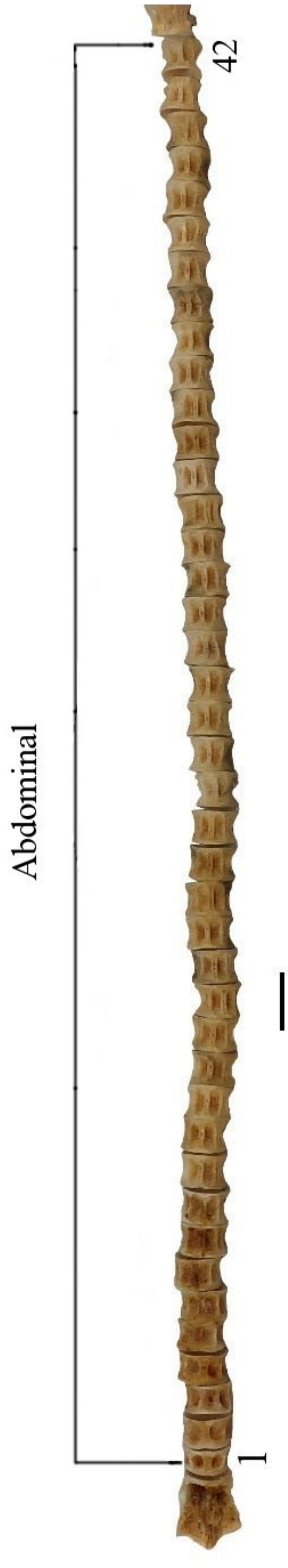
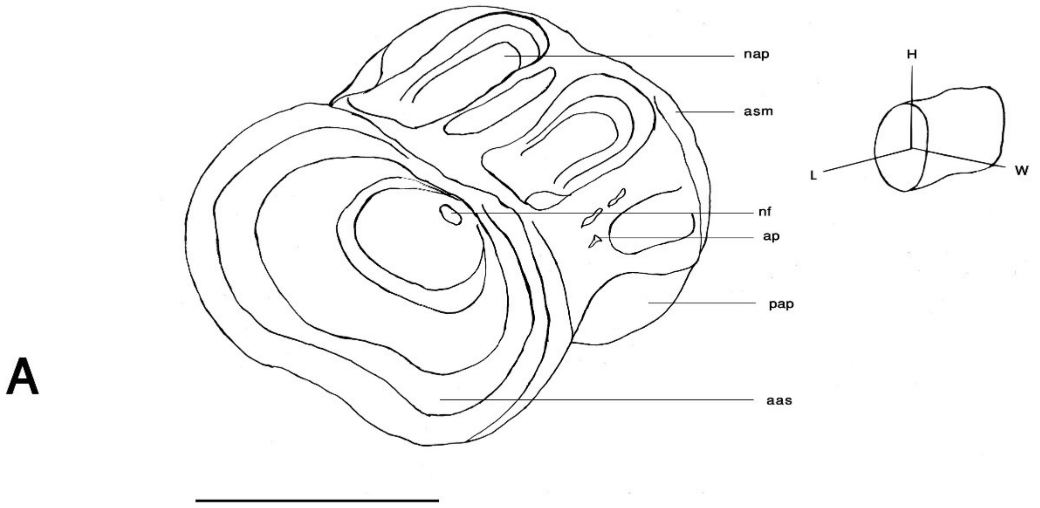


FIGURE 4-1 B. Abdominal region of the vertebral column (UAMZ F8552) in dorsal view. Scale bar equals 1 cm.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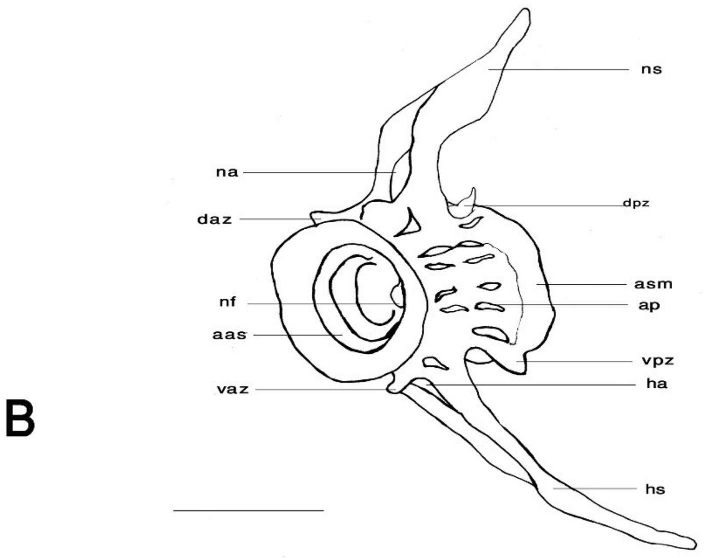
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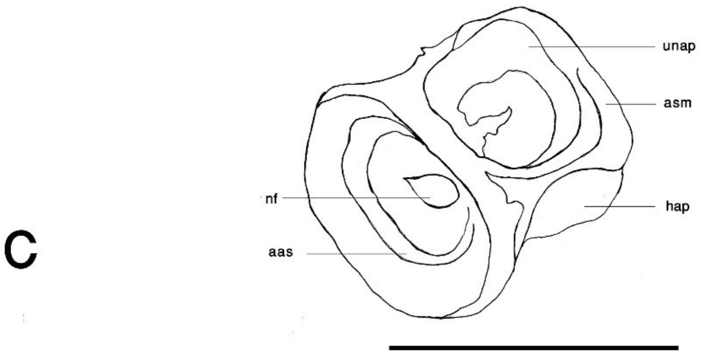
unap
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FIGURE 4-2. Generalized diagram showing different components of a pike vertebra. A, anterior abdominal centrum; B, caudal centrum; C, ural centrum. Abbreviations: aas, anterior articular surface; ap, accessory pitting; asm, articular surface margin; daz, dorsal anterior zygapophysis (= prezygapophysis); dpz, dorsal posterior zygapophysis (= postzygapophysis); H, height; ha, haemal arch; hap, hypural articular pit; hs, haemal spine; L, length; na, neural arch; nap, neural arch pit; nf, notochordal foramen; ns, neural spine; p, parapophysis; pap, parapophyseal articular pit; unap, uro neural articular pit; vaz, ventral anterior zygapophysis (= prezygapophysis); vpz, ventral posterior zygapophysis (= postzygapophysis); W, width. Note: surface bony texture is omitted for clarity. Scale bar equals 0.5 cm. The diagram showing the L, H and W is not to scale.

