

TELEOST ABDOMINAL CENTRA FROM THE BELLY RIVER GROUP OF ALBERTA, CANADA

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ABSTRACT

Teleost fish assemblages of the Late Cretaceous are of particular interest with respect to both the structure of paleocommunities and the evolutionary history of the group because crown teleost fishes are thought to have diversified during that time. However, the diversity and distribution of teleost fishes of the non-marine environments remains poorly understood because the fossil record consists primarily of isolated elements, many of very small size. In this paper, a combined taxonomic/morphotype approach is used to evaluate the diversity of teleosts present in the late Campanian Belly River Group of Alberta on the basis of abdominal centra. Both surface collected specimens and specimens collected from vertebrate microfossil localities by mass sampling techniques are included in the study. Twenty-five taxonomic groups are recognized on the basis of centra. These include three elopomorphs, four osteoglossomorphs, four clupeomorphs, four ostariophysans, one esocid, five acanthomorphs, and four teleosts of uncertain affinities. All occur in fully non-marine environments of deposition. The diversity of teleosts in the Belly River Group is higher than both the temporally equivalent Kaiparowits Formation of Utah and the younger Hell Creek Formation of Montana. This high diversity can be attributed in part to the diversity of the environments of deposition because localities in both fluvial sandstones and fine-grained sediments were sampled, and these differ in both the relative abundance and taxonomic composition of the assemblages.

INTRODUCTION

Vertebrate microfossil localities offer unique insights into the paleocommunities of the Late Cretaceous. Such localities generally yield taxonomically diverse aggregations of remains that include most of the vertebrate taxa known as macrofossils from the beds in which they occur, as well as many taxa not preserved in other taphonomic settings. Also, large sample sizes can be obtained through the use of screen washing techniques. These attributes give vertebrate microfossil localities a unique position in both taxonomic and paleoecological studies, as well as providing the remains of taxa that are very rare outside such settings, and they have allowed quantitative approaches to be used to develop and test paleoecological hypotheses. One group that remains particularly challenging are the teleost fishes. Early studies of isolated elements of teleost fishes from vertebrate microfossil localities resulted in some taxa being named on the basis of tooth bearing elements (Estes, 1964, 1969a, 1969b; Wilson et al., 1992) although it was recognized that the diversity of teleost fishes was being underestimated because many distinctive elements were present that could not be placed in any taxonomic group. More recent studies have found that abdominal centra are also an important source of information on the diversity and distribution of teleosts of the Cretaceous (Brinkman and Neuman,

2002; Neuman and Brinkman, 2005; Brinkman et al., 2013, 2014, 2017a). These are often abundant, morphologically distinctive, and well preserved. However, establishing the diversity and relationships of the fish represented by isolated centra has proved challenging as the features seen in the three-dimensional elements can rarely be seen in articulated specimens. Because of this, a morphotype approach has been used in the study of teleost centra (Brinkman and Neuman, 2002; Brinkman et al., 2013, 2014, 2017a, b). Morphologically distinctive centra that could not be identified but were judged to be from taxonomically distinct kinds of fish, rather than a result of variation within a taxon, were given alpha-numeric designations and treated as operational taxonomic units in the faunal analyses. This approach allowed teleost fishes to be more fully incorporated in studies of patterns of diversity and distribution of vertebrates through the Late Cretaceous.

The goal of this paper is to document, as fully as possible, the teleost centra present in the Late Campanian Belly River Group of Alberta, Canada. The Belly River Group (previously known as the Judith River Group) has played a pivotal role in paleoecological studies of the Late Cretaceous because it preserves an exceptionally rich and diverse assemblage of vertebrates from a restricted geographic area and time period. Vertebrate microfossil localities are well represented and a program of bulk sampling of

these localities, using underwater screen washing techniques, has resulted in large samples of vertebrate microfossils from a variety of environments of deposition.

The first study that used a morphotype approach to incorporate teleosts into a paleoecological study was by Eberth and Brinkman (1997). They showed that the teleost assemblage present in a series of fine-grained deposits near the top of the Dinosaur Park Formation northeast of Onefour, Alberta, differed from the assemblage present in the fluvial deposits of Dinosaur Provincial Park. Later, a more comprehensive study of the diversity of teleosts from the Belly River Group was published by Brinkman and Neuman (2002) and a review of the diversity of fish from Dinosaur Provincial Park was published by Neuman and Brinkman (2005). Subsequent studies applied the morphotype approach to the study of teleost assemblage to other Late Cretaceous assemblages, including the early Maastrichtian portion of the Horseshoe Canyon Formation of Alberta (Larson et al., 2010), a series of assemblages of Cenomanian to Campanian age of southern Utah (Brinkman et al., 2013), the late Maastrichtian Hell Creek Formation of Montana (Brinkman et al., 2014), and the late Santonian Milk River Formation of Alberta (Brinkman et al., 2017a, b). Furthermore, studies of the morphology and development of teleost centra in extant teleosts through the use of high-resolution micro-CT scans (Sakashita et al., 2019), and studies of the variation along the column in extant species of *Esox* (Sinha et al., 2019) have provided additional information on extant teleost centra that facilitates the interpretation of fossil material. This additional information, together with the results of further collecting efforts leading to much larger sample sizes, provide a much more complete documentation of the teleosts from this geological unit. With the larger sample sizes, refined taxonomic interpretations are possible in many cases. Also, additional, previously unrecognized, morphotypes can be defined. Together, this additional information allows teleost centra to be used more effectively in studies of the paleoecology of the Belly River Group and facilitates the use of teleost centra in future paleoecological studies of the Late Cretaceous of the Western Interior of North America.

GEOLOGY

The Belly River Group (previously referred to as the Judith River Group) is comprised of three formations. In ascending order, these are the Foremost, Oldman, and Dinosaur Park Formations. The material described here comes from localities in the upper part of the Oldman Formation and the Dinosaur Park Formation. Sedimentological studies (Eberth, 2005) showed that both of these formations were deposited in fluvial-lacustrine settings, although the geometry of the

rivers depositing the sediments differs. The Oldman Formation was deposited by shallow, braided rivers, whereas the Dinosaur Park Formation was deposited by large meandering rivers. In addition, transitional beds at the top of the Dinosaur Park Formation document a series of marine and brackish-water deposits associated with the transgressing Bearpaw Sea.

This study is based on material collected from the exposures of The Belly River Group in two regions of Alberta: Dinosaur Provincial Park, north-east of the town of Brooks, and a small area of exposure north-east of the Onefour Research Station in south-eastern Alberta. The exposures of the Belly River Group in Dinosaur Provincial Park include the upper beds of the Oldman Formation and the entire Dinosaur Park Formation. In Dinosaur Provincial Park, the Dinosaur Park Formation has been dated as extending from 76.5 to 74.8 Ma (Eberth, 2005). Information on the stratigraphic position and environment of deposition of vertebrate microfossil localities in Dinosaur Provincial Park referred to in the text is given in Table 1. Additional information, including UTM coordinates and stratigraphic position, for localities in Dinosaur Provincial Park is given in Currie and Koppelhus (2005). A detailed description of the sedimentology of many of these localities was described by Eberth and Brinkman (1990). With two exceptions, the localities sampled are all in the lower two thirds of the formation. The two localities near the top of the formation are locality L2371 (Wolf Coulee Site), and BB 180 (Cretin locality). Both of these are within a series of coal-bearing beds marking the transition from the fluvial to marine environments called the Lethbridge Coal Zone.

The exposures in the Onefour area of southeastern Alberta are all within the Dinosaur Park Formation. The base of the Dinosaur Park Formation becomes younger towards the south, so that the exposures of the formation in the Onefour area are equivalent to approximately the upper third of the exposures in Dinosaur Provincial Park. The exposures of the Dinosaur Park Formation in this area include both fluvial deposits and fine-grained sediments deposited in quiet water environment. The fine-grained sediments were deposited in incised valleys and have been referred to as the Onefour Mud-filled Channel Complex (Eberth 1996). The sedimentology of these sites was described by Eberth (1996) and paleoecological interpretations were presented by Eberth and Brinkman (1997). This complex is of particular importance for studies of aquatic paleocommunities of the Dinosaur Park Formation because it was interpreted as a largely autochthonous assemblage. It is overwhelmingly dominated by aquatic vertebrates, and among these, teleost fishes are well represented. In addition to the localities deposited in quiet water settings, two localities in the Onefour area are preserved in fluvial deposits. These are localities

L1104 and L1108. Both are stratigraphically below the Onefour Mud-filled Channel Complex. A list of localities from the Onefour area is included in Table 1.

METHODS

This study is based primarily on material from vertebrate microfossil localities that were bulk-sampled using underwater screening techniques. As typical for such localities, fishes are represented by disarticulated, isolated elements. The combined taxonomic/morphotype approach adopted by Brinkman et al. (2013, 2014, 2017a) in studies of fish material from the Grand Staircase/Escalante region of Utah, the Hell Creek Formation of Montana, and the Milk River Formation of Alberta is used to ensure that all available material is incorporated into the analysis of the diversity of teleosts present. The taxonomic significance of morphological variation in vertebral elements must be evaluated cautiously because of potential variations along the column of a single individual. The range in variation along the column in extant teleosts provides a framework in which to evaluate whether distinct morphotypes are from different regions of the vertebral column or represent taxonomically distinct groups. Additionally, hypotheses of association of morphologically distinct centra were tested using distribution patterns. Centrum morphotypes that have a different stratigraphic or geographic distribution pattern are unlikely to be from a single kind of fish.

In an attempt to identify the taxa represented by the elements present in the vertebrate microfossil assemblages, comparisons were made with extant and fossil specimens. The osteological collections of the University of California Museum of Paleontology, Berkeley (California, USA), Royal Ontario Museum (Toronto, Ontario, Canada), Canadian Museum of Nature (Ottawa, Ontario, Canada), University of Michigan (Ann Arbor, Michigan), and Royal Tyrrell Museum of Palaeontology (Drumheller, Alberta, Canada) provided a broad range of comparative specimens of recent fish. The collections of fossil fishes in the University of Alberta (Edmonton, Alberta) and the Royal Tyrrell Museum of Palaeontology were also particularly useful. In addition to articulated specimens of teleosts of Cretaceous and Paleocene age, Eocene Green River Formation fishes were examined because Divay and Murray (2016) were able to use articulated Green River specimens to identify isolated elements of *Diplomystus* and *Notogoneus* in the Wasatch Formation, and these taxa are present in the Cretaceous (Cavin 2017). For the classification of teleost fishes, the taxonomic system of Nelson et al. (2016) is followed.

To document the morphological variation within the taxonomic units recognized, an extensive series of photographs of the elements described here is included.

Specimens were whitened with ammonium chloride before photography to emphasize relief. All specimens used in this study are housed in the Royal Tyrrell Museum of Palaeontology (TMP). Because of the large number of catalogued specimens for many taxa, only representative specimens are listed as voucher specimens in an attempt to document the variation within a morphotype and the distribution of the morphotype.

SYSTEMATIC PALEONTOLOGY

Division TELEOSTEOMORPHA Arratia, 2001
Subdivision TELEOSTEI Müller, 1844 (sensu
Patterson and Rosen, 1977)

Cohort ELOPOMORPHA Greenwood et al., 1966
Paratarpon apogerontus Bardack 1970
Figure 1 A-C

Paratarpon apogerontus, Bardack, 1970: 1-8

Paratarpon apogeontus, Peng, Russell, and Brinkman, 2001:16, Plate 4, figs1-2

Morphoserries IA-1, Brinkman and Neuman, 2002:140-141, fig. 1.1- 1.13

Paratarpon apogerontus, Neuman and Brinkman, 2005:173, fig. 9.5

Voucher Specimens.—TMP 1964.004.0099, one caudal centrum; TMP 1980.030.0015, one centrum from BB 9; TMP 1980.031.0014, one centrum from BB 14; TMP 1980.031.0015, one centrum from BB 14; TMP 1981.020.0016, one centrum from BB 37; TMP 1981.028.0022, one centrum from BB 102; TMP 1981.041.0164, one centrum from BB 102; TMP 1982.019.0033, one centrum from BB 75; TMP 1982.019.0335, one centrum from BB 69; TMP 1982.030.0054, one centrum from BB 83; TMP 1982.031.0029, one centrum from BB 23; TMP 1982.031.0032, one centrum from BB 23; TMP 1984.036.0036, one centrum from BB 10; TMP 1985.044.0011, one centrum from BB 102; TMP 1985.058.0063, one centrum from BB 102; TMP 1986.036.0167, one centrum from BB 10; TMP 1986.128.0014, one centrum from BB 95; TMP 1987.099.0009, one centrum from BB 75; TMP 1993.036.0558, one centrum from BB 25; TMP 1994.012.0847, one centrum from BB 9; TMP 2001.012.0105, one centrum from BB 14; TMP 2019.060.0235, one caudal centrum from Dinosaur Provincial Park.

Remarks.—The extinct teleost fish *Paratarpon* is an elopomorph, closely related to the extant *Megalops* (tarpon) and *Elops* (ladyfish). However, in contrast to its extant relatives, *Paratarpon* appears to be strictly freshwater since it has only been recovered from non-marine beds of the Dinosaur Park Formation (Bardack, 1970;

TABLE 1. List of localities referred to in the text.

Locality Number	Locality Name	Formation	Environment of Deposition
Onefour Area			
L1101	Above Coal Zone	Dinosaur Park	Mud-filled Channel
L1102	Turtle Locality	Dinosaur Park	Mud-filled Channel
L1103	Pachy Site	Dinosaur Park	Mud-filled Channel
L1104	DP SS Unit	Dinosaur Park	Fluvial
L1105	Jane's Site	Dinosaur Park	Mud-filled Channel
L1106	Above Janes Site	Dinosaur Park	Mud-filled Channel
L1108	Millar Bonebed	Dinosaur Park	Fluvial
L1109	GB #1	Dinosaur Park	Mud-filled Channel
L1110	GB #2	Dinosaur Park	Mud-filled Channel
L1111	GB #3	Dinosaur Park	Mud-filled Channel
L1112	GB #4	Dinosaur Park	Mud-filled Channel
L1113	Lost Maggot Mine	Dinosaur Park	Mud-filled Channel
L1114	Baby Ceratops	Dinosaur Park	Mud-filled Channel
L1115	Car Park Loc	Dinosaur Park	Mud-filled Channel
	JMC Site 2;	Dinosaur Park	Mud-filled Channel
	JMC 700.	Dinosaur Park	Mud-filled Channel
	JMC Mammal site 2	Dinosaur Park	Mud-filled Channel
Dinosaur Provincial Park area			
BB 31	Egg Shell Site	Dinosaur Park	Crevasse Splay
BB 54		Dinosaur Park	Muddy channel fill
BB 78	Pumposaur site	Dinosaur Park	Fluvial
BB 86		Dinosaur Park	Fluvial
BB 97	JMC 1044	Dinosaur Park	Fluvial
BB 98	New Egg Shell Site	Dinosaur Park	Fluvial
BB 100	MANC	Oldman	Crevasse Splay
BB 102	RR Gr	Dinosaur Park	Fluvial
BB 104	U-4	Dinosaur Park	Crevasse Splay
BB 105	U-2	Oldman	Fluvial
BB 107	Chris's Site	Oldman	Crevasse Splay
BB 117		Dinosaur Park	Fluvial
BB 121	Mathews Site	Oldman	Crevasse Splay
BB 135		Dinosaur Park	Fluvial
BB 137		Dinosaur Park	Fluvial
BB 180	Cretin	Dinosaur Park	Fluvial
L1118	Ken's site	Dinosaur Park	Crevasse Splay
L2370	H&M Site	Dinosaur Park	Fluvial
L2371	Wolf Coulee Site	Dinosaur Park	Fluvial
L2453		Oldman	Fluvial
	Marie's Site	Dinosaur Park	Muddy channel fill
	Vipond's Site	Dinosaur Park	Crevasse Splay

Neuman and Brinkman, 2005). *Paratarpon* is the largest fish in the Belly River Group vertebrate assemblage and one of the few fishes from the Late Cretaceous Belly River Group represented by articulated skeletons. Two partial skeletons are known, both missing the skull. One of these was described by Bardack (1970). The second, a specimen in the collections of the Royal Ontario Museum, was illustrated by Neuman and Brinkman (2005).

Centra were referred to *Paratarpon* by Brinkman and Neuman (2002) on the basis of comparison with the articulated specimens from the Dinosaur Park Formation and with extant members of the order. These are short, plate-like elements with widely separated neural arch and parapophyseal articular pits and with numerous fine ridges extending between the ends of the centrum. The shape of the centra varies, with some being taller than wide (Figure 1A) and others being nearly circular in end view (Figure 1 B). The circular centra are assumed to be from a posterior position along the column because caudal centra have a similar shape (Figure 1C). In the anterior abdominal centra the parapophyseal pits are widely separated and face laterally. A second pit of unknown function is present ventral and medial to the parapophyseal articular pits. In the posterior abdominal centra, the parapophyseal pits are located close together on the ventral edge of the centrum and the accessory pits merge with the parapophyseal articular pits.

Distribution.—Centra of *Paratarpon* are widely distributed in the Dinosaur Park Formation but because of their size are usually found as isolated specimens in macro-bonebeds rather than in vertebrate microfossil localities. They have not been observed in other non-marine formations of the Western Interior of North America.

Order ALBULIFORMES sensu Forey et al., 1996
Suborder ALBULOIDEI sensu Forey et al., 1996
Family ALBULIDAE Bleeker, 1859
Subfamily PHYLLODONTINAE Estes and Hiatt,
1978

Paralbula casei Estes 1969b
Figure 1 D-E

Morphoserries IA-2, Brinkman and Neuman, 2002:141,
fig. 1.14-1.17

Paralbula, Neuman and Brinkman, 2005:174, fig. 9.8A
Paralbula, Brinkman et al., 2013:210, fig. 10.13A

Voucher Specimens – From Onefour Mud-filled Channel Complex: TMP 1990.048.0058, one centrum from locality L1106; TMP 1990.067.0045, one centrum from locality L1113; TMP 1993.0093.0056, two centra from locality L1104; TMP 1993.091.0038, one centrum

from L1101; TMP 1993.0097.0009, one centrum from locality L1105; TMP 1993.0093.0125, five centra from locality L1105; TMP 1993.093.0118, three centra from locality L1102; TMP 1993.116.0065, one centrum from locality L1115; TMP 1993.093.0044, one centrum from locality L1113; TMP 1993.093.0124, one centrum from locality L1101; TMP 1993.124.0046, one centrum from locality L1114; TMP 1994.023.0032, one centrum from locality L1102; TMP 2016.009.0040, one complete centrum fragments of at least three others from JMC 700.

From Dinosaur Provincial Park: TMP 2008.68.1, one centrum from locality L2371 (Wolf Coulee Microsite).

Remarks.—The Albulidae, represented today by *Albula vulpes*, the bonefish, are represented in the non-marine deposits of the Western Interior of North America by the Phyllodontinae. As in the Albulinae, robust pharyngeal tooth-plates are present, but, rather than pillar-like teeth like those of *Albula*, the teeth are flattened button-like teeth arranged in multiple superimposed sets of replacement teeth. Two members of the Phyllodontinae are present in the Late Cretaceous of the Western Interior of North America: *Phyllodus*, and *Paralbula*. *Phyllodus* is restricted to the late Maastrichtian and younger formations. An indeterminate phyllodontine with similarities to *Phyllodus* was reported from the Belly River Group on the basis of button-shaped tooth-like elements thought to be isolated teeth (Peng et al., 2001), but these have subsequently been identified as gastroliths from a freshwater shrimp. Thus, the only phyllodontine currently recognized in the late Campanian is *Paralbula*.

Centra were referred to *Paralbula* by Neuman and Brinkman (2005) on the basis of similarity with those of *Albula*. As in other members of the Elopidae these are short, plate-like elements with multiple fine ridges extending between the ends of the centrum. However, they differ from centra of *Paratarpon* and are similar to *Albula* in that the bony ridges extending between the ends of the centra are grouped into bundles.

Distribution.—Although teeth of *Paralbula* are widespread in the late Campanian of the Western Interior, centra of *Paralbula* have only been recovered from the Dinosaur Park Formation. All but one specimen have been collected from localities in the Onefour Mud-filled Channel complex. One specimen has been collected in Dinosaur Provincial Park. This is from a locality high in section that also has fine-grained sediments. The restricted distribution of centra of *Paralbula* contrasts with the wide distribution of teeth of this taxon. This difference is likely a result of taphonomic biases favoring the preservation of nodular, enamel-covered elements like isolated *Paralbula* teeth.