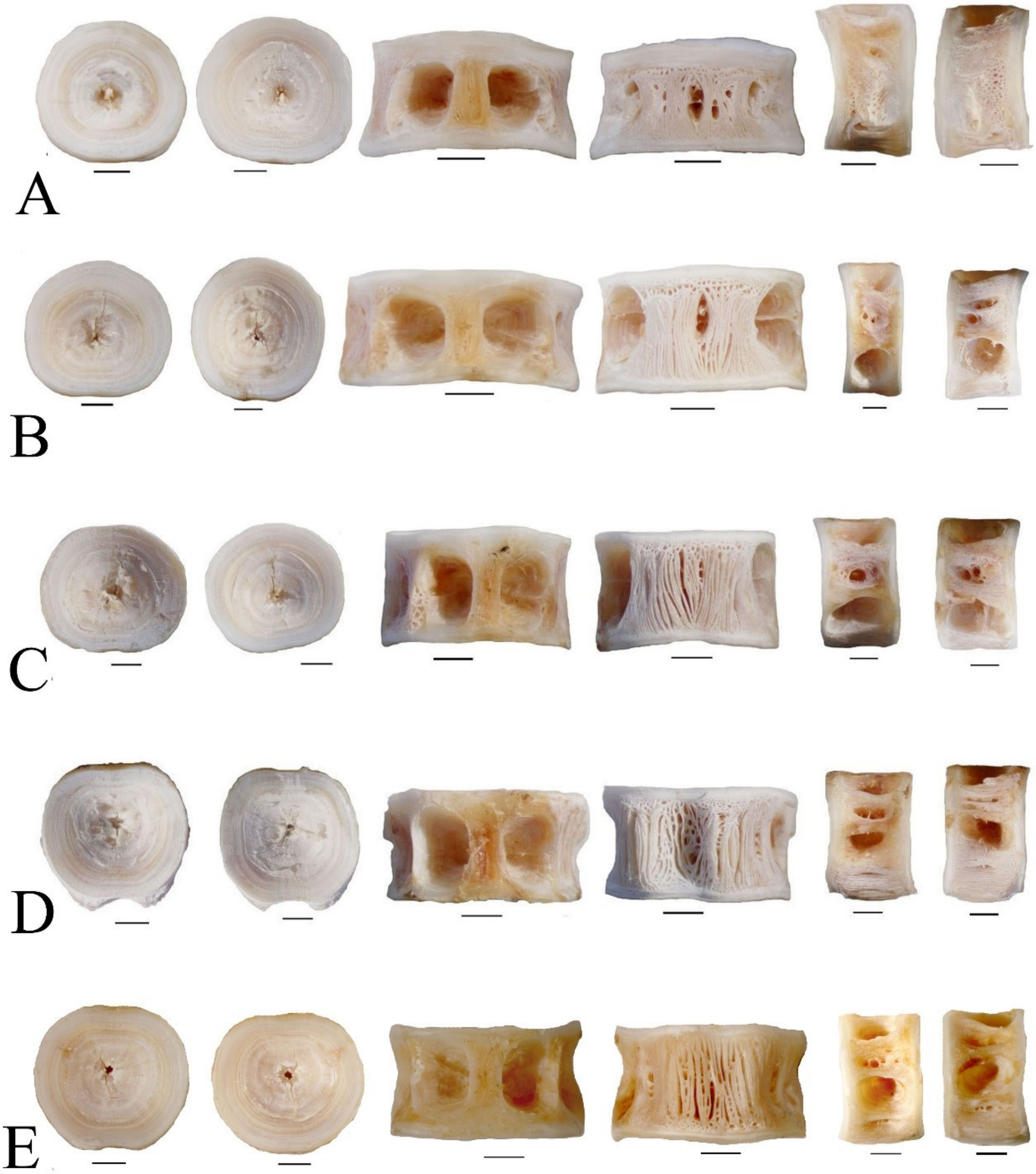

FIGURE 4-3. *Esox lucius* abdominal centra (UAMZ F8552). A, Centrum 1; B, Centrum 2; C, Centrum 3; D, Centrum 4; E, Centrum 5. Centra are presented from left to right, in anterior, posterior, dorsal, ventral, left lateral and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