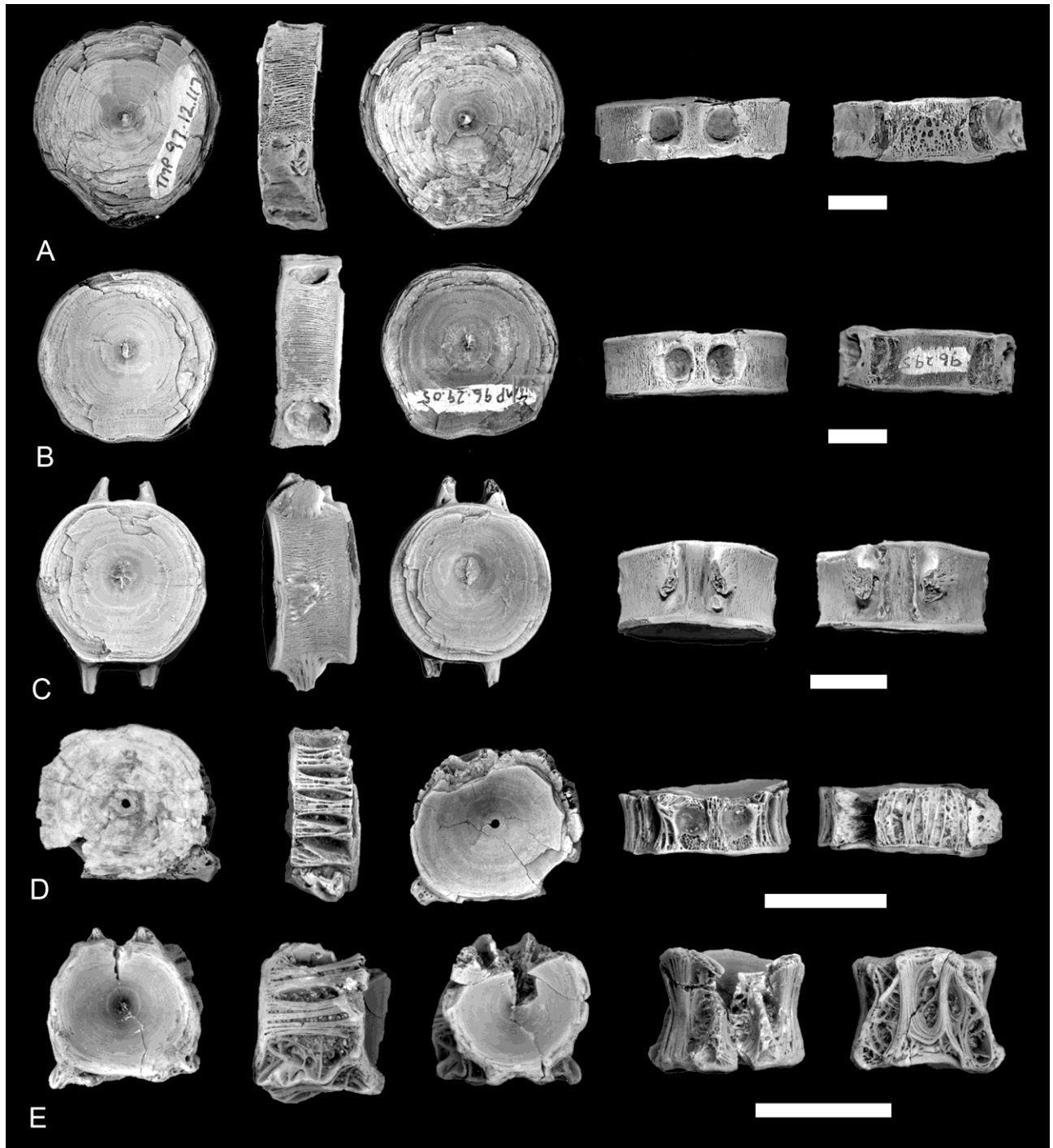


FIGURE 1. Centra of large elopomorphs from the Dinosaur Park Formation shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-C**) centra of *Paratarpon*. **A**, anterior abdominal centrum, TMP 1997.012.0117; **B**, posterior abdominal centrum, TMP 1996.029.0005; **C**, caudal centrum, TMP 2019.060.0235. **D-E**) centra of *Paralbula*. **D**, mid abdominal centrum, TMP 1993.093.0056; **E**, posterior abdominal centrum, TMP 1993.116.65. Figure 1B is from Neuman and Brinkman (2002:fig.9.5C). Figure 1D is from Neuman and Brinkman (2005:fig. 9.8A). Scale bar equals 1 cm.

Family indet.
gen. indet. (small elopomorph)
Figure 2

Teleost F, Eberth and Brinkman, 1997:57
Morphoserries IA-3, Brinkman and Neuman, 2002:141,
figs. 1.18-1.27.
Elopiiformes, Brinkman et al., 2010:210, fig. 10.14A-C
Elopiiformes genus et sp. indet., Brinkman et al.,
2017:18-19, fig. 8

Voucher Specimens.—from Onefour Mud-filled
Channel complex: TMP 1990.048.0059, four centra
from locality L1105; TMP 1990.067.0019, one centrum,
from locality L1113; TMP 1993.091.0025, one centrum,
from L1101; TMP 1993.091.0037, one centrum, from
locality L1101; TMP 1993.092.0012, one centrum, from
locality L1102; TMP 1993.093.0057, three centra, from
locality L1101; TMP 1993.093.0123, one centrum, from
L1104; TMP 1993.093.0054, one centrum, from L1105;
TMP 1993.093.0046, three centra, from locality L1110;
TMP 1993.093.0047, one centrum from locality L1112;
TMP 1993.093.0052, four centra, from locality L1109;
TMP 1993.093.0048, four centra in articulation, from
locality L1102; TMP 1997.019.0012, one centrum, from
locality L1102; TMP 1997.019.0011, one centrum, from
L1101; TMP 1997.019.0013, one centrum, from L1101;
TMP 2008.025.0017, four centra from JMC Stake Site;
TMP 2019.060.0204, three centra from locality L1115.

Remarks.—Based on isolated centra described by
Brinkman and Neuman (2002) as morphoserries IA-3,
and referred to as centrum type F in Eberth and
Brinkman (1997), a small elopomorph fish distinct from
Paratarpon and *Paralbula* is represented in the
Dinosaur Park Formation. These centra conform to the
general elopomorph pattern in being short, having
widely spaced neural and rib articular pits, and in having
numerous fine ridges extending between the ends of the
centra. The centra differ from those of *Paratarpon* and
Paralbula in their shape as seen in end view. Rather than
being round or higher than wide, centra of the small
elopomorph are wider than high. Variation in shape of
the centra is present that can be interpreted as a
reflection of variation along the column. More anterior
abdominal centra are sub-triangular in end view, with
parapophyseal articular pits widely spaced (Figure 2A).
Posterior abdominal and anterior caudal centra are sub-
rectangular in end view and parapophyseal articular pits
are close to one another (Figure 2B-C). Posterior caudal
centra are distinctly wedge-shaped in lateral view, with
the ventral edge of the centrum much narrower than the
dorsal edge (Figure 2E). The small size of these centra
raises the possibility that these are from juvenile
individuals of one of the larger elopomorphs although

this is considered unlikely because growth lines are
present, indicating that these centra are from individuals
more than a year old.

Distribution.—Within the Dinosaur Park
Formation, centra of the small elopomorph have been
encountered only in the mud-filled channel complex
northeast of Onefour. Outside Dinosaur Park, they have
also been reported from the late Santonian Milk River
Formation of southern Alberta (Brinkman et al.,
2017a,b) and from the Cenomanian to early Santonian
in Utah (Brinkman et al., 2013). They were not observed
in the late Maastrichtian Hell Creek of Montana.

Cohort OSTEOGLOSSOMORPHA Greenwood,
Rosen, Weitzman & Myers, 1966
Coriops Estes, 1969a
Figure 3

Coriops amnicolus, Estes, 1969:7-9, plate 4
Teleost D, Brinkman and Eberth, 1990:44-45, fig. 1
Teleost D, Peng, Russell, and Brinkman, 2001:18, Plate
4, figs. 7-9
Morphoserries IIA-1, Brinkman and Neuman, 2002:144-
146, fig. 4.1-4.11
Coriops, Neuman and Brinkman, 2005:174-176, fig.
9.6B-D, 9.8D
Coriops, Larson, Brinkman, and Bell, 2010:1165, fig.
5A
Coriops, Newbrey et al., 2013:fig. 3
Coriops, Brinkman et al., 2013:207-209, fig. 10.11
Coriops, Brinkman et al. 2014:252-253, fig. 4
Coriops, Murray et al., 2018:fig. 12D-F

Voucher Specimens.—Because of the large
number of catalogued specimens, only a few
representative specimens are listed here. TMP
1986.023.0035, approximately 20 centra from BB 86;
TMP 1986.217.0036, seven complete centra and many
partial centra from BB 51; TMP 1987.004.0018,
approximately 40 centra from BB 54; TMP
1988.215.0054, approximately 15 centra from BB 105;
TMP 1993.117.0007, approximately 30 centra from
locality L1104.

Remarks.—*Coriops* was originally described on
the basis of basibranchial tooth plates and was included
in the Albulidae because of the presence of blunt, pillar-
like teeth (Estes, 1969a). However, based on
comparison with members of the Osteoglossomorpha,
specifically *Scleropages*, the Malaysian Bonytongue,
Brinkman and Neuman (2002) suggested that it is an
osteoglossomorph. Dentaries, premaxillae and centra
were referred to *Coriops* because they share with the
basibranchial elements a similar pattern of geographic

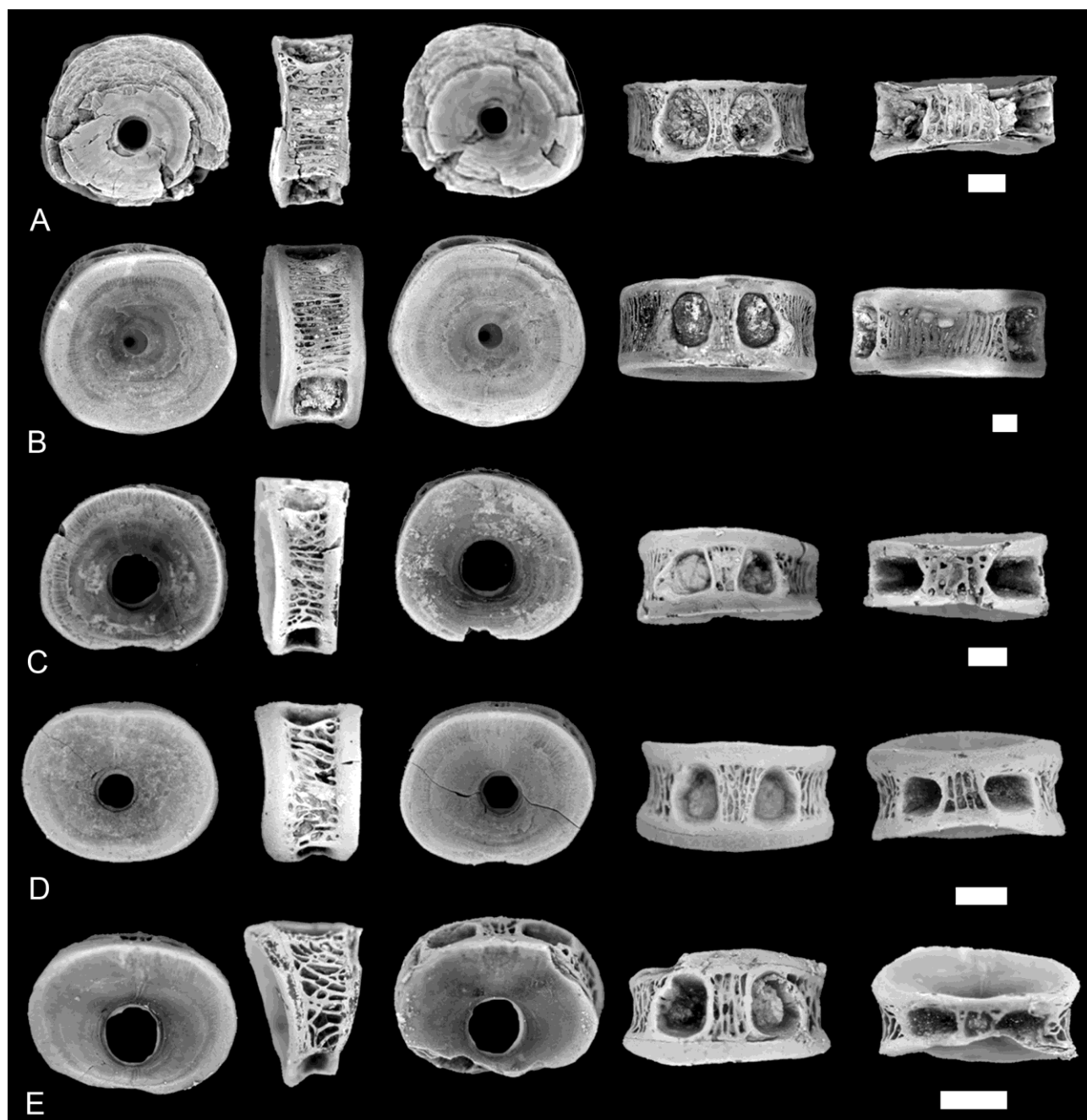


FIGURE 2. Centra of small-bodied elopomorph shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A)** mid-abdominal centrum, TMP 1997.019.0012; **B)** posterior abdominal centrum, TMP 1997.019.0013; **C)** posterior abdominal or anterior caudal centrum, TMP 1997.019.0011; **D)** anterior caudal centrum, TMP 1993.093.0046; **E)** posterior caudal centrum, TMP 1993.093.0057. Scale bar equals 1 mm.

and stratigraphic distribution, and a similar size-frequency distribution. The centra were originally described by Brinkman and Neuman (2002) as morphoserries IIA-1 and were subsequently referred to *Coriops* by Neuman and Brinkman (2005).

Centra from the anterior, mid, and posterior regions of the vertebral column can be recognized. The centra from the mid-abdominal region (Figure 3B-C) are most common and distinctive. These are shorter than wide and round or slightly higher than wide in end view.

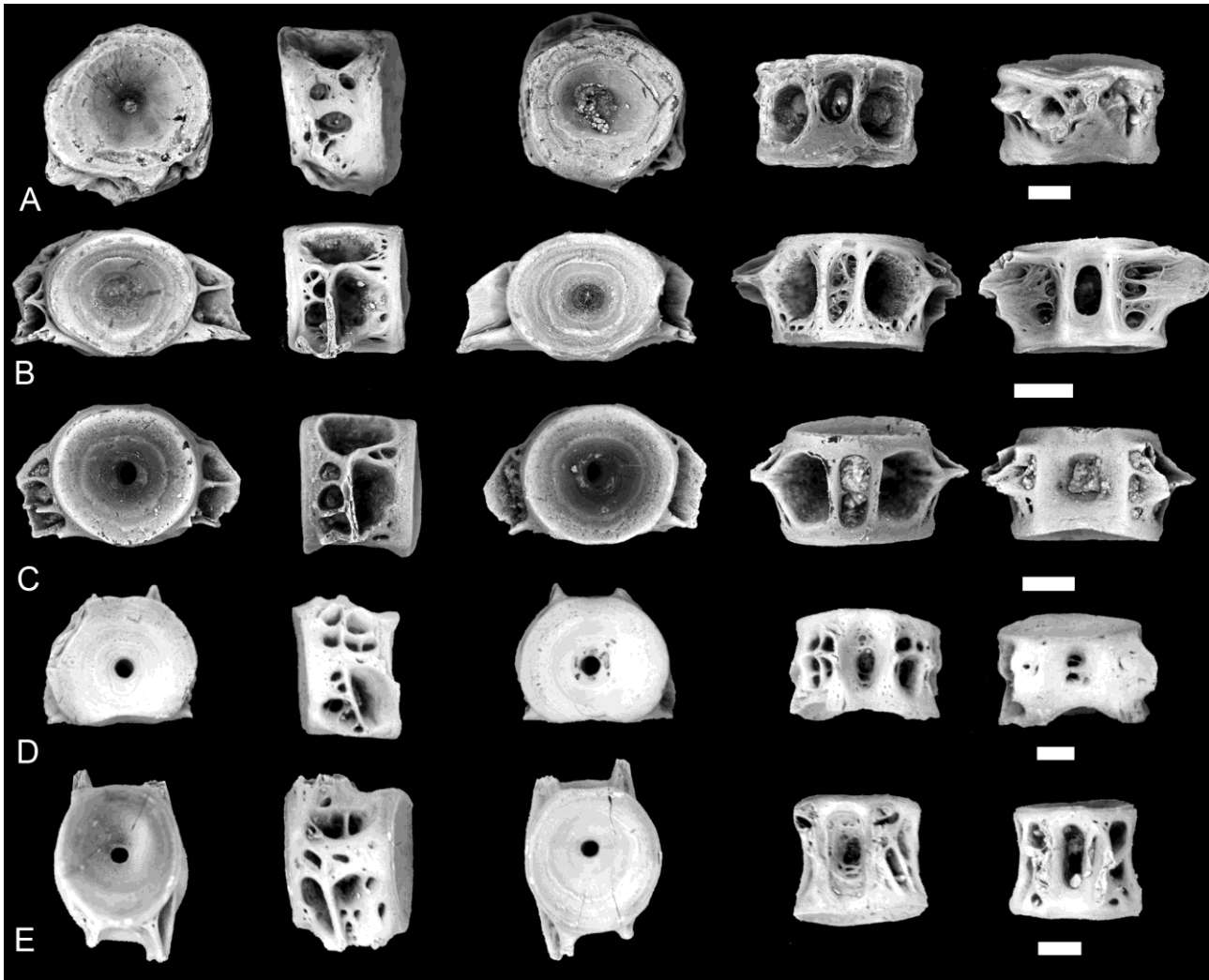


FIGURE 3. Centra referred to *Coriops* sp. shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. A) anterior abdominal centrum, TMP 1990.043.0046; B) mid- abdominal centrum, TMP 1990.043.0046; C) mid-abdominal centrum, TMP 1986.045.0064; D) posterior abdominal centrum, TMP 1990.115.0046; E) caudal centrum, TMP 1986.022.0043. Figure 3D are from Newbrey et al. (2013:fig. 3). Scale bar equals 1 mm.

The neural arches are autogenous and the articular surfaces for the neural arch are large, oval pits that extend the full length of the centrum. A mid-dorsal pit is present between the neural arch articular pits. This is typically a large oval pit about half the size of the neural arch articular pits (Figure 3C), although in some centra it is narrow and crossed by minor ridges (Figure 3B). Long parapophyses are present. When complete, these are vertical flanges that extend laterally from the centrum. The base of the parapophyses is located anterior to the middle of centrum and extends from the lateral edge of the neural arch articular pit to the ventral edge of the centrum. A pit posterior to parapophyses is identified as a rib articular pit. A mid-ventral pit is present ventrally.

The anterior abdominal centra (Figure 3A) are similar to the mid-abdominal centra in having autogenous neural arches and a mid-dorsal pit between the neural arch articular pits. They differ in that the parapophyses are short and are more ventrally oriented. The ventral surface of the centrum between the parapophyses is flat and featureless or has minor pits (Figure 3A).

Posterior abdominal centra (Figure 3D) differ from the mid-abdominal centra in having neural arches fused to the centrum. A ridge extends from the neural arch to the tip of the parapophyses, which are directed ventrolaterally. As in the more anterior centra, a mid-ventral pit is present.

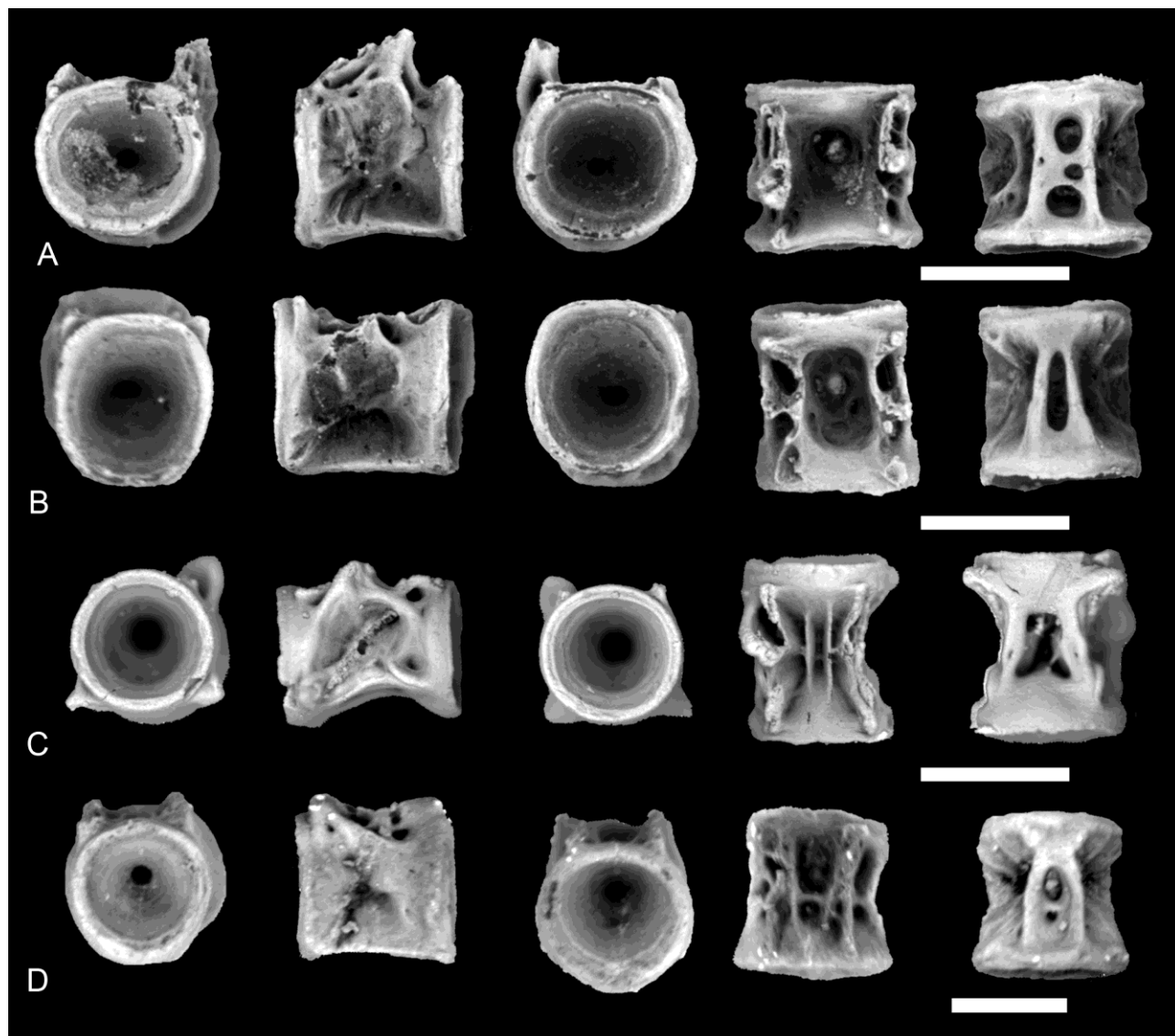


FIGURE 4. Centra referred to *Wilsonichthys* shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-B**) centrum morphotype B-vE; **A**, TMP 1995.182.0050; **B**, TMP 1995.063.0041; **C-D**) Centrum morphotype B-vA; **C**, TMP 1995.181.0066; **D**, TMP 1986.045.0066. Scale bar equals 1 mm.

Caudal centra (Figure 3E) are similar to the posterior abdominal centra in the presence of ridges on the lateral surface of the centrum, but differ in that a rib articular pit is absent and the base of the haemal arches are located close to the midline.

The osteoglossomorph affinities of the centra Neuman and Brinkman (2005) referred to *Coriops* was confirmed by Divay and Murray (2016), who showed that they are near-identical to the centra of *Phareodus*, including the presence of neural arches that are autogenous in anterior abdominals and fused in posterior positions. Additionally, the distinctive morphology of first centra is similar. Also, Murray et al. (2018) showed that centra of this type are similar to those present in

Lopadichthys, an osteoglossomorph from the Paleocene. The similarity of the centra here referred to *Coriops*, with those of *Phareodus* and *Lopadichthys* suggests that this centrum morphotype is probably shared by a higher taxonomic group that includes *Coriops*, as well as other related osteoglossomorphs. The specimens from the Dinosaur Park Formation are referred to *Coriops* because tooth-bearing elements show that this taxon is abundant in the formation whereas *Phareodus* and *Lopadichthys* are absent.

Distribution.—*Coriops* is one of the few fish taxa from the Dinosaur Park Formation of moderate size. It is the most abundant teleost fish in the Dinosaur Park Formation (Neuman and Brinkman, 2005:table 9.1). It

is also widely distributed in the Late Cretaceous of the Western Interior, occurring in the Hell Creek Formation of Montana and the Kaiparowits Formation of Utah (Brinkman et al., 2013, 2014). Fish centra from the Nemegt Formation of Mongolia with similarities to centra of *Coriops* were described by Newbrey et al. (2013).

Order OSTEOGLOSSIFORMES Berg, 1940
Wilsonichthys Murray, Newbrey, Neuman, and
Brinkman 2016

Remarks.—*Wilsonichthys* is a basal osteoglossomorph represented by two articulated skeletons from the late Maastrichtian Scollard Formation of Alberta, Canada. Abdominal centra are partially visible in one of the specimens, and based on these, Murray et al. (2016) recognized that centra of *Wilsonichthys* were generally similar to two of the centrum morphotypes that were described by Brinkman et al. (2013, 2014), as centrum morphotypes B-vE and B-vA. However, only one of these centrum morphotypes, B-vE, was present in the formation from which the articulated specimens of *Wilsonichthys* were found. Thus, it was considered most likely to be from that fish. However, the similarity in these centrum morphotypes suggests that they are from closely related taxa. Thus, both are included here as questionably belonging to *Wilsonichthys*.

? *Wilsonichthys* (centrum morphotype B-vE)
Figure 4A-B

Genus et sp. indet. BvE, Brinkman et al., 2013:225-226,
fig. 10.27

Genus and species indet. B-vE, Brinkman et al.
2014:261, fig. 11C-D

Wilsonichthys, Murray et al., 2016:1-14, fig. 7-8

Wilsonichthys, Brinkman et al., 2017a:24, fig. 13

Voucher Specimens.—from Dinosaur Provincial Park: TMP 1995.182.0050, five centra from BB 86; TMP 2017.020.0007, four centra from Lost River microsite; TMP 2019.060.0193, one centrum from BB 105; TMP 2019.060.0194, two centra from BB 107; TMP 2019.060.0209, one centrum from Vipond's Site.

Centra of morphotype B-vE from Onefour area: TMP 2014.10.15, three centra from locality L1115.

Remarks.—Teleost centrum morphotype B-vE includes centra in which the neural arch is fused to the centrum and in which the parapophyses are autogenous, there is a large shallow excavated area on the side of the centrum for the parapophyses, and a deep mid-ventral pit is present. This pit is bordered by a pair of ridges that extend between the ends of the centrum. The mid-dorsal pit has a smooth base and no processes are present on the posterior end of the centrum.

Distribution.—Within the Belly River Group, centrum morphotype B-vE occurs most frequently in the fluvial deposits of Dinosaur Provincial Park. Outside the Belly River Group, centrum morphotype B-vE occurs in the Kaiparowits Formation of southern Utah (Brinkman et al., 2013), the Hell Creek Formation of Montana (Brinkman et al., 2014), and the Scollard Formation of Alberta (Murray et al., 2016). This distribution corresponds to the distribution of dentaries referred to *Wilsonichthys*, adding support to the referral of these centra to that genus.

? *Wilsonichthys* (centrum morphotype B-vA)
Figure 4C-D

Genus and species indet. B-vA, Brinkman et al.,
2014:261, fig. 11A-B

Voucher Specimens.—Centra of morphotype B-vA from the Onefour area: TMP 2008.025.0020, one centrum from JMC Stake Site; TMP 2019.060.0207, four centra, from locality L1115. From fluvial beds of Onefour area: TMP 2019.060.0203 eight centra from L1108.

Centra of morphotype B-vA from Dinosaur Provincial Park: TMP 1986.043.0084, eight centra from BB 86; TMP 2017.011.0003, four centra from locality L2370; TMP 1995.181.0066, fifteen centra from locality BB 104; TMP 2008.051.0008, two centra from locality BB105; TMP 2019.060.0188, three centra from BB 100.

Remarks.—Centrum morphotype B-vA is similar to centrum morphotype B-vE in that the neural arch is fused to the centrum, the parapophyses are autogenous, a large shallow excavated area is present on the side of the centrum for the parapophyses, and a deep mid-ventral pit is present. These two morphotypes differ in that a pair of parasagittal ridges is present at the base of a mid-dorsal pit of morphotype B-vA (Figure 4C-D), but in centrum type B-vE, this pit has a smooth base (Figure 4A-B). Also, ventro-lateral processes are present on the posterior end of the centrum of B-vA but not B-vE and, as seen in ventral view, the anterior end of the centrum separating the parapophyseal surfaces is constricted in B-vA but not B-vE.

Distribution.—Within the Belly River Group, centrum morphotype B-vA occurs in both Dinosaur Provincial Park and the Onefour Mud-filled Channel complex in apparently equal frequency relative to other teleost centra. Outside of the Belly River Group, centrum morphotype B-vA occurs only in the Hell Creek Formation of Montana (Brinkman et al., 2014). This different distribution suggests that the fishes represented by centrum morphotypes B-vA and B-vE had a different distribution within the Western Interior of North America.

Family HIODONTIDAE Valenciennes in Cuvier &
Valenciennes, 1846
Gen et sp. indet.
Figure 5

Teleost indet., Peng, Russell, and Brinkman, 2001: 18,
Plate 4, fig. 10-11

Morphoserries IIB-1, Brinkman and Neuman,
2002:147149, fig. 6

Morphoserries IIB-1 (Hiodontidae), Neuman and
Brinkman, 2005:180, fig. 9.8F

Hiodontidae, Newbrey et al., 2013:fig. 2

Hiodontiformes, Brinkman et al., 2013:209, fig. 10.12

Hiodontidae gen et sp. indet 1, Brinkman et al.,
2014:253, fig. 5

Hiodontidae Genus et sp. indet., Brinkman et al.,
2017a:24-27, fig. 14

Voucher Specimens.—Because of the large number of catalogued specimens, only a few representative specimens are listed here. TMP 1995.145.0006, five centra from BB 51; TMP 1995.157.0049, three centra from locality L1108; TMP 1995.177.0066, four centra from BB 100; TMP 1995.180.0037, five centra from BB 107; TMP 1995.181.0034, fourteen centra from BB 104; TMP 2004.104.0064, three centra from Marie's Site; TMP 2004.104.0062, twenty-two centra from Marie's Site; TMP 2008.051.0005, one centrum from BB 105; TMP 2008.025.0011, two centra from JMC Stake Site; TMP 2017.011.0006, eight centra from locality L2370; TMP 2019.020.0213, approximately twenty-five specimens including a first centrum from locality L2370.

Remarks.—The Hiodontidae, which includes the extant Goldeye and Mooneye and the Eocene genus *Eohiodon*, is endemic to North America. The presence of a member of the Hiodontidae in the Dinosaur Park Formation is documented by a series of centra described by Brinkman and Neuman (2002) as morphoserries IIB-1 and referred to as Teleost centrum type E in Eberth and Brinkman (1997). These centra were referred to the Hiodontidae by Brinkman and Neuman (2002) because of the morphology of the first centrum, which has a distinctive quadripartite anterior surface and small round pits for the neural arch (Figure 5A). Additionally, as in *Hiodon*, the ribs articulate directly with the centrum, rather than the parapophyses, and a rib articular pit is present on the side of the centrum posterior to the parapophyses. The neural arches are autogenous except for the posterior-most abdominal centra (Figure 5E). Neural arch articular pits are shallow, oval depressions that extend the full length of the centrum. Parapophyses are fused to the centrum. These are laterally directed processes in the anterior to mid-abdominal centra (Figure 5B), and ventro-laterally directed processes in the posterior abdominal centra

(Figure 5C-E). As in specimens from the Dinosaur Park Formation, the sides and ventral surface of the centrum are pierced by numerous small pores.

Distribution.—Hiodontid centra are widely distributed in the Dinosaur Park Formation but are never abundant. They extend through the Late Cretaceous, being present in the Cenomanian of Utah and the late Maastrichtian of Montana (Brinkman et al., 2013, 2014).

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

Order ELLIMMICHTHYIFORMES Grande, 1985

Family SORBINICHTHYIDAE Bannikov and Bacchia
2000

Remarks.—Ellimmichthyiformes are a group of freshwater and marine clupeomorph fish. Freshwater members of the group include the genus *Diplomystus*, which is well represented by articulated specimens from the Eocene Green River Formation, and *Horseshoeichthys*, which was described on the basis of a partial skeleton from the Horseshoe Canyon Formation of Alberta, Canada (Newbrey et al., 2010). Both of these genera are present in the Dinosaur Park Formation and are represented by centra that can be identified by comparison with those from articulated specimens.

Diplomystus Cope, 1877

Figure 6

Teleost Q, Eberth and Brinkman, 1997:58

Morphoserries IIB-2 Brinkman and Neuman, 2002:149-
150, fig. 7

Diplomystus sp. Brinkman et al., 2013:213, fig. 10.15

Diplomystus, Divay and Murray, 2016:2-4, fig. 2

Voucher Specimens.—from Onefour Mud-filled Channel complex: TMP 1993.0116.0008, seven centra from locality L1115; TMP 1993.093.0028, twenty-three centra from locality L1101; TMP 1993.093.0032, seven centra from locality L1109; TMP 1993.093.0027, three centra from locality L1112; TMP 993.093.0029, eight centra from locality L1111; TMP 1993.093.0031, nineteen centra from locality L1112; TMP 2016.009.0002, eleven centra from JMC 700.

Remarks.—Centra described by Brinkman and Neuman (2002) as morphoserries IIB-2 and referred to as Teleost centrum type Q in Eberth and Brinkman (1997) were identified as the ellimmichthyiform *Diplomystus* by Brinkman et al. (2012) based on a comparison with centra of that genus from the Green River Formation. Additional detail on the centra from *Diplomystus* was subsequently proved by Divay and Murray (2016) who described isolated centra of this genus from the Wasatch Formation. Anterior abdominal centra are similar to

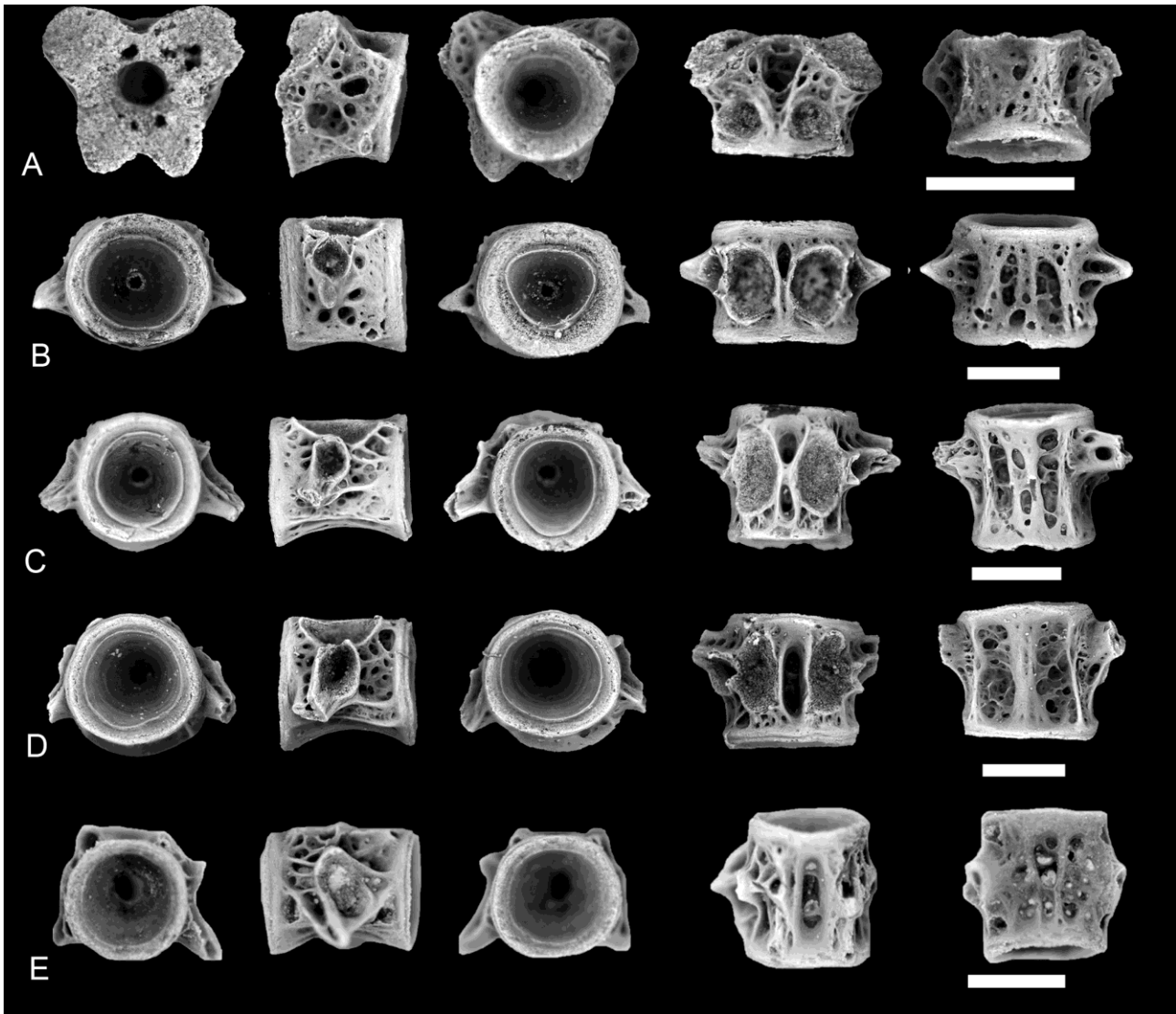


FIGURE 5. Centra referred to *Hiodontidae* gen. indet. shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A**) first centrum, TMP 2004.104.0062. **B-E**) abdominal centra, arranged from anterior to posterior to illustrate variation along the vertebral column. **B**, TMP 2004.104.0062; **C**, TMP 1995.181.0034; **D**, TMP 2004.104.0062; **E**, TMP 1995.181.0034. 5E is from Newbrey et al. (2013:fig. 2). Scale bar equals 1 mm.

centra of *Coriops* in having laterally directed parapophyses (Figure 6A). However, neural arch articular pits are restricted to the anterior portion of the centrum, mid-dorsal and mid-ventral ridges are present, the neural arch articular pits are shallow, and dorsal processes are present on the posterior edge of the dorsal centra. Posterior abdominal centra differ in that the centra are relatively higher and the neural arch articular pits are restricted to a more anterior position on the centra (Figure 6C-D). Regional variation in the shape of the neural arch pits along the vertebral column is present. In the anterior centra, these are widely separated (Figure 6A-B). More posteriorly, they become

positioned more closely to one another (Figure 6C-D), and in the most posterior abdominal centra, the neural arch is fused to the centrum.

Distribution.—In the Belly River Group, *Diplomystus* has a patchy distribution, being very abundant in some localities but absent in most. Centra of *Diplomystus* are also present in the Cenomanian and early Santonian of Utah (Brinkman et al., 2013).

Horseshoeichthys Newbrey, Murray, Brinkman,
Wilson and Neuman, 2010

Figure 7

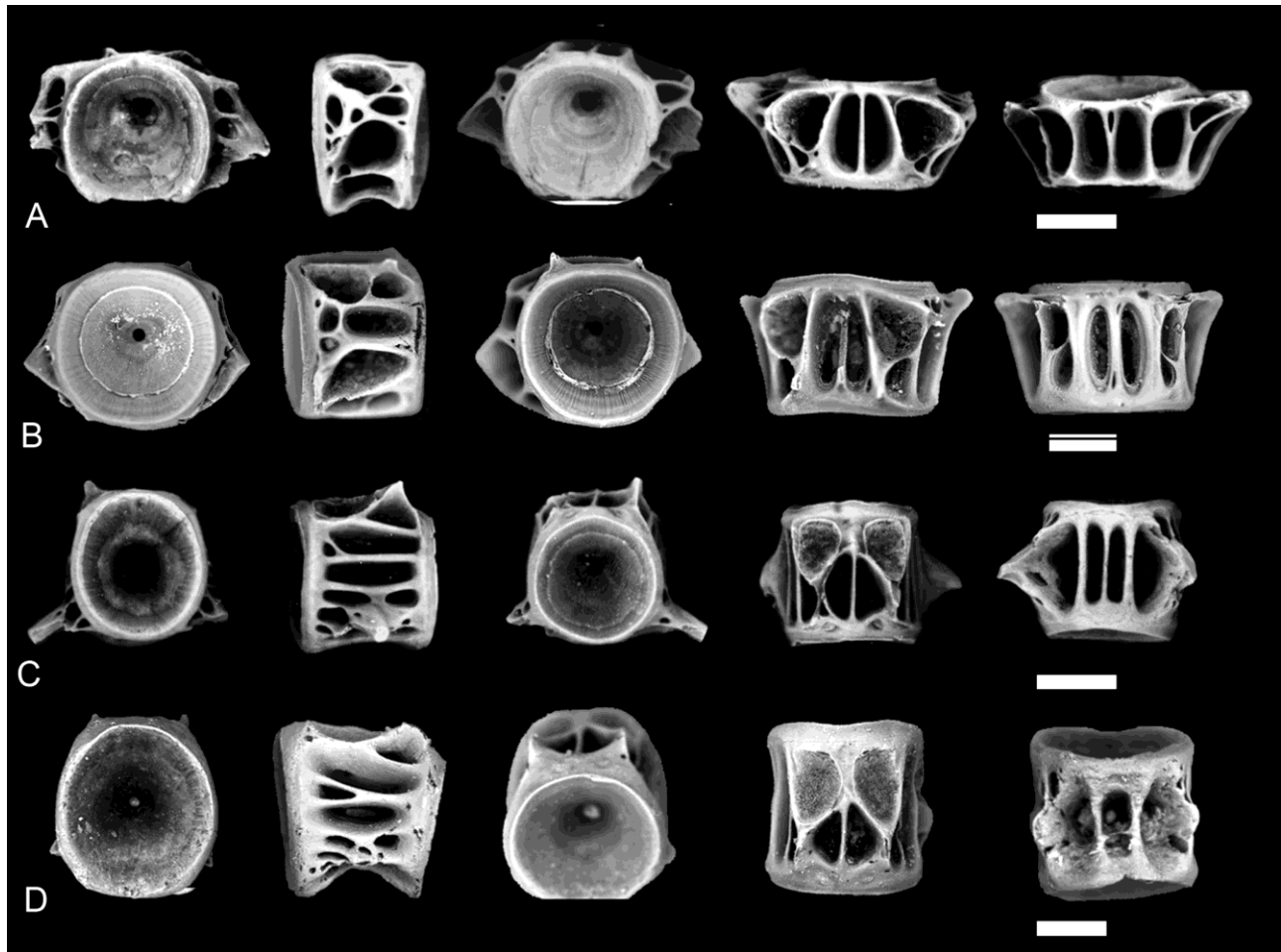


FIGURE 6. Centra of *Diplomystus* sp., showing variation along the column shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. A) TMP 93.124.40; B) TMP 1993.93.28; C) TMP 2016.009.0002; D) TMP 1987.001.0066. Figs. 6A and 6C from Brinkman and Neuman (2002:fig. 7). Scale bar equals 1 mm.