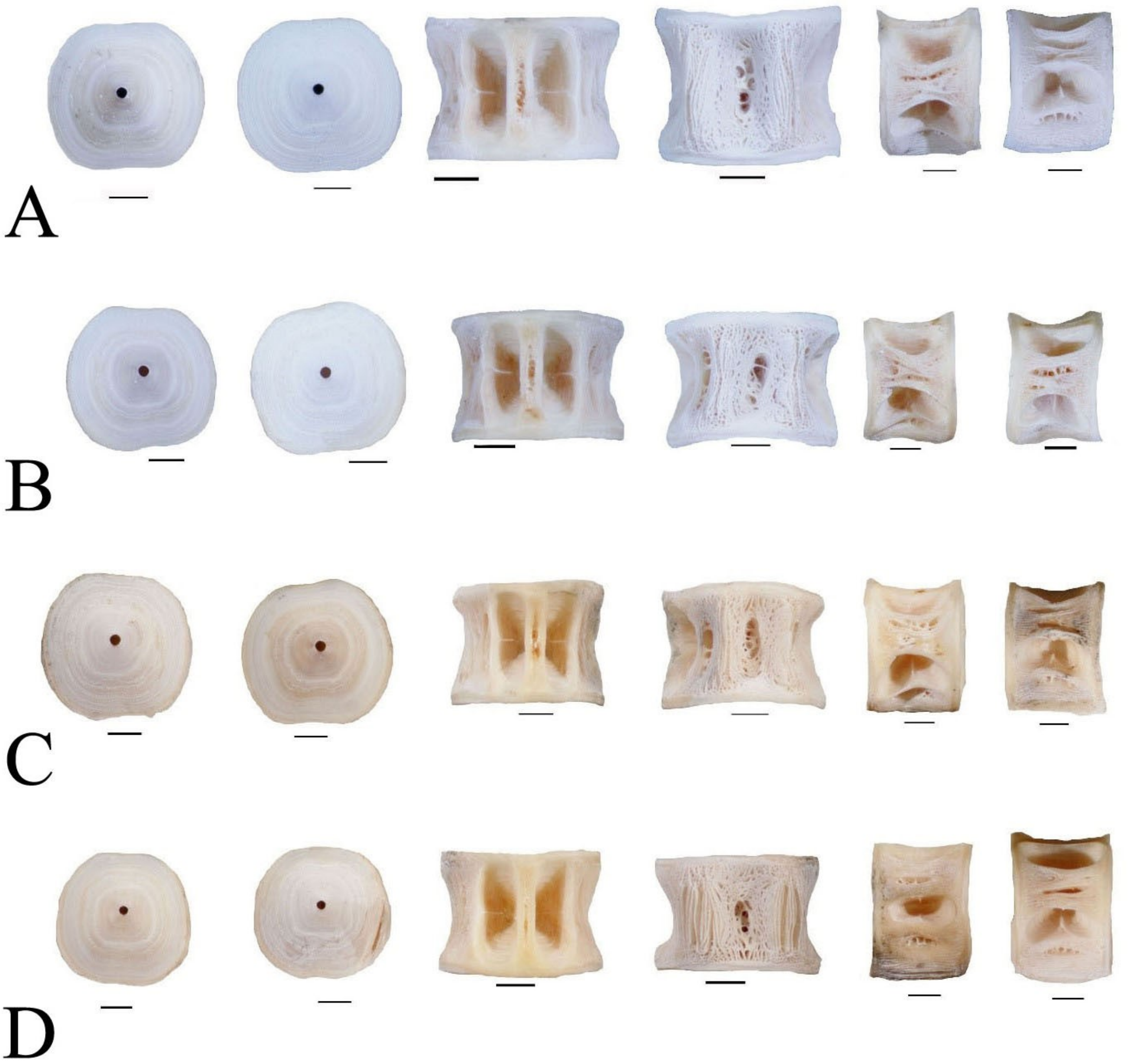

FIGURE 4-4. *Esox lucius* abdominal centra (UAMZ F8552). A, Centrum 10; B, Centrum 15; C, Centrum 16; D, Centrum 17. The centra are presented from left to right in anterior, posterior, dorsal, ventral, left lateral and right lateral views; for lateral views, dorsal is towards the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