Teleost L, Eberth and Brinkman, 1997:57
 Teleost S, Eberth and Brinkman, 1997:48
 Morphoserries IB-2, Brinkman and Neuman, 2002:143, fig. 2.15-2-28
 Morphoserries IIA-2, Brinkman and Neuman, 2002:146, fig. 4.12- 4.22
 Morphoserries IB-2 (?esocoid indeterminate), Brinkman and Neuman, 2005:180, fig. 9.8C
 Morphoserries IIA-2 (possibly *Cretophareodus*), Brinkman and Neuman, 2005:180, fig. 9.8E
 Ellimmichthyiformes gen et sp. nov., Larson, Brinkman, and Bell, 2010:1165, fig. 5B
Horseshoeichthys sp. Newbrey et al., 2010:1183-1195, figs, 1-5, 9
Horseshoeichthys sp. Newbrey et al., 2013:fig. 4
Horseshoeichthys, Brinkman et al., 2013:214-215, fig. 10.16C
Horseshoeichthys, Brinkman et al., 2017a:27. Fig. 15

Voucher Specimens.—Anterior abdominal centra (teleost centrum morphotype S): TMP 1986.158.0046, one centrum from BB 100; TMP 1986.199.0048, one centrum from BB 97; TMP 1986.053.0013, two centra from BB 102; TMP 1986.217.0047, one centrum from BB 51; TMP 1993.144.0001, one centrum from BB 94; TMP 1993.093.0103; twenty-eight centra from locality L1105; TMP 1993.093.0105, twelve centra from locality L1112; TMP 1993.093.0099, five centra from locality L1101; TMP 1993.093.0104, seven centra from locality L1110; TMP 1995.180.0057, one centrum from BB 107; TMP 2008.025.0010, sixteen centra from JMC Stake Site; TMP 2016.009.0024, more than 100 centra from JMC 700; TMP 2019.020.0214, one centrum from L2370.

Posterior abdominal centra (teleost centrum morphotype L): TMP 1986.0185.0024, one centrum from BB 54; TMP 1987.004.0011, two centra from BB

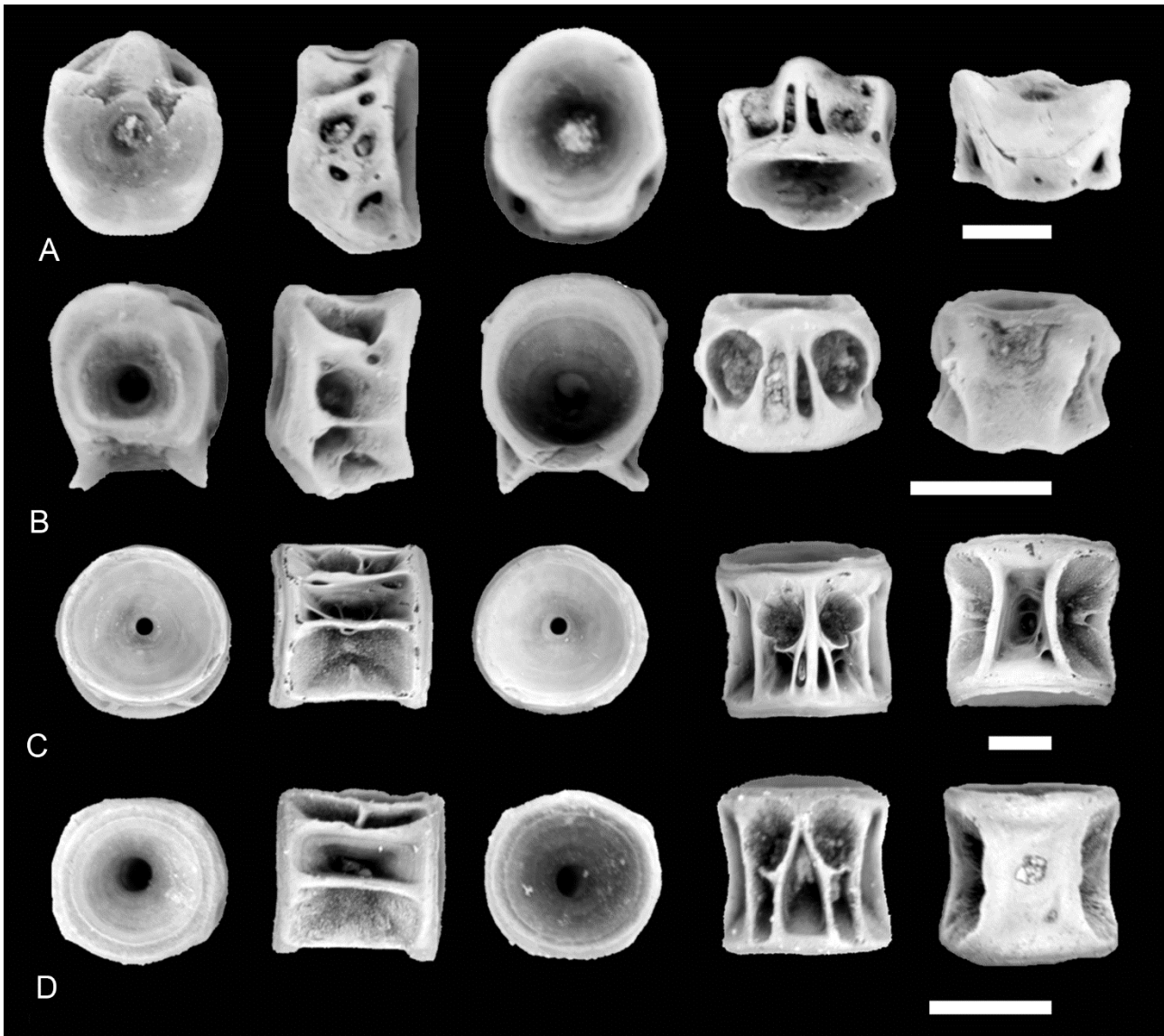


FIGURE 7. Centra of *Horseshoeichthys* sp. shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-B**) anterior-most centra, **A**, TMP 1993.093.0097; **B**, TMP 1993.93.0103. **C-D**) more posterior abdominal centra; **C**, TMP 1986.010.0064; **D**, TMP 1993.093.0025. Scale bar equals 1 mm.

54; TMP 1986.038.0045, one centrum from BB 86; TMP 1988.007.0070, one centrum from BB 98; TMP 1986.045.0089, one centrum from BB 54; TMP 1986.033.0050, one centrum from BB 31; TMP 1995.180.0039, one centrum from BB 107; TMP 1993.116.0014, twenty-four centra from locality L1115; TMP 1993.093.0023, ten centra from locality L1105; TMP 2016.009.0003, approximately 30 centra from JMC 700.

Remarks.—*Horseshoeichthyes* was described on the basis of an articulated specimen from the early Maastrichtian beds of the Horseshoe Canyon Formation

of Alberta, Canada (Newbrey et al., 2010). Two of the anterior abdominal centra were preserved as three-dimensional isolated elements. These showed that two centrum morphotypes that had been previously assumed to be taxonomically distinct were regional variants from along the vertebral column of this genus. The anterior abdominal centra of *Horseshoeichthyes* were described by Brinkman and Neuman (2002) as morphoseries IIA-2 and informally referred to as teleost centrum type S by Eberth and Brinkman (1997) (Figure 7A-B). These typically have short ventro-laterally directed parapophyses and neural arches that are unfused. In

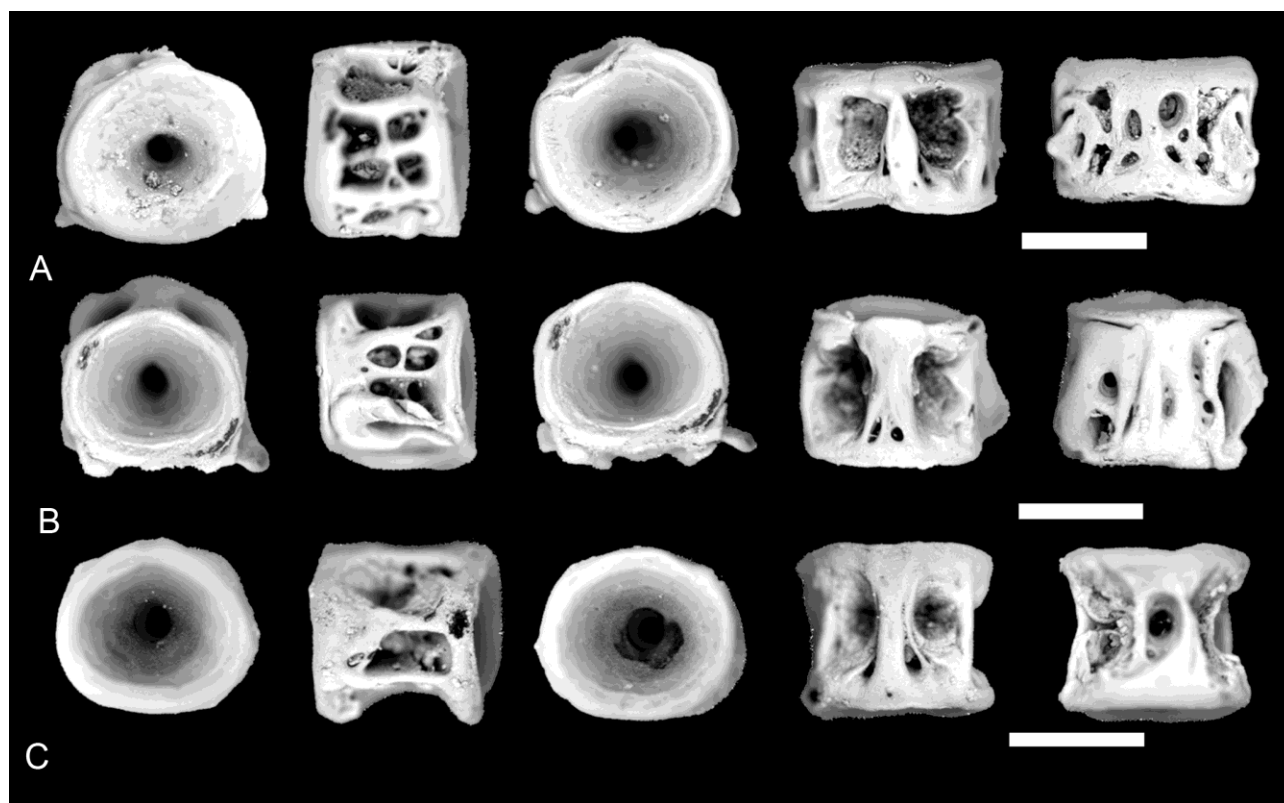


FIGURE 8. *Ellimmichthyiformes* indet. type U-7. **A**, TMP 2007.027.0021; **B**, TMP 2007.027.0022; **C**, TMP 2007.027.0024. Scale bar equals 1 mm.

these features, the centra are like the anterior abdominal centra of *Coriops*, although they differ in having a mid-dorsal bar extending between the ends of the centrum and not having a mid-ventral pit. A distinctive feature of this centrum morphology is a smooth ventral surface between the parapophyses.

The more posterior abdominal centra, designated morphoserries 1B-2 by Brinkman and Neuman (2002) and referred to as teleost centrum type L in Eberth and Brinkman (1997), are simple spools with autogenous parapophyses and neural arches (Figure 7C-D). The neural arch articular pits are restricted to the anterior portion of the centrum. These are separated by a mid-dorsal ridge. Large, rectangular parapophyseal pits are present on the ventro-lateral side of the centrum. Ventrally, a mid-ventral pit is usually present (Figure 7C), although in some centra this can be restricted to a small circular opening (Figure 7D).

Distribution.—Centra of *Horseshoeichthys* have a patchy distribution in the Belly River Group of Alberta, generally being rare but being of high abundance in some localities. They are also present in the Milk River Formation of Alberta and the Cenomanian to Turonian of Utah (Brinkman et al.,

2013), as well as the early Maastrichtian Horseshoe Canyon Formation of Alberta (Newbrey et al., 2010; Larson et al. 2010). They were not present in the late Maastrichtian Hell Creek Formation (Brinkman et al., 2014).

Family Indet.

Gen. et sp. indet type U-7

Figure 8

Genus et sp. indet. type U-7, Brinkman et al., 2013:215, fig. 10.17

Voucher Specimens.—TMP 2007.027.0021, from locality L1115; TMP 2007.027.0022 from locality L1115; TMP 2007.027.0024 from locality L1115; TMP 2019.060.0205, one centrum from locality L1115.

Remarks.—*Ellimmichthyiform* gen. et sp. indet. type U-7 was recognized by Brinkman et al. (2014) on the basis of a centrum that had similarities with the posterior abdominal centra of *Horseshoeichthys*. As in that genus, the neural arch articular pits are separated by a mid-dorsal bar and a pair of small pits are present posterior to the neural arch articular pits (Figure 8A-C).

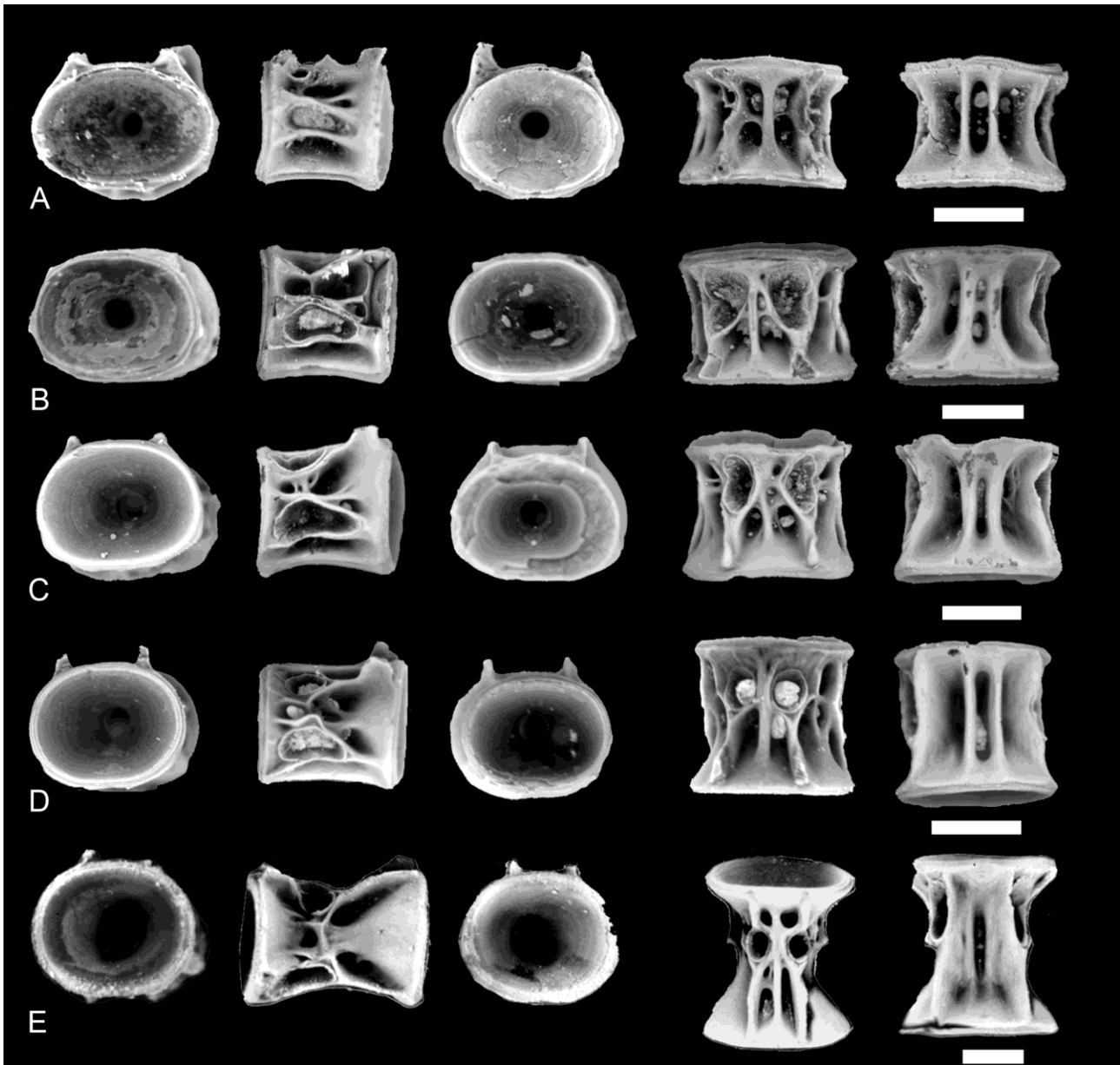


FIGURE 9. Centra of *Clupeiformes* gen. et sp. indet. type G, showing variation along the column. Shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A)** TMP, 1993.093.0031 from L1102; **B)** TMP 1993.116.0009; **C)** TMP 1989.001.0058; **D)** TMP 1993.093.0013; **E)** TMP 1989.001.0058. Fig. 9F from Neuman and Brinkman (2002:Figure 3). Scale bar equals 1 mm.

Parapophyseal pits are large, and a broad network of ridges separates the neural arch and parapophyseal pits. The ventral surface of the centrum varies in the number and size of pits. In some, multiple pits are present (Figure 8A), while in others this surface is relatively solid (Figure 8B) or has a single large pit (Figure 8C). The centra of *ellimmichthyiform* gen. et sp. indet. type U-7 differ from those of *Horseshoeichthys* in that the neural arch articular pits are relatively larger, generally

extending the full length of the centrum, and the centra are more robust.

Distribution.—In the Belly River Group, centrum morphotype U-7 has only been recovered from one locality in the Onefour Mud-filled Channel Complex. The presence of centra of morphotype U-7 in both the Cenomanian of Utah and late Campanian of Alberta suggests that it is a late-surviving member of a lineage present in the Western Interior of North America at the very base of the Late Cretaceous.

Order CLUPEIFORMES

Family indet.

Gen. et sp. indet. type G.

Figure 9

Clupeiformes, gen. et sp. indet type G, Brinkman et al., 2013:215, fig. 10.18A-B

Voucher Specimens.—from Onefour Mud-filled Channel complex: TMP 1990.048.0017, two centra from locality L1106; TMP 1990.067.0033, three centra from L1113, TMP 1993.116.0009, approximately 20 centra from locality L1115; TMP 1993.093.0031, seven centra from L1102; TMP 1993.124.0039, five centra from locality L114; TMP 2008.025.0006, approximately 20 centra from JMC Stake Site; TMP 1993.093.0013, approximately 20 centra from locality L1102; TMP 1994.023.0025, thirteen centra from locality L1102, TMP 1994.023.0029, seven caudal centra from locality L1102; TMP 2016.009.0001, approximately 40 centra from JMC 700.

Remarks.—Centra that Brinkman and Neuman (2002) described as morphoserries IC-1 and referred to as teleost G by Eberth and Brinkman (1997) were included in Clupeiformes gen. et sp. indet. type G by Brinkman et al. (2013). Characteristic features include the gracile structure, dorsal processes at the posterior end of the centra, and small articular pits for the neural arch restricted to the anterior end of the centra. As well as showing these features, the Dinosaur Park clupeiform typically has a mid-dorsal ridge, and a mid-ventral pit. However, the anterior-most abdominal centra differ in that neural arch articular pits are absent (Figure 9A). Also, anterior abdominal centra are short and oval in end view (Figure 9A-C) whereas the more posterior abdominal centra are elongate and round in end view (Figure 9E).

Distribution.—In the Dinosaur Park Formation, centra of Clupeiformes gen. indet. type G have only been recovered from a series of vertebrate microfossil localities preserved in mud-filled channels at Onefour, south-eastern Alberta. However, they have also been described from the Kaiparowits Formation of Utah (Brinkman et al., 2013).

Order OSTARIOPHYSI Sagemehl, 1885
Series ANOTOPHYSI Rosen and Greenwood, 1970
Order GONORYNCHIFORMES Berg, 1940
Family GONORYNCHIDAE Bonaparte, 1850
Notogoneus Cope, 1885
Figure 10

Teleost R, Eberth and Brinkman, 1997:57
Morphoserries IIIA-2, Brinkman and Neuman, 2002:151, fig. 8.5-8.8

Voucher Specimens.—from Onefour Mud-filled

Teleost G, Brinkman and Eberth, 1997:57

Morphoserries IC-1, Brinkman and Neuman, 2002:143-144, fig. 3.1-3.12

Channel complex: TMP 1993.093.0093, centra from L1104; TMP 1993.097.0007, centra from L1107; TMP 2009.120.0007, one centrum from locality L1101; TMP 2016.009.0008, two centra from JMC 700; TMP 2008.025.0013, centrum fragments from JMC Stake Site.

From Dinosaur Provincial Park: TMP 206.11.11, four centrum fragments from locality L2371 (Wolf Coulee microsite).

Remarks.—The gonorynchiform *Notogoneus* is one of the few teleosts represented by articulated skeletons from the late Campanian of the Western Interior of North America (Grande and Grande, 1999). Recently, material including distinctive skull bones and centra found abundantly in the Onefour mud-filled channels were identified as being from *Notogoneus* by Divay et al. (in press), partly based on comparison with elements removed from an articulated specimen of *Notogoneus* from the Green River Formation.

The centra identified as being from *Notogoneus* by Divay et al. (in press) were described by Brinkman and Neuman (2002) as morphoserries IIIA-2 and referred to as teleost centrum type R in Eberth and Brinkman (1997). Variation along the vertebral column in articulated specimens of *Notogoneus* allows isolated centra from different vertebral regions to be recognized. The most abundantly encountered isolated centra are from the middle to posterior regions of the abdominal series (Figure 10A-B). These centra are often large, reaching 1 cm in length. Neural arches are fused to the centra and the neural arch bases are located close together. Parapophyses are fused to the centrum and are widely spaced at the antero-ventral corner of the centra. This arrangement results in the mid-abdominal centra having a triangular appearance in anterior and posterior views (Figure 10A). A ridge is present dorsally between the neural arches, and a mid-ventral pit is present between the transverse processes. One of the most characteristic features of this centrum morphotype is the presence of a strong rounded bar running antero-posteriorly on the lateral surface of the centrum above the transverse process.

Distribution.—Centra of *Notogoneus* are most abundant in the Onefour mud-filled channels but also occur in the fluvial beds of Dinosaur Provincial Park.

Order GONORYNCHIFORMES Berg, 1940
Gen. et sp. indet. type H
Figure 11

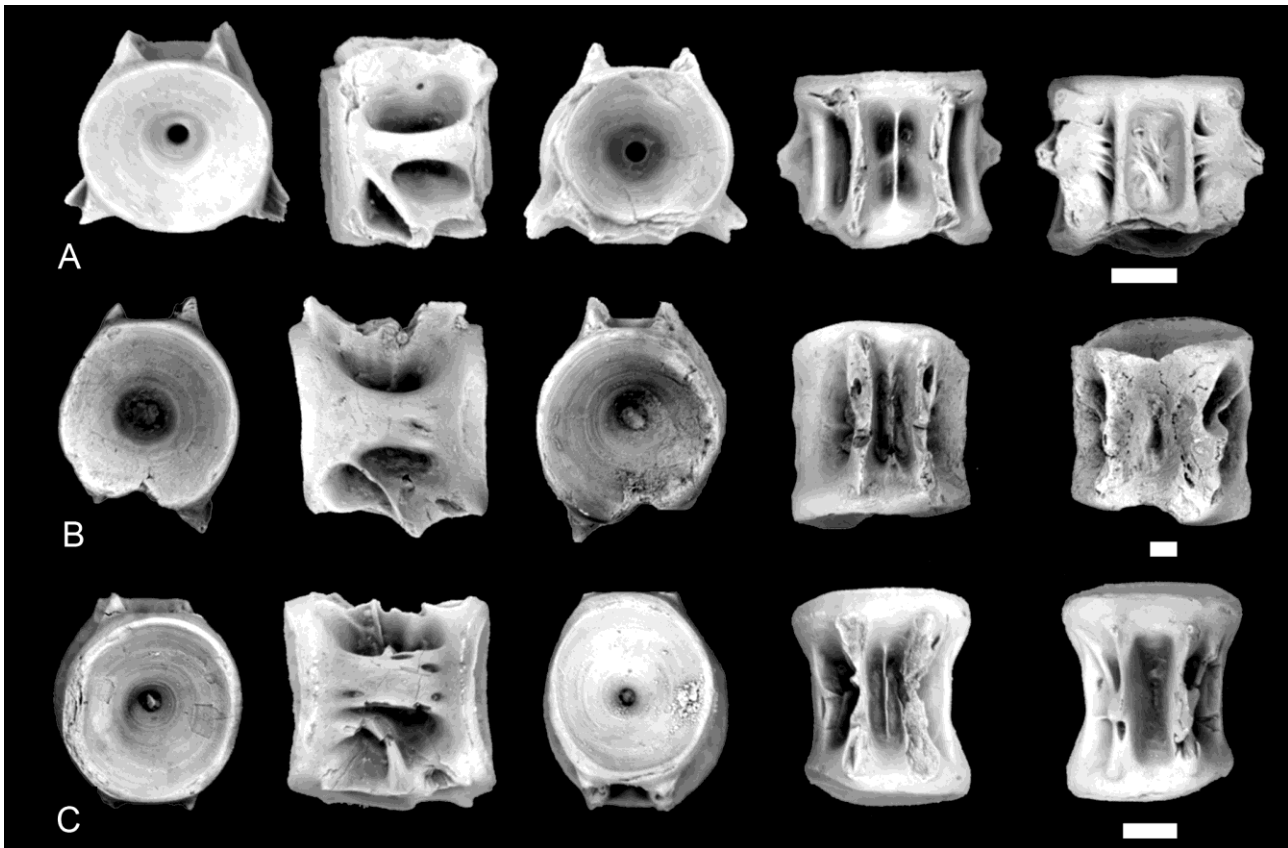


FIGURE 10. Centra of *Notogoneus* sp. from the mid and posterior region of the abdominal series shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. A) TMP 1993.093.0093; B) TMP 1993.097.0007; C) TMP 1993.093.0093. Figure 10A from Neuman and Brinkman (2002:fig. 8). Scale bar equals 1 mm.

Morphoserries IIIA-1, Brinkman and Neuman, 2002:150-151, fig. 8.1-8.4

Morphoserries IIIA-1 (teleost indeterminate), Neuman and Brinkman, 2005:180, fig. 9.8G

Genus et sp. indet. type HvB, Brinkman et al., 2013:225, fig. 10.26

Genus and species indet H-vB, Brinkman et al., 2014:261, fig. 10C

?*Ostariostoma*, Brinkman et al., 2017:21, fig. 10-11

Voucher Specimens.—From Onefour area: TMP 1995.157.0052, approximately 21 post-Weberian centra from locality L1108; TMP 2016.009.000.9 seven first abdominal centra (morphotype HvB) and 4 abdominal centra (morphotype HvA), from JMC 700; TMP 1993.116.0020, three abdominal centra (morphotype HvA) from locality L1115; TMP 2000.022.0010, four seven first abdominal centra (morphotype HvB) from locality L1108; TMP 2008.025.0012, four abdominal centra (morphotype HvA) and four seven first abdominal centra (morphotype HvB) from locality

L1108; TMP 1997.019.0003, one abdominal centrum (morphotype HvA) from locality L1109.

From Dinosaur Provincial Park: TMP 1996.1.45, one abdominal centrum (morphotype HvA) from BB105; TMP 1986.45.79, two abdominal centra (morphotype HvA) from BB 54.

Remarks.—The presence of a second kind of gonorynchiform in the Dinosaur Park Formation, here referred to as Gonorynchiform gen. et sp. indet. type H, is documented by centra. It is included in the Gonorynchiformes because one of the variants included in this morphotype, described by Brinkman et al. (2013) as morphotype HvB, matches both the centrum identified as a gonorynchiform Weberian centrum by Divay and Murray (2016:fig. 4 A-B) and the first centrum in *Notogoneus* (Divay et al., in press:fig 6A). Following Divay et al. (in press) these are here referred to as first abdominal centra rather than Weberian centra because, although they are part of a sound-conductive system, only otophysans have a true Weberian system. In these centra (Figure 11A), the neural arches are not

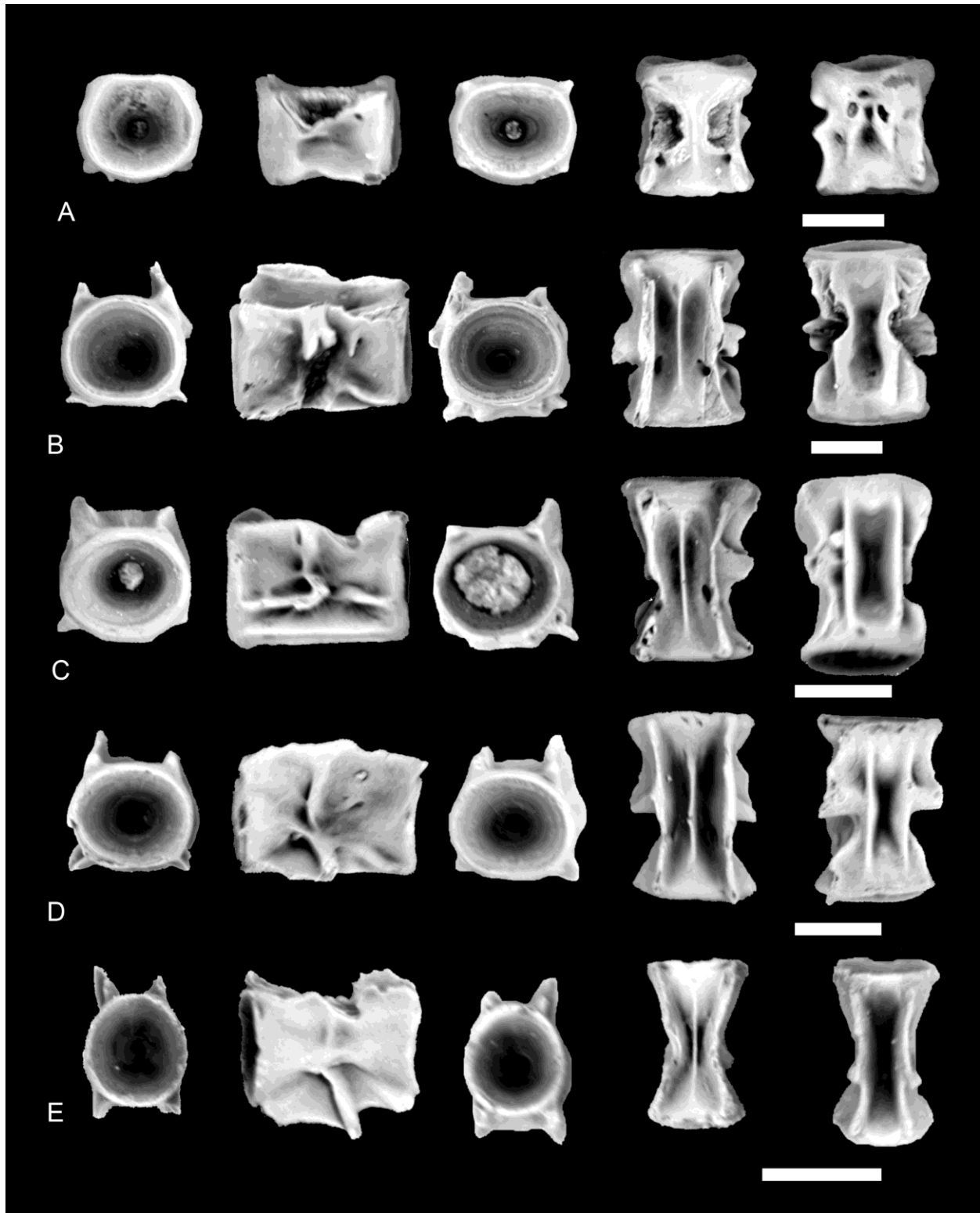


FIGURE 11. Centra of *Gonorynchiformes* gen. et sp. indet. type H shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A**) centrum morphotype HvB, TMP 2000.022.0010; **B-D**) centrum type HvA, showing variation along the column; **B**), TMP 1997.018.0007; **C**) TMP 2000.022.0011; **D**) TMP 2000.022.0009. **E**) caudal centrum, TMP 1995.180.0041. Figure 11B from Neuman and Brinkman (2005:fig. 9.8G). Scale bar equals 1 mm.

fused to the centrum. Instead, oval pits are present separated by a solid bar of bone. Parapophyseal pits are absent. The ventral surface of the centrum is flat and a mid ventral pit is present.

The more posterior abdominal centra of Teleost type H were described by Brinkman and Neuman (2002) as morphoserries IIIA-1 (referred to in catalogue records as centrum morphotype HvA). Both morphotypes HvA and HvB are elongate. Centrum morphotype HvA (Figure 11B-D) has neural arches fused to the centrum with the bases of the neural arch extending the length of the centrum. A narrow mid-dorsal ridge is present between the bases of the neural arch. On centra interpreted as from a more anterior position, the parapophyses are autogenous (Figure 11B). The parapophyseal pit is a shallow area on the lateral surface of the centrum. A stout ridge extends from the neural arch to the dorsal edge of the parapophyseal articular pit. On centra interpreted as being from a more posterior position, the parapophyses are fused to the centrum (Figure 11C-D). A mid-ventral pit is present on centra from both regions. In the more anterior abdominal centra this pit is bordered by a flat flange with a notch for the parapophyses midway along its length (Figure 11B). In the more posterior abdominal centra the pit is bordered by two narrow ridges (Figure 11C-D). Caudal centra differ from the posterior abdominal centra in being narrower (Figure 11E).

Based on patterns of distribution and comparison with the centra partially visible in an articulated specimen, Brinkman et al. (2017a) suggested that centrum morphotype H may be from *Ostariostoma*, raising the possibility that this fish was a gonorynchiform rather than an osteoglossomorph. However, pending additional support for this association, the teleost represented by centrum type H is treated here as a distinct taxon.

Distribution – Centra of Teleost type H are widely distributed in the Dinosaur Park Formation. They are also present in the Turonian of Utah (Brinkman et al., 2013) and late Santonian Milk River Formation of southern Alberta (Brinkman et al., 2017a), but were not encountered in the late Maastrichtian Hell Creek Formation of Montana.

Superorder OSTARIOPHYSI Sagemehl 1885 (sensu Fink and Fink, 1996)

Series OTOPHYSI Garstang, 1931 (sensu Rosen and Greenwood, 1970)

Gen. et sp. indet. type U3/BvD
Figures 12, 13B

Otophysi gen et sp. indet. type U3/BvD, Brinkman et al., 2013:215-219, figs. 10.19A-C, 10.20A-C, 10.21A-C

Otophysi, gen et sp. indet. Brinkman et al., 2014:255-256, fig. 7A-D

Otophysi genus et sp. indet U-3/BvD, Brinkman et al., 2017a:30-33, figs. 16-17, 18B

Voucher Specimens.—Anterior centra of Weberian apparatus (also referred to as centrum morphotype U-3): TMP 1995.157.0071, six centra from locality L1108; TMP 2016.011.007, five centra from locality 2371; TMP 2016.009.0011, three centra from JMC 700; TMP 2000.019.0036, one centrum from locality L1104; TMP 2017.011.0010, approximately 15 centra from locality L2370; TMP 2019.060.0206, one centrum from L1115; TMP 2019.060.0208, three centra from locality L2370.

Third centrum of the Weberian apparatus (also referred to as centrum morphotype BvC): TMP 2004.104.67, one centrum from Maries Site; TMP 2019.020.0212 two centra from locality L2370.

Abdominal centra (also referred to as centrum morphotype BvD): TMP 2016.009.0010, two centra from Onefour area; TMP 2017.020.0002, one centrum from Lost River Ranch microsite; TMP 2017.011.0011, seven centra from locality L2370 (H&M Site); TMP 2004.104.0077, one centrum from Marie's Site; TMP 2019.060.0195, one centrum from BB 107 (Chris's Site); TMP 2019.060.0190, one centrum from BB 104; TMP 2019.060.0191 one centrum from BB 105; TMP 2019.060.0187, three centra from BB 100; TMP 2019.060.0196; one centrum from BB 78.

Remarks.—Brinkman et al. (2017a) concluded that three distinct centrum morphotypes that had been informally designated as U-3, BvD, and BvC were regional variants from the vertebral column of a single kind of otophysan fish, which was designated gen. et sp. indet. type U3/BvD. This was included in the Otophysi by Brinkman et al. (2013) because they identified two of these centrum morphotypes, U3, and BvC, as being part of the Weberian apparatus. The third centrum morphotype, BvD, was interpreted as including the post-Weberian abdominal centra.

The centrum identified as the anterior centrum of the Weberian apparatus had previously been referred to as centrum morphotype U-3 (Fig.12A). As in extant members of the Otophysi, this centrum is greatly foreshortened. The anterior surface is nearly flat, while the posterior surface is shallowly concave. A pair of small circular pits separated by a rounded bar of bone about equal in width to the diameter of the pits is present on the dorsal surface. These pits were interpreted as the articular surfaces for the second pair of Weberian ossicles, the scaphium. As preserved, the parapophyses appear to be low vertically oriented ridges. The length of the parapophyses is unknown because of breakage. The centra differ from the anterior-most centrum of extant otophysians in the presence of a large circular

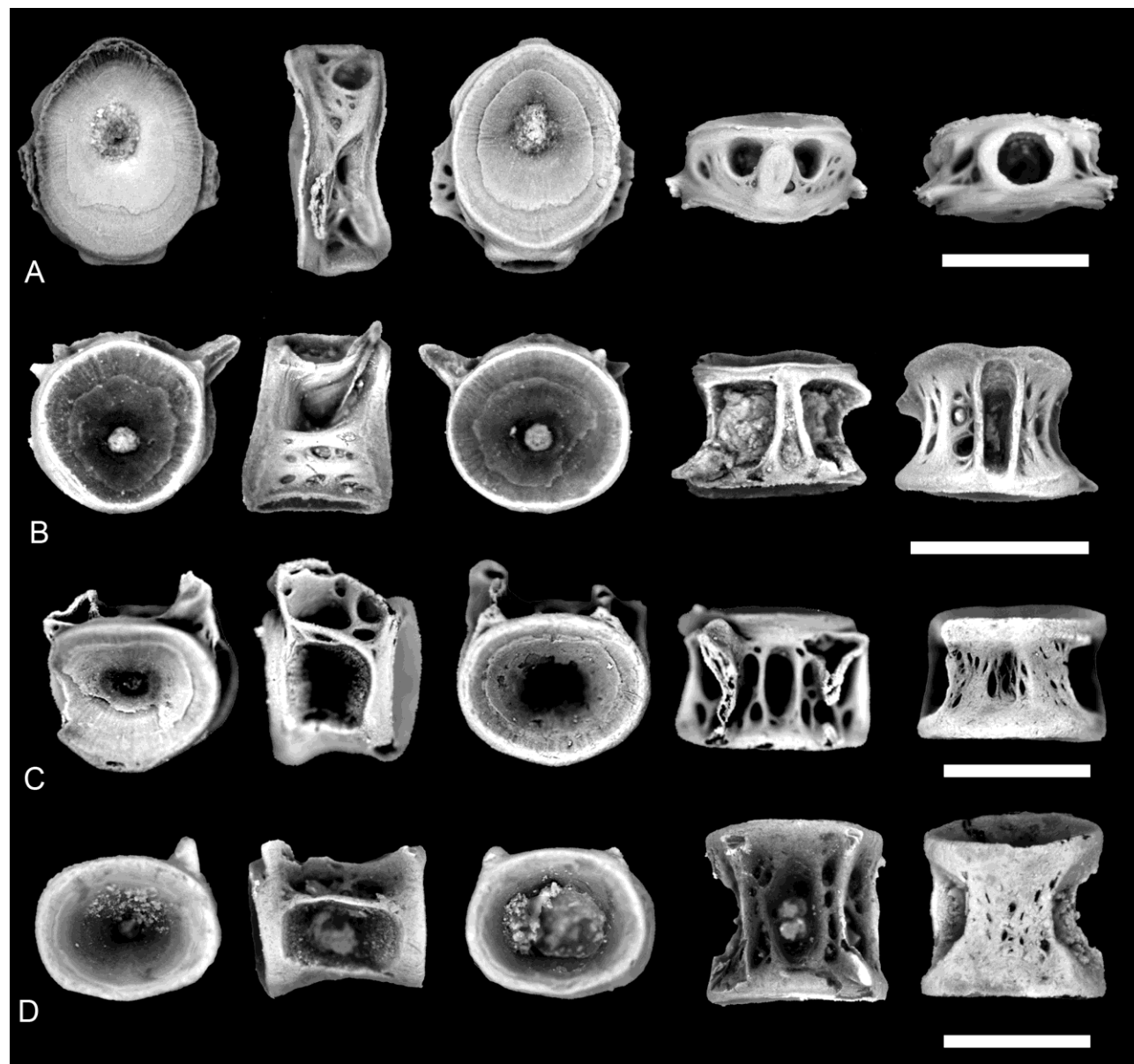


FIGURE 12. Centra *Otophysi* gen. et sp. indet. type U3/BvD shown in, from left to right, anterior left lateral, posterior dorsal and ventral views. **A)** anterior-most Weberian centrum (centrum morphotype U3), TMP 2004.104.0075; **B)** third centrum of the Weberian apparatus (centrum morphotype BvC), TMP 2019.060.0230; **C-D)** post-Weberian abdominal centra (centrum morphotype BvD); **C)** TMP 2019.060.0196, from locality L1131; **D)** TMP 2019.060.0195 from locality BB 107. Scale bar equals 1 mm.

fossa on the ventral surface of the centrum. The diameter of this fossa is greater than half the length of the centrum.