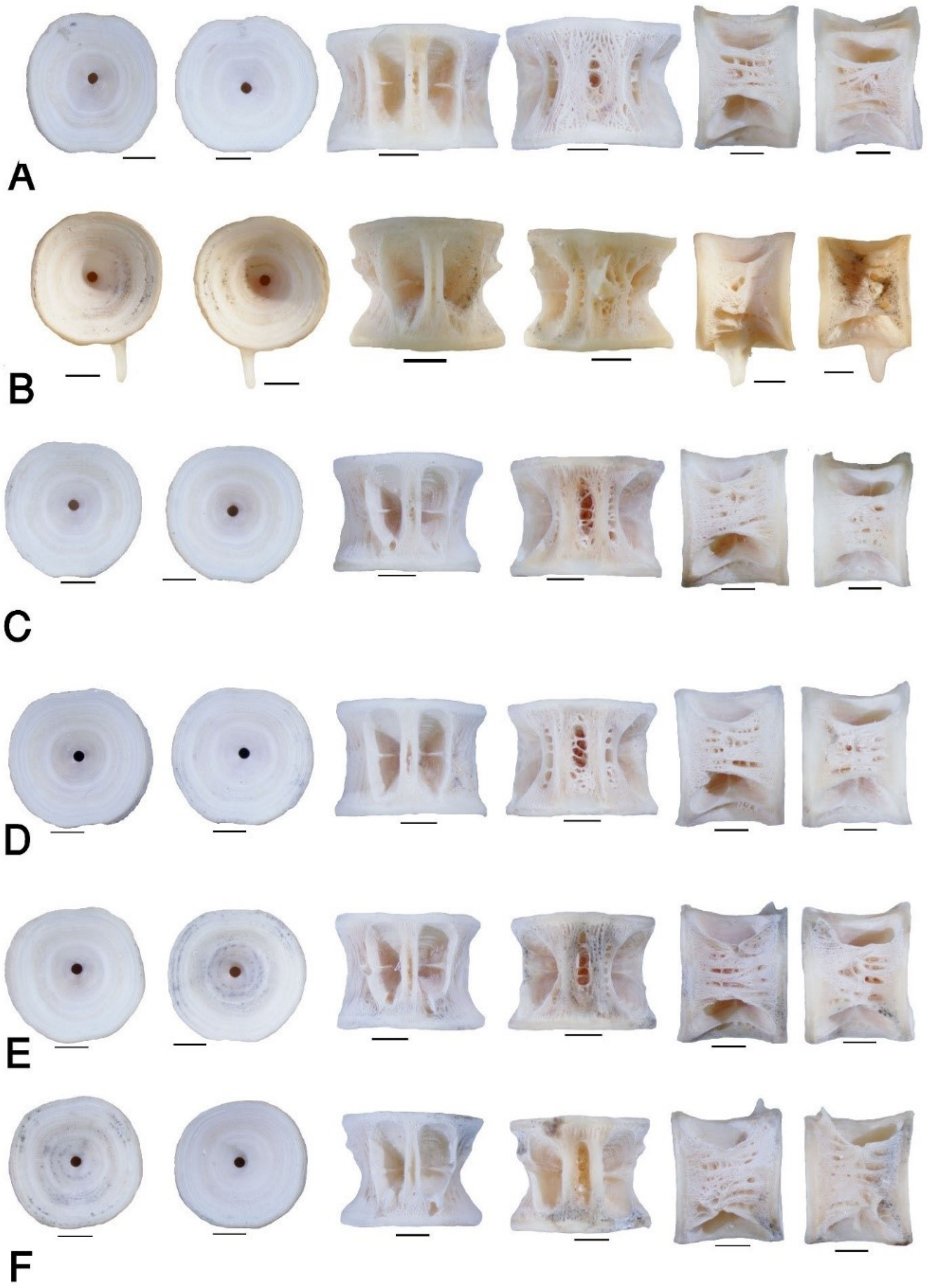

FIGURE 4-5. *Esox lucius* abdominal centra (UAMZ F8552). A, Centrum 20; B, Centrum 21; C, Centrum 25; D, Centrum 30; E, Centrum 35; F. Centrum 40; Centra are presented from left to right in anterior, posterior, dorsal, ventral, left lateral and right lateral views; for lateral views, dorsal is to the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

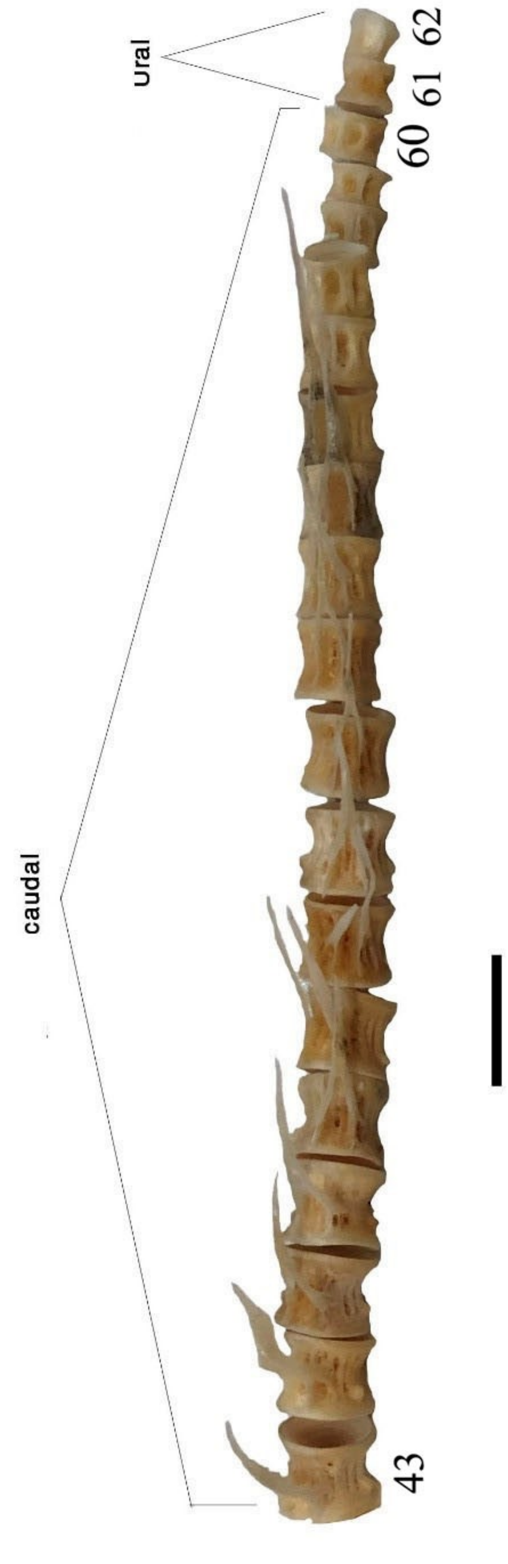

FIGURE 4-6. The caudal and ural vertebrae of the vertebral column (UAMZ F8552) in dorsal view. Scale bar equals 1 cm.

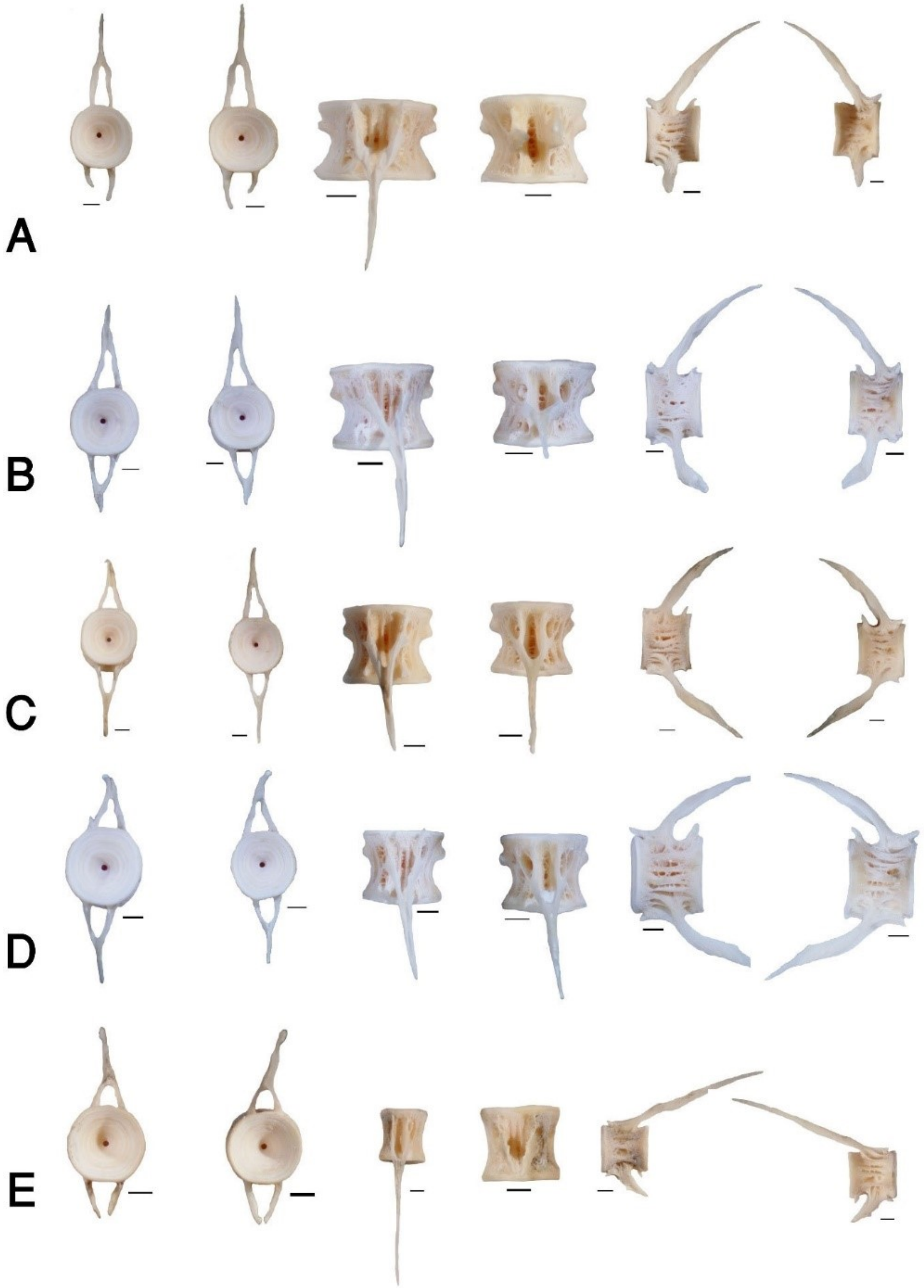

FIGURE 4-7. *Esox lucius* caudal centra (UAMZ F8552). A, Vertebra 43; B, Vertebra 45; C, Vertebra 47; D, Vertebra 50; E, Vertebra 54. Centra are presented from left to right in anterior, posterior, dorsal, ventral, left lateral and right lateral views; for lateral views, dorsal is to the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

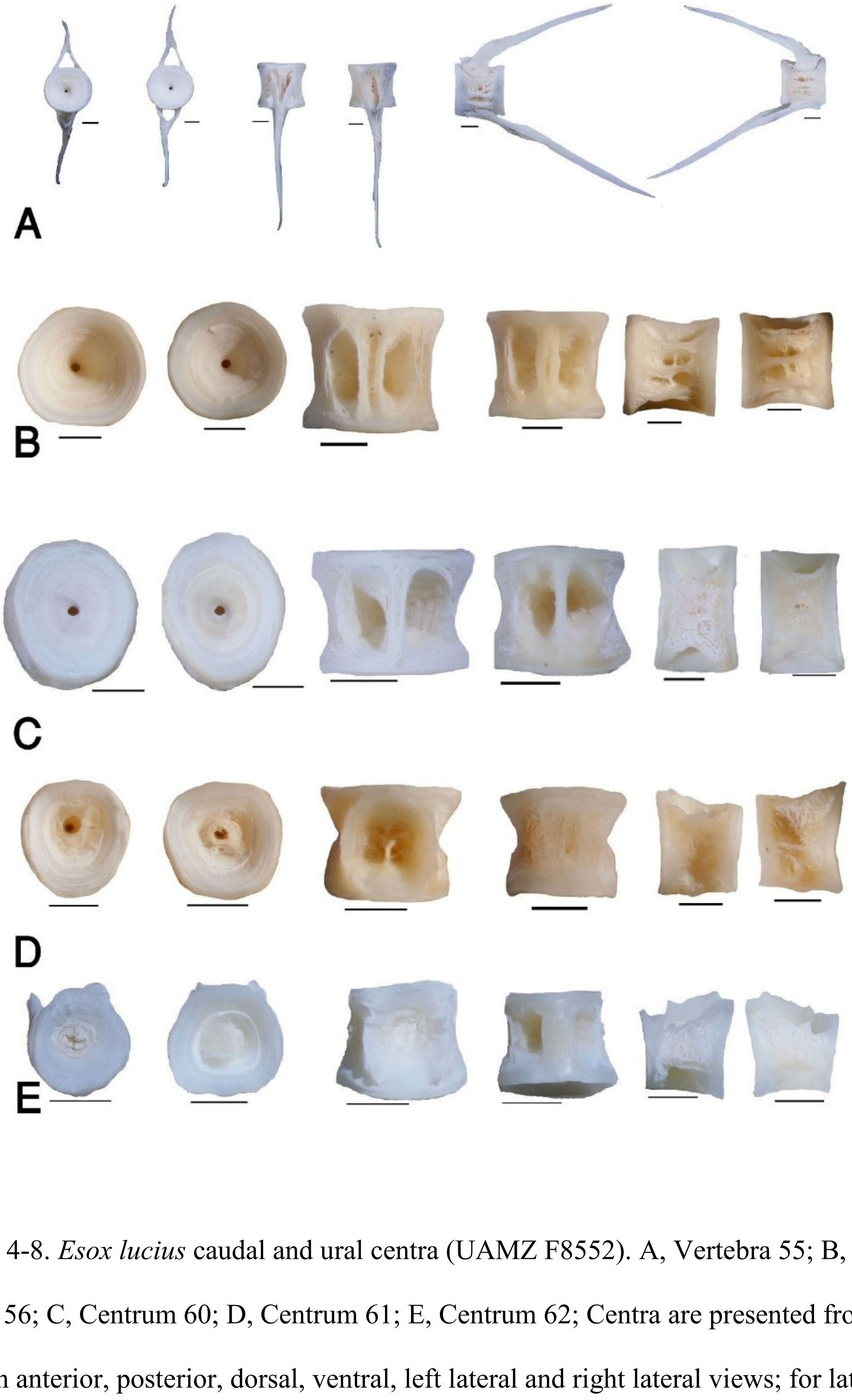

FIGURE 4-8. *Esox lucius* caudal and ural centra (UAMZ F8552). A, Vertebra 55; B, Centrum 56; C, Centrum 60; D, Centrum 61; E, Centrum 62; Centra are presented from left to right in anterior, posterior, dorsal, ventral, left lateral and right lateral views; for lateral views, dorsal is to the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