The centrum identified as the third centrum of the Weberian apparatus by Brinkman et al. (2017a) had been referred to as centrum morphotype BvC (Fig. 12B, 13B). The dorsal surface of the centrum is distinct in having large, rectangular neural arch articular pits. A mid-dorsal pit is present between the neural arch articular pits, and, laterally, a depression is present

below the neural arch articular pit. The dorsal edge of this depression projects laterally and forms the lateral border of the neural arch articular pit. A groove at the base of this depression that extends posterodorsally to the postero-dorsal edge of the centrum was interpreted as the articular surface for one of the Weberian ossicles, the tripus, by Brinkman et al. (2017a:fig. 18).

The centra identified as the post-Weberian abdominal centra of teleost U3/BvD by Brinkman et al. (2013) had been referred to as centrum morphotype BvD

(Figure 12C-D). Neural arches are fused to the centrum and a deep mid-dorsal pit is present between the neural arches. Parapophyses are autogenous and large parapophyseal pits are present on the ventro-lateral sides of the centrum. These pits are sub-rectangular in shape and are separated from the neural arch articular pit dorsally by a sharp ridge. The ventral surface of the centrum is covered by a network of antero-posteriorly oriented bone ridges.

Distribution.—In the Dinosaur Park Formation, Teleost indet. type U3/BvD occurs in both Dinosaur Provincial Park and the Onefour area of southeastern Alberta. However, it is relatively rare in both areas. In contrast, it is abundant in Turonian to Campanian localities of southern Utah. Based on this distribution pattern, Brinkman et al. (2013) suggested that this fish had a limited latitudinal distribution pattern. The intermediate abundance of this taxon in the late Santonian Milk River Formation of Alberta suggests that its distribution shifted in response to climate change (Brinkman et al. 2017a)

Order CHARACIFORMES Regan, 1911
Gen. Indet.
Figures 13C, 14

Teleost C, Eberth and Brinkman, 1997:58
Morphoserries IIA-3, Brinkman and Neuman, 2002:146-147, Figure 5
Characiformes, Newbrey et al., 2009:3829-3833.
Characiformes gen. et sp. indet., Brinkman et al., 2013:219-221, Figure 10.22A-B

Voucher Specimens.—First centrum of the Weberian apparatus: TMP1989.001.0061, one centrum from locality L1105; TMP1993.093.0040, one centrum from locality L1103; TMP1993.093.0042, one centrum from locality L1111; TMP1993.093.0036, one centrum from locality L1105; TMP1993.093.0037, one centrum from locality L1103; TMP1997.019.0014, one centrum from locality L1113; TMP1989.001.0076, one centrum from locality L1105; TMP1989.001.0078, one centrum from locality L1105; TMP1989.001.0079, one centrum from locality L1105; TMP1989.001.0080, one centrum from locality L1105; TMP1989.001.0083, five centra from locality L1105; TMP1994.023.0051, one centrum from locality L1102; TMP1993.116.0066, three centra from locality L1115.

Third Weberian centrum: TMP 1990.048.0011, one centrum from Onefour area; TMP 2008.025.0018, one centrum from JMC Stake Site; TMP 2016.009.0013, six centra from JMC 700; TMP 1989.001.0064, six centra from locality L1105; TMP 2019.060.0201, three centra from L1102.

Abdominal centra: TMP1994.023.0052, eight centra from locality L1102; TMP1993.124.0067, one centrum from locality L1114; TMP1993.116.0068, one

centrum from locality L1115; TMP1994.023.0023, one centrum from locality L11102; TMP1993.092.0030, one centrum from locality L1102; TMP1993.093.0039, two centra from locality L1101; TMP1993.093.0043, one centrum from locality L1101; TMP1990.048.0020, two centra from locality L1106; TMP1993.093.0045, four centra from locality L1105; TMP1989.001.0077, one centrum from locality L1105; TMP1989.001.0081, one centrum from locality L1105.

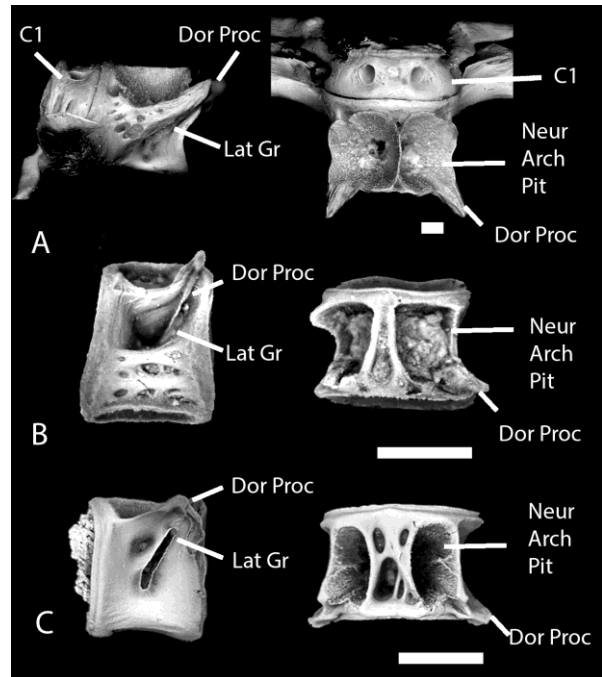


FIGURE 13. Third Weberian centrum of *Cyprinus cyprinus* compared with the third Weberian centra of the ostariophysan designated U3/BvD and Characiformes gen. et sp. indet. A) first and third Weberian centrum of *Cyprinus cyprinus* in lateral and dorsal views, specimen TMP 2007.030.0009. B) third Weberian centrum of the ostariophysan designated U3/BvD, TMP 2019.060.0230; C) third Weberian centrum of the Characiformes gen. et sp. indet., TMP 2016.060.00013. Abbreviations: C1, first Weberian centrum; Dor Proc, dorsal process; Lat Gr, lateral groove; Neur Arch Pit, neural arch articular pit. Scale bar equals 1 mm.

Remarks.—Characiformes are a group of ostariophysans that originated in the southern hemisphere and have generally been assumed to have been absent from North America until the Miocene. A characteristic feature of characiforms is the presence of a distinctive hinge joint between the dentaries, and the presence of a characiform in the Dinosaur Park Formation was documented by Newbrey et al. (2009) on the basis of dentaries with this feature. Based on comparison with extant members of the group, Brinkman et al. (2013) referred a series of distinctive centra, including elements from the Weberian apparatus,

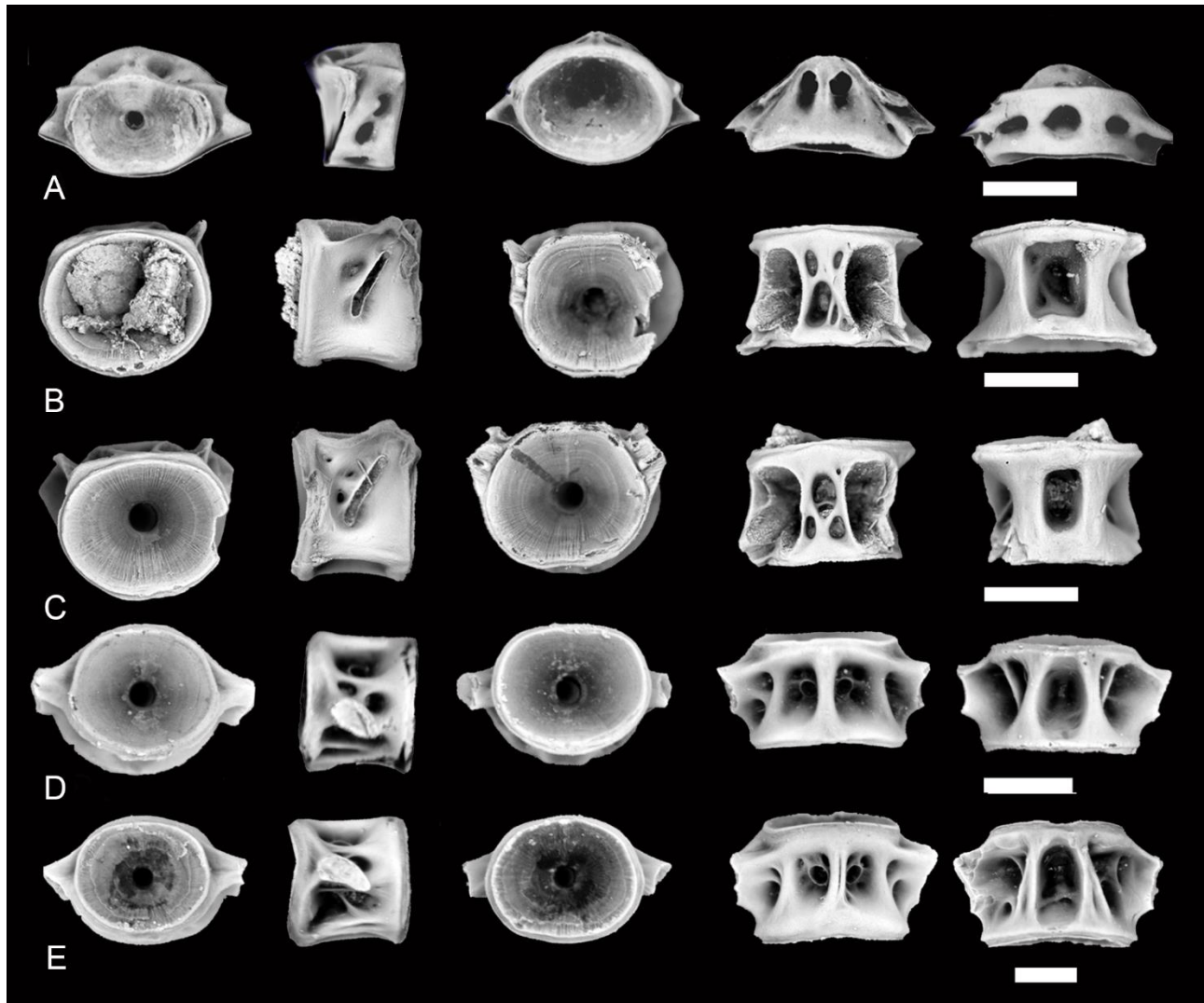


FIGURE 14. Centra of Characiformes gen. et sp. indet. shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A**) anterior-most centrum of the Weberian apparatus, TMP 1997.019.0014; **B-C**) third centrum of the Weberian apparatus, both included in TMP 2016.009.0013; **D-E**) abdominal centra, **D**, TMP 1991.113.0006; **E**, TMP 1993.093.0039. Figure 13A from Brinkman and Neuman (2002:fig.5). Scale bar equals 1 mm.

to the Dinosaur Park Formation characiform. These centra had been described by Brinkman and Neuman (2002) as morphoseries IIA-3, and had been referred to as teleost C by Eberth and Brinkman (1997).

Ostariophysan affinities of the teleost represented by these centra is supported by two centrum morphologies that can be identified as being from the Weberian apparatus. The centrum interpreted as the anterior-most centrum of the Weberian apparatus is distinctive in the presence of a saddle-shaped anterior articular surface (Figure 14A). The first centrum of the Weberian apparatus in extant characiforms has a similar shape (Brinkman et al. 2013:fig. 10.22), further supporting the interpretation that this fish is a member

of the Characiformes. A centrum interpreted as the third centrum of the Weberian apparatus is also present (Figure 13C, 14B-C). This centrum is similar to the corresponding centrum in *Cyprinus* (Figure 13A) in having large articular pits for the neural arch and a depression on the side of the centrum with a groove for articulation with the tripus. This groove is more distinct than in the corresponding third Weberian centrum of teleost U3/BvD, suggesting that the tripus-centrum articulation was more fully developed than in teleost U3/BvD.

Post-Weberian abdominal centra, here referred to the Dinosaur Park characiform, were described by Brinkman and Neuman (2002) as part of teleost centrum

morphoserries IIA-3. These centra are shorter than wide and wider than high (Figure 14D-E). Parapophyses are fused to the centrum. These are long, laterally directed parapophyses, although they are usually broken at their base. The parapophyses are simple rods of bone with few struts or flanges at their base. The antero-dorsal edge of the parapophyses are continuous with a ridge that borders that antero-dorsal edge of the centrum. Neural arch articular pits are separated by a rounded mid-dorsal ridge. Three fossa of sub-equal size are present ventrally.

Distribution.—Centra referred to the Dinosaur Park characiform are relatively abundant in a series of vertebrate microfossil localities in the Onefour area of Alberta. They have only been recovered from one locality in Dinosaur Park, L2371, which is a locality very high in section and is preserved in fine-grained sediment. Centra of the characiform also occur in the Kaiparowits Formation of Utah (Brinkman et al. 2013). As well, dentaries of the characiform are also present in the Mesa Verde Formation (pers. obs., University of Wyoming specimen UW 34886). They have not been observed in any of the Maastrichtian localities examined. Thus they appear to be stratigraphically restricted to a short interval during the late Campanian but widely distributed in the Western Interior of North America during this time.

Cohort EUTELEOSTEI sensu Arratia, 1999
Order SALMONIFORMES Bleeker 1859
Family ESOCIDAE Cuvier, 1817
Estesesox or *Oldmanesox*
Figs. 15-16

Teleost N, Eberth and Brinkman, 1997:57
Teleost indet. Peng, Russell, and Brinkman, 2001:18, Plate 4, fig. 12-13
Morphoserries IB-1, Brinkman and Neuman, 2002:141-143, fig. 2-1 to 2-14
Morphoserries IB-1, Neuman and Brinkman, 2005:176, fig. 9.8B
2010: Esocoidea, Larson, Brinkman, and Bell, p. 1165, fig. 5C
2013: Salmoniform, Brinkman et al., p. 223-225, fig.10.25
Salmoniform, Brinkman et al., 2014:257-259, fig. 9
Estesesox, Brinkman et al., 2017a:33-34, fig. 19

Voucher Specimens.—Centrum morphotype NvA: TMP 1986.043.0080, one centrum from BB 86; TMP 1993.093.0002, one centrum from locality L1105; TMP 1993.093.0002, one centrum from locality L1115; TMP 1986.203.0024, one centrum from BB 107; TMP 1986.218.0036, one centrum from BB 51; TMP 1986.060.0031, two centra from BB 54; TMP 1986.004.0037, one centrum from BB 31; TMP

1986.019.0065, one centrum from BB 54; TMP 1986.023.0087, one centrum from BB 86; 2007.039.0001 one centrum from BB 97; TMP 1995.151.0028, one centrum from BB 137.

Centrum morphotype NvB: TMP 1986.219.0040, two centra from BB 51; TMP 1986.044.0016, one centrum from BB 97; TMP 1986.041.0072, one centrum from BB 54; TMP 1995.143.0021, one centrum from BB 135. TMP 1993.116.0005, one centrum from locality L1115.

Centrum morphotype NvC: TMP 1986.045.0065; two centra from BB 54; TMP 1986.060.0033, five centra from BB 54; TMP 1986.242.0067, one centrum from BB 104; TMP 1986.006.0050, one centrum from BB 31; TMP 1986.193.0008, one centrum from BB 104; TMP 2017.011.0008, one centrum from L2370; TMP 2008.025.0007, two centra from JMC Stake Site; TMP 1987.028.0060, two centra from BB 105; TMP 1995.157.0114, one centrum from locality L1108; TMP 1995.157.0115, one centrum from locality L1108.

Centrum morphotype NvD: TMP 1995.180.0040, one centrum from BB 107; TMP 1987.154.0040, one centrum from BB 121; TMP 1987.019.0040, one centrum from BB 104; TMP 1993.093.0006, one centrum from locality L1112; TMP 1986.008.0089, one centrum from BB 102.

Centrum morphotype NvE: NvE TMP 1986.053.0012, one centrum from BB 102; TMP 1987.029.0074, two centra from BB 103; TMP 1993.093.0001, two centra from locality L1105; TMP 1995.157.0098, two centra from locality L1108.

Remarks.—The Esocidae (pikes and mud minnows) were first recognized in vertebrate microfossil localities of the Late Cretaceous by Wilson et al. (1992) on the basis of dentaries and palatines. Two genera were recognized, *Estesesox*, and *Oldmanesox*. In *Oldmanesox*, a single row of large teeth is present and replacement pits are present between groups of one to three teeth. In *Estesesox*, the anterior portion of the dentary bears three to four rows of teeth. Subsequently, Brinkman et al. (2014) recognized a second, unnamed species of *Estesesox* based on the presence of fewer tooth rows.

Esocids have centra that are simple spools with unfused parapophyses and neural arches in the abdominal series. Neural arch and parapophyseal articular pits are close together (in contrast to the condition in elopomorphs), and the centra tend to be as long as they are wide. Centra from Dinosaur Park Fm. that show these features were designated morphoserries IB-1 Brinkman and Neuman (2002) and were referred to as Teleost centrum type N by Eberth and Brinkman (1997) and Brinkman et al. (2014).

Five distinct variants of centrum type N can be recognized. These are referred to as NvA, NvB, NvC, NvD, and NvE. These centrum morphotypes were

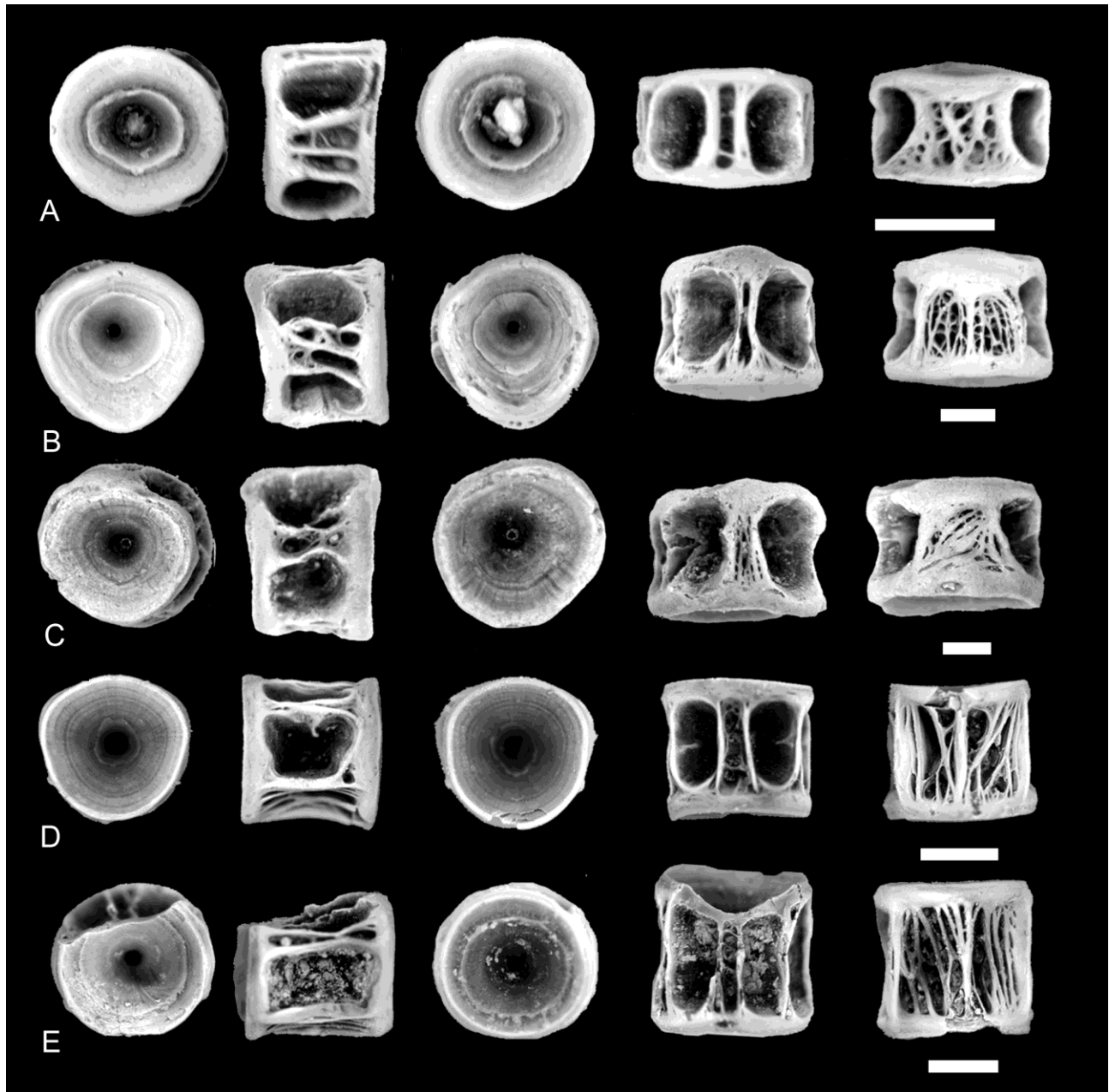


FIGURE 15. Esocidae centrum morphotypes NvA and NvB shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-C**) esocid centrum morphotype NvA. **A**, TMP 1995.157.0067; **B**, TMP 1993.093.0008; **C**, TMP 1995.151.0028. **D-E**) esocid centrum morphotype NvB. **D**, TMP 1989.001.0060; **E**, TMP 1993.116.0005. Figure 14C from Neuman and Brinkman (2005:fig.9.8B). Scale bar equals 1 mm.

considered to be taxonomically distinct by Brinkman et al. (2013, 2014), although, based on a study of the range in variation along the column in extant species of *Esox* (Sinha et al., 2019) it is likely that at least some are regional variants from along the column of a single taxon. Pending resolution of this question, the individual morphotype designations are described separately but

are included in a single operational taxonomic unit for estimates of diversity of teleosts in the assemblage.

Centrum Morphotype NvA.—Centrum morphotype NvA has a ventral network of bone ridges converging towards the midline (Figure 15A-C). A mid-ventral ridge is weakly developed (Figure 15B) or absent (Figure 15A, C). The neural arch pits extend for the full length of centra. The neural and parapophyseal

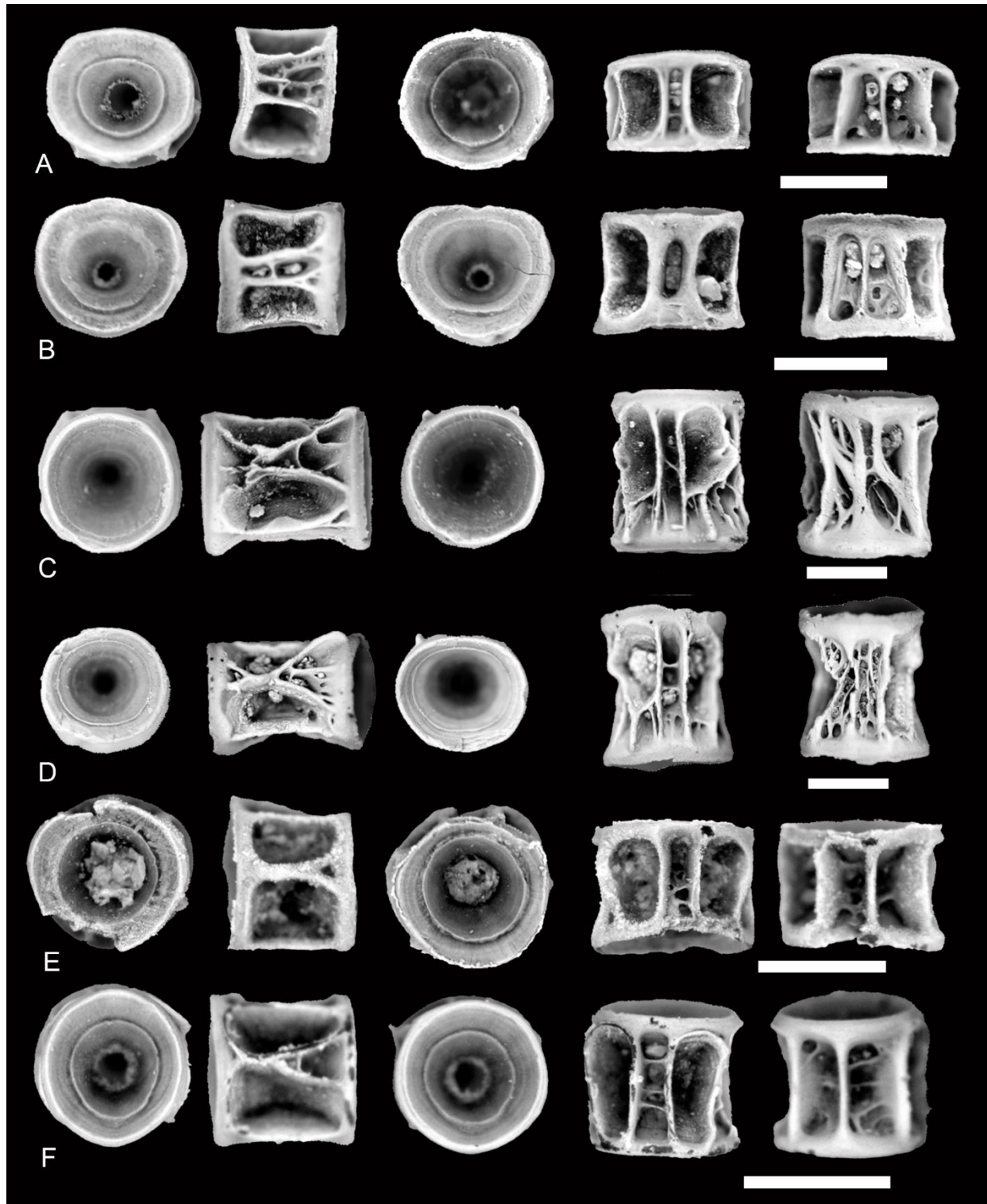


FIGURE 16. Esocidae centrum morphotypes NvC, NvD and NvE shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. A-B) esocid centrum morphotype NvC. A, TMP 1995.157.0114; B, TMP 1995.177.0057. C-D) esocid centrum morphotype NvD. C, TMP 1986.008.0089; D, TMP 1995.180.0040. E-F) esocid centrum morphotype NvE. E, TMP 1995.157.0098; F, TMP 1995.157.0098. Scale bar equals 1 mm.

articular pits are separated from one another by two or three ridges.

Centrum Morphotype NvB.—Centrum morphotype NvB (Figure 15D-E) has a mid-ventral ridge with a network of bone fibers arranged longitudinally on either side of this ridge. A mid-dorsal pit is generally present. This pit is narrow and elongate, extending the full length of the centrum. The neural and parapophyseal articular pits are located close to one another and may be separated by a single bar of bone (Figure 15D) or two closely spaced ridges (Figure 15E). The centra are relatively more elongate than centrum morphotype NvA and thus are likely from a more posterior position along the column.

Centrum Morphotype NvC.—Centrum morphotype NvC has large neural arch articular pits that extend the full length of the centrum. These pits are separated by a narrow area formed of two strong ridges with a narrow mid-dorsal pit between them (Figure 16A-B). Parapophyseal pits are large rectangular pits that extend the full length of the centrum. They are separated from the neural arch articular pits by two or three strong ridges with finer ridges crossing the space between these. Ventrally, a mid-ventral ridge and two lateral ridges are present, with a shallow fossa between these ridges. The lateral ridges diverge posteriorly, so the fossae are wider posteriorly than they are anteriorly. Based on variation in the relative length of the centra, Sinha et al. (2019) suggested that centrum morphotype NvC included centra from the anterior end of the abdominal series.

Centrum Morphotype NvD.—Centrum morphotype NvD (Figure 16C-D) are longer than wide. Neural arch articular pits are distinctly rounded in outline and do not extend for the full length of the centrum. A posterior-dorsal process is present posterior to the neural arch pits. Ventrally, a mid-ventral ridge is present with the space between the ridge and the edge of the parapophyseal articular pit crossed by a network of bone. In the reduced length of the neural arch articular pits and the presence of dorsal processes posterior to these pits, and the more elongate centra, centrum morphotype NvD is similar to the posterior abdominal centra of extant species of *Esox* (Sinha et al., 2019). Thus it is likely that centrum morphotype NvD include centra from the posterior region of the abdominal series.

Centrum Morphotype NvE.—Esocid centrum morphotype NvE (Figure 16E-F) is similar to morphotype NvC in having a mid-ventral ridge separating lateral pits. However, the ridges lateral to these pits are parallel with one another, in contrast to morphotype NvC, where these ridges diverge posteriorly. The neural and parapophyseal articular pits are located close to one another along the anterior half

of their length, where they are separated by a single bar of bone. This contrasts with the centra of morphotype NvC where the pits are more widely separated. Based on the pattern of variation along the column in extant species of *Esox* described by Sinha et al. (2019), it is likely that centrum morphotype NvE are transitional between the anterior and posterior regions of the vertebral column.

Superorder ACANTHOMORPHA Rosen 1973 (sensu Stiassny, 1986)

Remarks.—Acanthomorph teleosts include the teleosts characterized by the presence of true fin spines in the dorsal, and pelvic fins (Nelson, Grande and Wilson, 2016). They first appear in the mid-Cretaceous and had their initial phase of diversification during the Late Cretaceous. In a review of the fossil record of the major groups of non-marine acanthomorphs by Cavin (2017), none of the extant groups of non-marine acanthomorphs were recognized in the Late Cretaceous, although recently a percopsiform from the late Maastrichtian Scollard Formation of Alberta was described by Murray et al. (2019). However, isolated elements, especially centra, demonstrate that acanthomorphs were diverse and abundant members of Late Cretaceous freshwater paleocommunities. The abundance of acanthomorph centra, relative to those of other teleosts, demonstrates that acanthomorphs increased in abundance from their first occurrence in the Coniacian to the late Maastrichtian, when they constituted an average 50% of all teleost abdominal centra based on samples from three vertebrate microfossil localities (Brinkman et al., 2017a:fig. 23). They also document an increase in diversity through the Late Cretaceous. In the late Santonian Milk River Formation of Alberta, a single morphotype is present, but in the late Maastrichtian Hell Creek Formation of Montana, four distinct morphotypes are present, indicating that the assemblage included at least four kinds of acanthomorphs.

Acanthomorphs show an exceptionally high degree of morphological variation along the vertebral column. The first centrum has a tripartite anterior articular surface with separate surfaces for articulation with the basioccipital and exoccipitals. The more posterior abdominal centra are distinctive in the presence of zygapophyseal articulations between the centra and in that the ribs in the anterior region of the vertebral column articulate on the lateral surface of the neural arch rather than low on the centrum (Rosen and Patterson, 1969; Grande, 1988). However, the high degree of variation along the column increases the risk that morphologically distinct centra represent regional

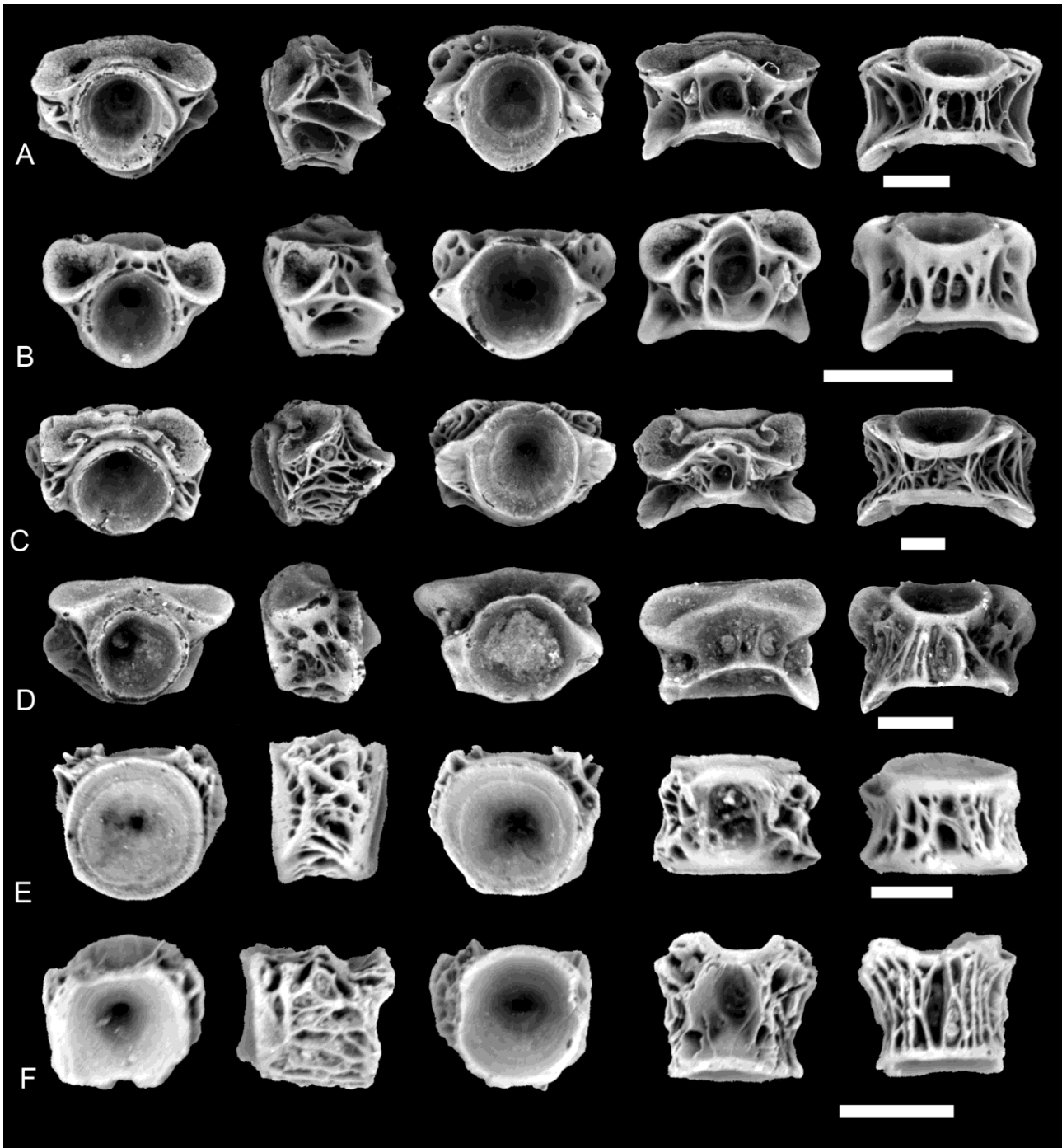


FIGURE 17. Acanthomorph centrum morphotype AvA shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-D**) first centrum. **A**, TMP 1995.180.0036, from BB 107; **B**, TMP 1995.180.0036, from BB 107; **C**, TMP 1999.177.0068, from BB 100; **D**, TMP 1986.044.0019, from BB 54. **E-F**) abdominal centra, **E**, TMP 1986.196.0028; **F**, TMP 1986.205.0005. Figure 16C from Neuman and Brinkman (2002:fig.9). Scale bar equals 1 mm.

variants from along the column, rather than distinct taxa. To minimize this possibility, the morphotypes were defined on the basis of the first abdominal vertebra. In

some cases, more posterior abdominal centra were included in these morphotypes based on the presence of shared features.

Acanthomorph centrum morphotype AvA
Figure 17

Morphoserries IIB-1, Brinkman and Neuman, 2002:151-152, fig. 9.1-9.5
Morphoserries IIB-1 (acanthomorph), Neuman and Brinkman, 2005:180, fig. 9.8H
Acanthomorph #1, Larson, Brinkman and Bell, 2010:1167-1168, fig. 5E
Acanthomorph, Brinkman et al., 2013:227, fig. 10.28
Acanthomorph atlas centrum type HC-2, Brinkman et al., 2014:263-264, fig. 15A
Brinkman et al., 2017a:34-35
Brinkman et al., 2017b:62, fig. 20

Voucher Specimens—First abdominal centra: TMP 1986.242.0059, two centra from BB 104; TMP 1993.093.0068, ten centra from L1101; TMP 1986.020.0050, two centra from BB 54; TMP 1986.161.0017, approximately 30 centra from BB 100; TMP 1986.159.0014, one centrum from BB 100; TMP 1995.180.0036, eight centra from BB 107; TMP 1986.044.0019, two centra from BB 54.

Abdominal centra: TMP 1986.196.0028, one centrum, from BB 104; TMP 2008.025.0015, approximately 15 centra from JMC Stake Site; TMP 1993.093.0074, approximately 14 centra from locality L1105; TMP 1995.168.0044, five centra from BB 117.

Description.—In the first centrum of acanthomorph centrum morphotype AvA the antero-dorsal articular surfaces broadly contact one another above the basioccipital articular surface, the centra are short and tend to be wedge-shaped in lateral view, and mid-dorsal and mid-ventral pits are present (Figure 17A-D). The mid-dorsal pit varies in size. Most specimens have a large, smooth-walled pit, (Figure 17A-B), although in some the pit is relatively small (Figure 17C-D). The mid-ventral pit is generally bordered by enlarged ridges of bone. The sides of the centrum are formed by a network of relatively coarse bone ridges generally oriented between the ends of the centrum with smaller branches extending dorso-ventrally between these.

More posterior abdominal centra referred to acanthomorph centrum morphotype AvA share with the first centrum the presence of a mid-dorsal and mid-ventral pits with the mid-ventral pit generally bordered by distinct ridges (Figure 17C-E). As with the first centrum, the sides of the centra are formed by a relatively low number of ridges extending between the ends of the centrum with smaller ridges connecting these.

Remarks.—Centra of acanthomorph centrum morphotype AvA are abundant in all the localities examined. Variation in the size of the mid-dorsal pit of

the first centrum is of potential taxonomic significance but was considered more likely a result of variation within a taxon because a similar range of variation is present in the first centra of acanthomorphs in the Milk River Formation (Brinkman et al., 2017a, b).

Acanthomorph centrum morphotype AvA is comparable to the morphotype from the Hell Creek Formation described as HC-2 (Brinkman et al., 2014). It is also similar to the acanthomorph centra from the late Santonian Milk River Formation described by Brinkman et al. (2017a, b). Thus the operational taxonomic unit represented by this centrum morphotype likely includes several lower-level taxa.

Acanthomorph centrum morphotype AvC
Figure 18

Morphoserries IIB-2, Brinkman and Neuman, 2002:152, fig. 9.6-9.10

Voucher Specimens.—TMP 1990.0048.100, one first centrum; TMP 1990.113.0074, one first centrum, from South Saskatchewan River, west of Hilda; TMP 1993.093.0062, two first abdominal centra, from locality L1103; TMP 1993.0093.059, one abdominal centrum, from locality L1105; TMP 1992.023.0022, approximately ten centra from L1102; TMP 2000.022.0004, six first centra from locality L1101; TMP 2000.022.0002, one abdominal centrum from locality L1101; TMP 2008.025.0016, seven first centra, from Stake Site; TMP 2008.025.0037, seven abdominal centra from Stake Site; TMP 2014.010.0007, seventeen first centra, from locality L1115; TMP 2019.060.0067, one first centrum from locality L1101; TMP 2019.060.0068, 2 first centra, from L1108; TMP 2019.060.0069 five first centra, from L1103; TMP 2019.060.0072, six first centra from JMC Mammal site 2; TMP 2019.060.0066, five first centra from Baby Ceratops locality; TMP 2019.060.0071, two first centra from L1102; TMP 2019.060.0070, four first centra from JMC 700.

Description.—Acanthomorph centrum morphotype AvC is recognized on the basis of a first centrum in which the centrum has a rounded ventral surface, a mid-ventral pit is absent, and the lateral surface of the centrum is formed by a lacy network of bone (Figure 18A). A distinct small, rounded, smooth area is present on the lateral surface of the centrum that has the appearance of an articular surface. The exoccipital articular surfaces are separated by a short distance or just barely touch above the basioccipital articular surface. A deep smooth-walled mid-dorsal pit is present.

More posterior abdominal centra that have a rounded ventral surface and either lack a mid-ventral pit or have a small, slit-like pit are likely from the same kind

of teleost as first centrum morphotype AvC (Figure 18B-C).