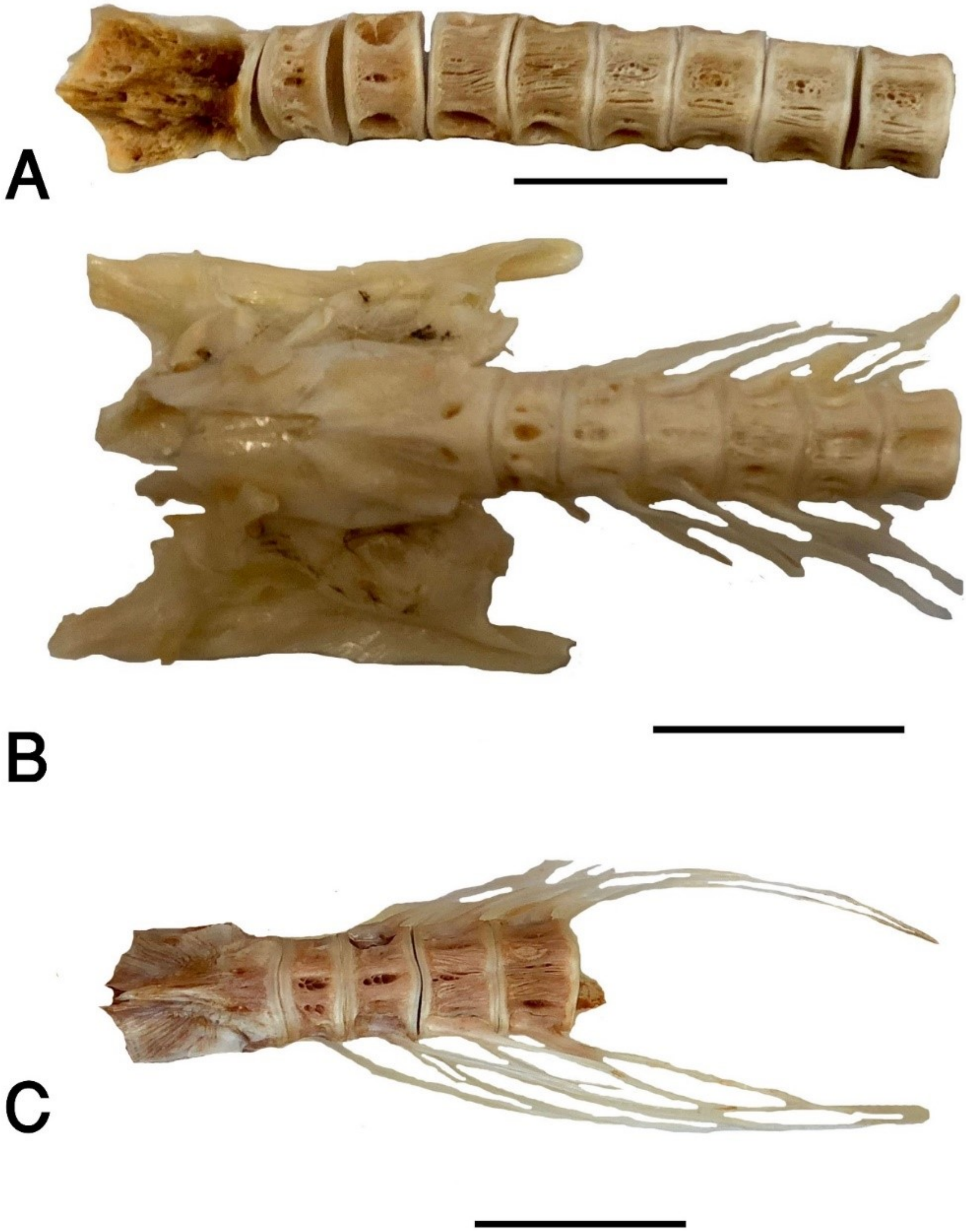

FIGURE 4-9. Comparison of the first 4 abdominal vertebrae (ventral view) of vertebral column of *Esox lucius*. Scale bar equals 2cm. A, studied specimen (UAMZ F8552); B, comparative specimen (UAMZ F4879); C, comparative specimen (UAMZ F4877).

FIGURE 4-10. Comparative specimen of *Esox lucius* (UAMZ F9102) in ventral view. Scale bar equals 3 cm.

FIGURE 4-11. Comparative specimen of *Esox lucius* (UAMZ F9102) in ventral view. Scale bar equals 2 cm (missing anterior portion).

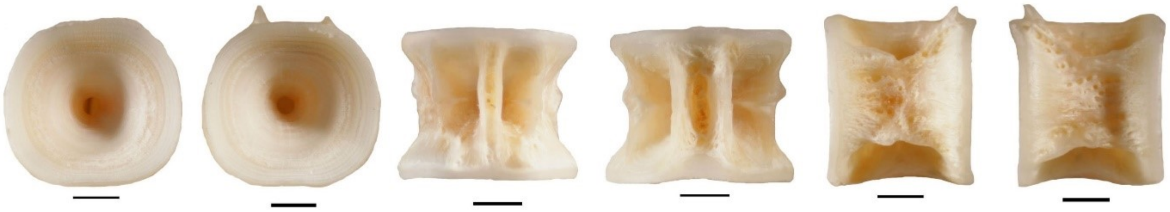

FIGURE 4-12. Centrum 34 of *Esox lucius* (Specimen number UAMZ F9102). Centrum is presented from left to right in anterior, posterior, dorsal, ventral, left lateral and right lateral views; for lateral views, dorsal is to the top of the page; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

Chapter 5: General discussions, comparisons, and conclusions

In this chapter, I compare the fauna from the two localities of the Ravenscrag Formation and then compare the fauna of the Ravenscrag Formation with the Late Cretaceous and the Eocene- Oligocene faunas reported in North America, review the main objectives of the thesis, and finally, derive the main conclusions.

Faunal comparison between Roche Percée (UAR2A site) and Croc Pot localities

The two Ravenscrag localities represent similar kinds of ichthyofauna with the UAR2A site of the Roche Percée locality being more diverse than the Croc Pot locality. Two tables (Table 5-1 and Table 5-2) have been included that show the number and type of different specimens from each locality. Apart from the unidentified species, the esocids are missing from the Croc Pot locality. Faunas reported from the Paleocene Ravenscrag Formation were already present in its Late Cretaceous counterparts; however, many of the Eocene-Oligocene Cypress Hills faunal sites have additional fish taxa such as the siluriforms, centrarchiforms, etc., but do not have other taxa such as the osteoglossomorphs and gonorhynchiforms. This indicates that the K/Pg extinction event did not have a drastic effect on the Cretaceous - Tertiary ichthyofauna in North America. However, the absence of certain groups of fishes such as the osteoglossomorphs and gonorhynchiforms from the Eocene formation is most likely due to the increase in seasonality in North America between the middle and late Eocene (Storer, 1996). The Eocene-Oligocene ichthyofauna is similar in composition to the modern-day fauna. This could be due to the previously mentioned increased seasonality as well as due to the gradual cooling of the climate prior to the Plio-Pleistocene glaciations (Zachos et al., 2008). Another reason for the Eocene-Oligocene Cypress Hills ichthyofaunal composition being different from the Ravenscrag Formation could be due to the local environment being unsuitable or the ichthyofauna was restricted to southern Saskatchewan.

Faunal comparison of the Ravenscrag Formation with the Late Cretaceous and the Eocene- Oligocene faunas reported in North America

Several taxa reported in the Paleocene of North America have already been reported in the Cretaceous. For instance, the lepisosteids were present in North America from the Early Cretaceous (Grande, 2010). The amiids were also present in the Cretaceous (Grande and Bemis, 1998). Hiodontids have been documented in the Late Cretaceous (Campanian) Dinosaur Park Formation, Alberta, Canada (Brinkman and Neuman, 2002). In the United States, they have been reported from the Late Cretaceous (Cenomanian) Dakota Formation to the late Campanian Kaiparowits Formation in Utah and in the Late Cretaceous (Maastrichtian) Hell Creek Formation in Montana (Brinkman et al., 2014). Late Cretaceous esocids have been reported from the Santonian Milk River Formation and in the Campanian Belly River Group of Alberta, Canada. They have been also reported in the Maastrichtian Hell Creek and Lance formations of Montana and Wyoming (Wilson et al., 1992; Brinkman et al., 2013; Brinkman et al., 2014), and in the Campanian Kaiparowits Formation of Utah (Brinkman et al., 2013) from the United States. Osteoglossomorphs have been reported in the Late Cretaceous (Campanian) Oldman Formation of Alberta (Li, 1996). The first Cretaceous (Campanian) report of gonorhynchiforms is in the Two Medicine Formation of Montana (Grande and Grande, 1999), Dinosaur Park Formation, Alberta (Brinkman et. al., 2013), Maastrichtian Hell Creek Formation in Montana (Brinkman, et al., 2014).

The thesis reports the first appearance of Paleocene hiodontid from the Roche Percée locality (chapter 2). Prior to this, the first report of *Hiodon* was considered to be in the

Eocene- Oligocene Kishenehn Formation, Montana (Li and Wilson, 1994). Apart from the hiodontid, other taxa that are reported in this thesis have been reported previously in the Paleocene of North America. For example, *Amia* has been previously reported from the Paskapoo Formation, Alberta (Grande et al., 2000). First appearance of *Esox* has been previously reported in the Ravenscrag Formation and Paskapoo Formation (Wilson, 1980). Osteoglossomorphs first occurred in the Paleocene Paskapoo Formation in Alberta (Li and Wilson, 1996) and the Sentinel Butte Formation of North Dakota (Newbrey and Bozek, 2000). The Gonorhynchiforms that appeared in North America in the Late Cretaceous persisted into the Paleocene (chapter 2 and 3). They have not been reported in the Cypress Hills Formations but have been reported in the Eocene of North America in the Green River Formation (Grande, 1984) and in the Horsefly beds close to Horsefly, British Columbia (Wilson, 1977).

Reviewing the objectives

Reconstruction of paleoenvironment from several localities of a formation may need to take into consideration a diverse array of environment because of lateral mixing of fauna. The use of multiple sites gives us an idea of the surrounding basins as well, compared to formations whose paleoenvironmental reconstruction is based on fauna from a single locality. Hence, the two localities studied in this thesis gives us a better idea of the floodplain deposits of the Ravenscrag Formation. For example, the presence of both hypoxic and normoxic species indicate that the water was stagnant or had low velocity water current at places but was well connected to an oxygenated component of the fluvial system too. Similarly, presence of wood fragments and finer grain size of sandstone indicate presence of several components of a fluvial system. In addition, the abundance of disarticulated material is indicative of a high velocity proximal over bank deposits. Articulated materials would only get deposited in relatively low velocity current as they would allow the fishes to be buried intact and not get carried away to the depositional basins by higher velocity currents.

The thesis reports the fish fauna as well as the paleoenvironment from two different localities. However, there are another three localities of the Ravenscrag Formations namely, the Ravenscrag 1, Pine Cree, and French Fry, where microfossils have been reported. Ichthyofaunas and sedimentology of these three localities have not been studied. Thus, in order to get a better idea of the ichthyofaunal and paleoenvironmental diversity in the formation, these three localities also need to be studied.

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TABLES

Table 5-1. Table of specimens examined from late Paleocene Roche Percée locality, Ravenscrag Formation, near Roche Percée, Saskatchewan. UALVP refers to University of Alberta Laboratory for Vertebrate Paleontology. The specimens were collected in 1971-1974 by David W. Krause and field crews.

Specimen number	Specimen	Number of specimens	Figure number in thesis	Page number in thesis	Page numbers of the figures
UALVP58691	*Lepisosteus* sp. scales	6635	2-2 A	11	34
UALVP58692	*Lepisosteus* sp. scales	475	2-2 B	11	34
UALVP58693	Holostean A Scales	115	2-2 C	12	34
UALVP58694	*Cyclurus* sp. teeth	900	2-2 D	12	34
UALVP58695	*Cyclurus* sp. teeth	200	2-2 E	12	34
UALVP58696	*Amia* sp. teeth	72	2-2 F	12	34
UALVP58697	Amiid basioccipital	1	2-2 G	12	34
UALVP58698	Amiidae abdominal centra	3	2-2 H	12	34
UALVP58699	Amiidae abdominal centra	44	2-2 I	12	34
UALVP58700	*Coriops* caudal centra	50	2-3 A	14	35
UALVP58701	*Coriops* caudal centra		2-3 B	14	35

UALVP58702	*Coriops* posterior pre caudal centrum	3	2-3 C	14	35
UALVP58703	?hiodontiform abdominal centrum	5	2-3 D	14	35
UALVP58704	hiodontiform centrum	1	2-3 E	15	35
UALVP58712	Gonorhynchyform centra	3	2-4 A	16	36
UALVP58713	Gonorhynchyform centra	1	2-4 B	16	36
UALVP58711	*Esox*sp. centra	3	2-4 C	17	36
UALVP58709	*Esox* sp. teeth	4	2-4 D	17	36
UALVP58710	*Esox* sp. partial jaw	1	2-4 E	17	36
UALVP58705	Acanthomorph basioccipital	3	2-5 A	17	37
UALVP58706	Acanthomorph centrum type HC-2	30	2-5 B	17	37
UALVP58707	indeterminate perciform anterior abdominal centrum	32	2-5 C	18	37
UALVP58708	unidet. perciform centra	10	2-5 D	19	37
UALVP58714	indet. teleost caudal centrum	1	2-6 A	19	38

UALVP58715	unidentified caudal centra	5	2-6 B	19	38
UALVP58716	unidentified teleost centra	1	2-6 C	19	38
UALVP58717	unidentified centra	3	2-6 D	19	38
UALVP58718	unidentified centrum	1	2-6 E	19	38
UALVP58719	unidentified centra	1	2-7 A	21	39
UALVP58720	unidentified centra	1	2-7 B	21	39
UALVP58721	unidentified centra	1	2-7 C	21	39
UALVP58722	unidentified centra	1	2-7 D	21	39
UALVP58723	unidentified centra	3	2-8 A	23	40
UALVP58724	unidentified centra		2-8 B	23	40
UALVP58725	unidentified centra	1	2-8 C	23	40
UALVP58726	unidentified centra	1	2-8 D	23	40

Table 5-2. Table of specimen examined from early Paleocene Croc Pot locality, Ravenscrag Formation, near Eastend, Saskatchewan. UALVP refers to University of Alberta Laboratory for Vertebrate Paleontology. Material collected by screen washing and were collected by Richard C Fox field crews in July 1996 and July 1997. Crews = RCF (Richard C Fox), CPY (Gordon P. Youswyshyn), DNS (?), CSS (Craig S. Scott). Note: Specimen number UALVP58745 was collected by Oksana Vernygora in July 2017.

Specimen number	Specimen	Number of specimens	Figure number in thesis	Page number in thesis	Page numbers of the figures
UALVP58727	*Lepisosteus* scale	over 5000	3-12 A	45	70
UALVP58728	*Lepisosteus* scale		3-12 B	45	70
UALVP58729	*Lepisosteus* scale		3-12 C	45	70
UALVP58730	*Lepisosteus* scale		3-12 D	45	70
UALVP58731	*Lepisosteus* scale		3-12 E	45	70
UALVP58732	*Lepisosteus* scale		3-12 F	45	70
UALVP58733	*Lepisosteus* scale		3-12 G	45	70

UALVP58734	*Lepisosteus* scale		3-12 H	45	70
UALVP58735	*Lepisosteus* scale		3-12 I	45	70
UALVP58736	*Lepisosteus* scale		3-12 J	45	70
UALVP58754	*Lepisosteus* teeth	Over 900	3-12 K	45	70
UALVP58737	unident. Holostean A scales	Over 300	3-12 L	46	70
UALVP58745	Amiidae caudal centrum	1 specimen, July 2017	3-13 A	43, 46	71
UALVP58744	Amiidae caudal centra	16	3-13 B	46	71
UALVP58739	Amiidae dentary	1	3-13 C	46	71
UALVP58738	*Cyclurus* sp. tooth plate fragment	30	3-13 D	47	71
UALVP58741	*Cyclurus* sp. coronoid teeth attached to the jaw	3	3-13 E	47	71

UALVP58742	*Cyclurus* sp. teeth	Over 1000	3-13 F	47	71
UALVP58743	*Cyclurus* sp. anterior coronoid teeth	9	3-13 G	47	71
UALVP58740	*Amia* tooth	6	3-13 H	47	71
UALVP58747	*Coriops* caudal centra	10	3-14 A	48	72
UALVP58748	*Coriops* centra	3	3-14 B	48	72
UALVP58749	*Coriops* centra	1	3-14 C	48	72
UALVP58750	*Lopadichthyes* sp. centrum	1	3-14 D	48	72
UALVP58752	Unidentified Gonorhynchidae centra	20	3-15 A	49	73
UALVP58753	*Notogoneus* basioccipital.	2	3-15 B	49	73
UALVP58746	Acanthomorph abdominal centra	3	3-15 C	50	73
UALVP58751	Unidentified teleost centrum	1	3-15 D	50	73

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