Remarks.—The first centrum of teleost centrum morphotype AvC is distinct in the absence of a mid-ventral pit and the presence of a distinct articular surface on the lateral side of the centrum. It is similar to centrum morphotypes AvE and AvF and different from centrum morphotypes AvA in that the exoccipital articular surfaces do not meet above the basioccipital surfaces.

Teleost centrum morphotype AvC has a restricted distribution. It was only recovered from localities in the Manyberries area of southern Alberta.

Acanthomorph centrum morphotype AvD
Figure 19

Acanthomorph #2, Larson, Brinkman and Bell, 2010:1167-1168, fig. 5F

Voucher Specimens.—TMP 1987.099.0012, three first centra from BB 75; TMP 1986.170.0001, one first centrum from BB 103; TMP 1986.021.0065, one first centrum from BB 54; TMP 1987.032.0037, one first

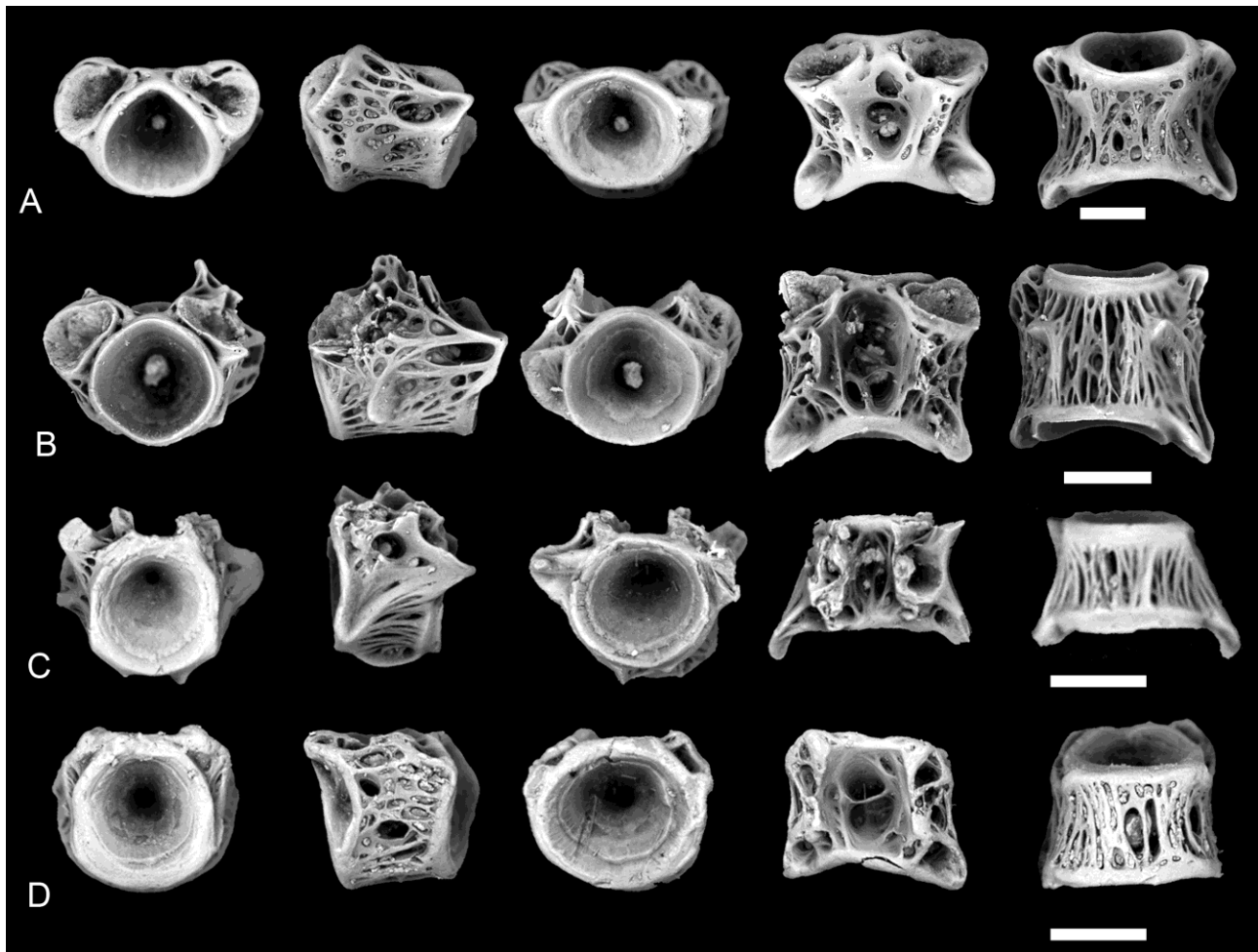


FIGURE 18. Acanthomorph centrum morphotype AvC shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-B**) first centrum, **A**, TMP 2008.025.0016; **B**, TMP 2019.060.0067. **C-D**), abdominal centra; both included in TMP 2008.025.0037. Scale bar equals 1 mm.

centrum from BB 106; TMP 2008.025.0035, two first centra from JMC Stake Site; TMP 1986.220.0018, one first centrum from BB 106; TMP 1986.053.0080, one first centrum from L0230; TMP 1995.181.0079, five first centra from BB 104; TMP 2019.060.0074, two atlas first centra from BB 54; TMP 2019.060.0075, three first centra from BB 104; TMP 2019.060.0076, six first

centra from L1105; TMP 2019.060.0077, three first centra from L1115; TMP 2019.060.0078, two first centra from JMC Mammal Site 2; TMP 2019.060.0079, two first centra from L2370; TMP 2019.060.0186, one first centrum from BB 100; TMP 2019.060.0080, eight first centra from locality L1108; 1986.009.0098, one first centrum from BB 86; TMP 1995.168.0044, one first

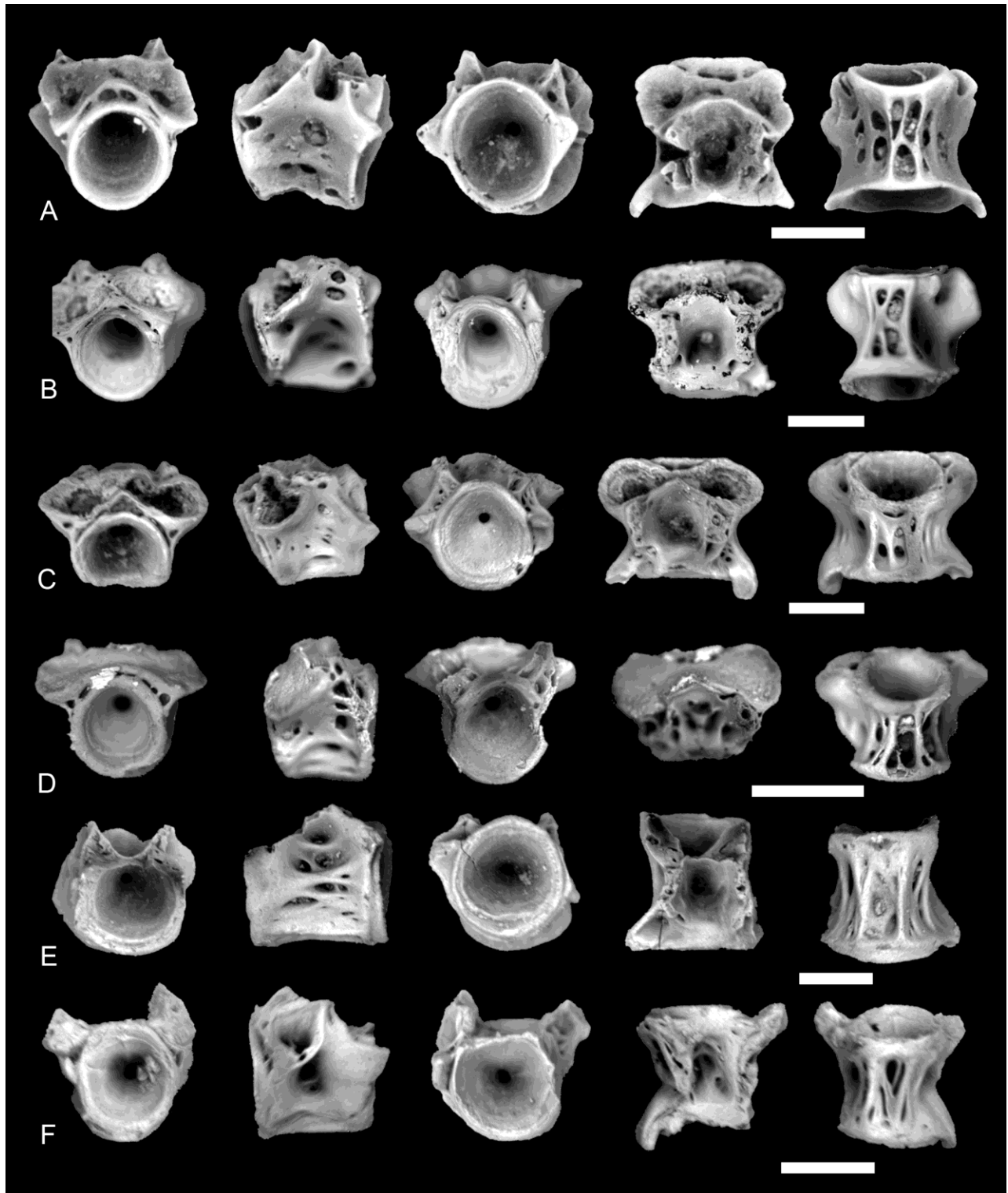


FIGURE 19. Acanthomorph centrum morphotype AvD shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A)** first centrum, TMP 1986.053.0080, from BB 102; **B)** TMP 1995.181.0079, from BB 104; **C)** TMP 1986.170.0001, from BB 103; **D)** TMP 1995.181.0079, from BB 104; **E)** abdominal centrum, TMP 1986.171.0037; **F)** abdominal centrum TMP 1995.181.0078 specimen from BB 104. Scale bar equals 1 mm.

centrum from BB 117; TMP 1995.147.0004, two first centra from Pumphosaur site; TMP 2000.009.0032, two first centra from BB 51; TMP 1986.242.0059, two first centra from BB 104.

Description.—Acanthomorph centrum morphotype AvD is recognized on the basis of first centra that are similar to centrum morphotype AvA in that the exoccipital articular surfaces broadly meet above the basioccipital articular surface but differ in that the sides of the centrum are smoother (Figure 19A-D). Rather than a series of ridges extending between the ends of the centrum, the sides of the centrum are pierced by relatively few foramina. As well, the centra are relatively narrower and the exoccipital articular surfaces do not extend as far laterally relative to the body of the centrum. A deep, smooth-walled, mid-dorsal pit is present. A mid-ventral pit is generally present, with multiple ridges crossing this space. Variation is present in the length of the centra, with most being longer than wide (Figure 19A-B) but some being distinctly shortened (Figure 19C-D).

Abdominal centra referred to acanthomorph centrum morphotype AvD (Figure 19D-F) are similar to the first centrum in having relatively few fenestrations on their lateral surfaces. They also differ from the abdominal centra of morphotype AvA in being more elongate.

Remarks.—The first centrum of morphotype AvD differs from centrum morphotype AvA primarily in the reduced number of fenestrae on the lateral wall. Centra of morphotype AvD occur both in the fluvial beds of Dinosaur Provincial Park and the fine-grained sediments of the Onefour Mud-filled Channel Complex.

Acanthomorph AvE
Figure 20

Acanthomorph #3, Larson, Brinkman and Bell, 2010:1167-1168, fig. 5G

Voucher Specimens.—TMP 1986.203.0036, one first centrum from BB 107; TMP 1995.181.0080, six first centra from BB 104; TMP 1995.145.0086, one first centrum from BB 51; TMP 1986.172.0024, one first centrum from BB 103; TMP 1986.158.0042, one first centrum from BB 100; TMP 2014.010.0001 one first centrum from BB 105; TMP 1986.021.0056, one first centrum from BB 54; TMP 1986.005.0027, one first centrum from BB 31; TMP 1995.180.0071, four first centra from BB 107; TMP 1995.177.0110, eight first centra from BB 100; TMP 2014.010.0009, five first centra from locality L1115; TMP 1995.157.0126, three first centra from L1108; TMP 1995.147.0059, three first centra from BB 78.

Description.—Acanthomorph centrum morphotype AvE is recognized on the basis of a first centrum in which the sides are deeply excavated and this excavation is bordered anteriorly by a buttress that extends laterally from the anterior articular surface. The exoccipital articular surfaces either do not meet dorsally above the anterior articular surface of the centrum (Figure 20A-B, D) or just barely meet (Figure 20C). As in acanthomorph centrum morphotype AvA, mid-dorsal and mid-ventral pits are present with the mid-ventral pit being bordered by bordered by robust ridges. Variation is present in length, with some centra being short and wide (Figure 20A) and others being elongate (Figure 20D). Also variation is present in the width of the ventral surface of the centrum, with some being narrower than wide (Figure 20A) and others being about as wide as long (Figure 20C).

No abdominal centra from a more posterior position along the column could be associated with the first centra.

Remarks.—Acanthomorph centrum morphotype AvE differs from all other acanthomorph morphotypes recognized here in the presence of a deeply excavated lateral surface on the first abdominal centrum with this excavation bordered anteriorly by a buttress extending laterally from the basioccipital articular surface. It is similar to morphotype AvC in that the exoccipital articular surfaces do not contact one another above the basioccipital articular surface and in the presence of a smooth-walled mid-dorsal pit. It differs from morphotype AvC in having a mid-ventral pit bordered by two stout ridges.

Centra of morphotype AvE are widely dispersed in the Belly River Group, occurring in both the fluvial beds of the Dinosaur Park Formation and the Onefour mud-filled channels.

Acanthomorph indet. type AvF
Figure 21

Acanthomorph centrum type HC-1, Brinkman et al., 2014:263-264, fig. 15C

Voucher Specimens.—TMP 2014.010.0010 three first centra, from locality L1115; TMP 2014.010.0002 five first centra, from BB 100; TMP 1986.060.0141, one first centrum, from BB 54; TMP 1995.177.0068, one first centrum, from BB 100; TMP 2014.010.0004, one first centrum, from BB 104; TMP 1995.177.0111, three first centra, from BB 100; TMP 2014.010.0003, two first centra, from BB 86; TMP 1995.145.0087, two first centra, from BB 51; TMP 2017.011.0030, two first centra, from L2370; TMP 1995.181.0074, seven first centra, from BB 104.

Description.—Acanthomorph centrum morphotype AvF is characterized by first centra that are similar to those of AvE in that the exoccipital articular surfaces are widely separated. However, they differ from AvE in that the lateral surface is little fenestrated (Figure 21A) or has ridges extending from the anterior end of the centrum to the posterior articular processes (Figure 21B-C). The posterior articular processes are distinct, and, when present, the ridges present on the lateral surface of the centrum converge on these processes. A mid-dorsal pit is present between the bases of the neural arch. As in centrum morphotype AvA, a mid-ventral pit bordered

by a pair of stout ridges is present. In some specimens of acanthomorph centrum morphotype AvF neural arches are fused to the centrum (Figure 21C).

No abdominal centra from a more posterior position along the column could be associated with the first centra.

Remarks.—The first centrum of morphotype AvF is similar to centrum morphotypes AvC, and AvE in that the exoccipital surfaces do not meet above the basioccipital articular surface. They differ from both AvC and AvE in that the exoccipital articular surfaces

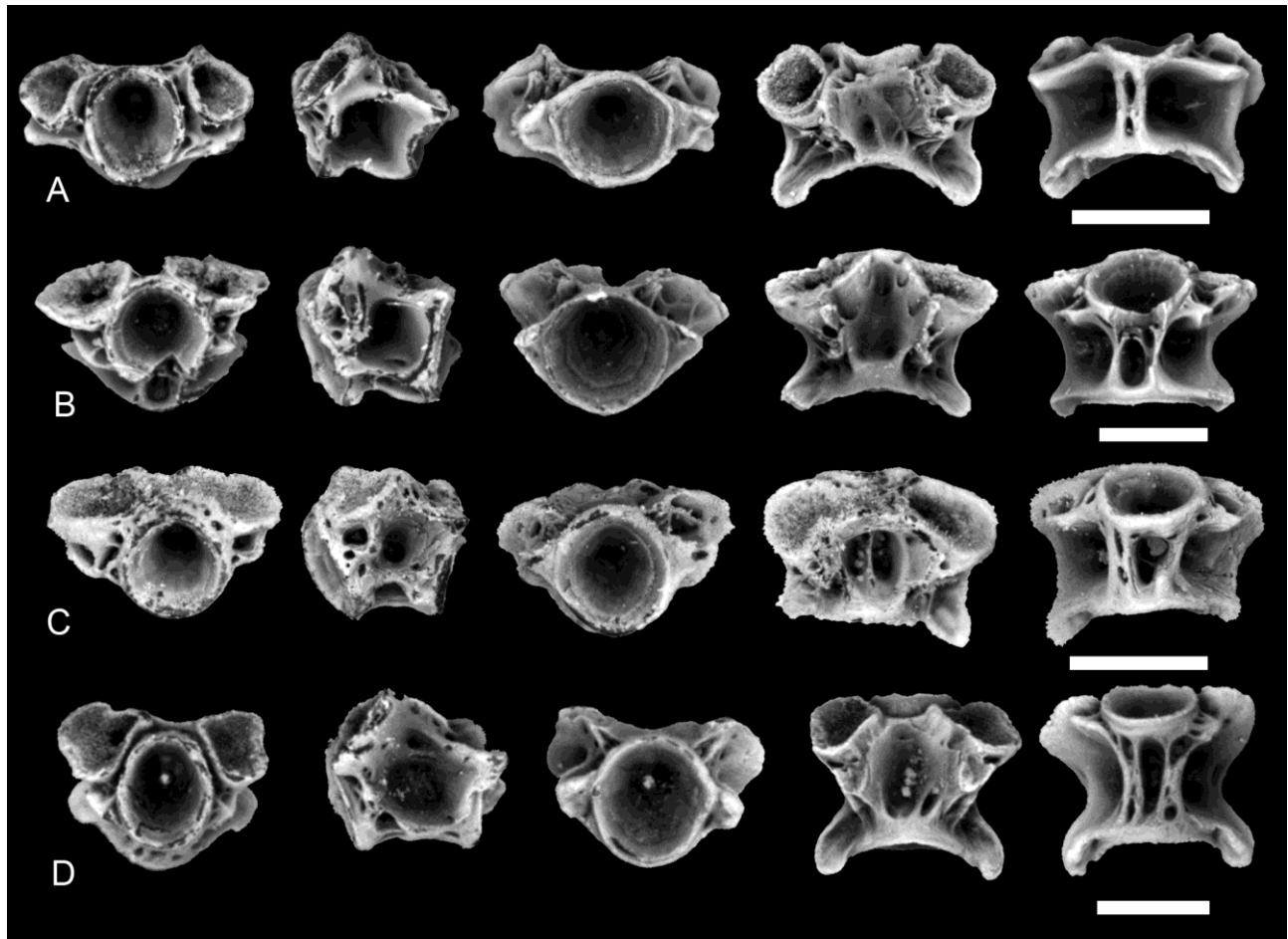


FIGURE 20. Acanthomorph centrum morphotype AvE shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-D**) first centrum: **A**, TMP 1995.177.0110, from BB 100; **B**, TMP 1995.177.0110, from BB 100; **C**) TMP 1995.177.0110, from BB 100. **D**) TMP 1995.181.0080, from BB 104. Scale bar equals 1 mm.

are much more widely separated, so they tend to be lateral to the basioccipital articular surface. In the presence of large, widely separated exoccipital articular surfaces, first centrum morphotype AvF is similar to centra from the Eocene Wasatch Formation identified as Aff. *Amblyopsidae* by Divay and Murray (2016) and to centra from the Hell Creek Formation described as

acanthomorph centrum morphotype HC-1 by Brinkman et al. (2014). Percopsiform affinities are supported by the presence of fused neural arches, which Divay and Murray (2016) identify as a feature of the group. However, they differ from the first centra of acanthomorph indet. type HC-1 in that mid-dorsal and a distinct mid-ventral pits are present. In acanthomorph

indet. type HC-1 the mid-dorsal pit is obscured by a network of fibers that is present on the dorsal surface of the centrum between the bases of the neural arch (Brinkman et al., 2014:fig. C). Similarly, the ventral surface of the centrum is covered by a fine network of ridges so lacks a mid-ventral pit like that seen in centrum morphotype AvF.

Centrum morphotype AvF is widely dispersed in the fluvial deposits of Dinosaur Provincial Park but was only observed in one of the samples taken from the Onefour Mud-filled Channel complex north-east of Onefour, Alberta.

Teleost Centra of Uncertain Affiliations

Remarks.—Although many of the morphoseries described by Brinkman and Neuman (2002) can now be placed in lower-level taxonomic groups, a series of distinct centrum morphotypes are present that remain taxonomically indeterminate. In order to incorporate the teleosts represented by these centra in studies of diversity and distribution of teleosts, these are given alpha-numeric designations and are described below as distinct morphotypes.

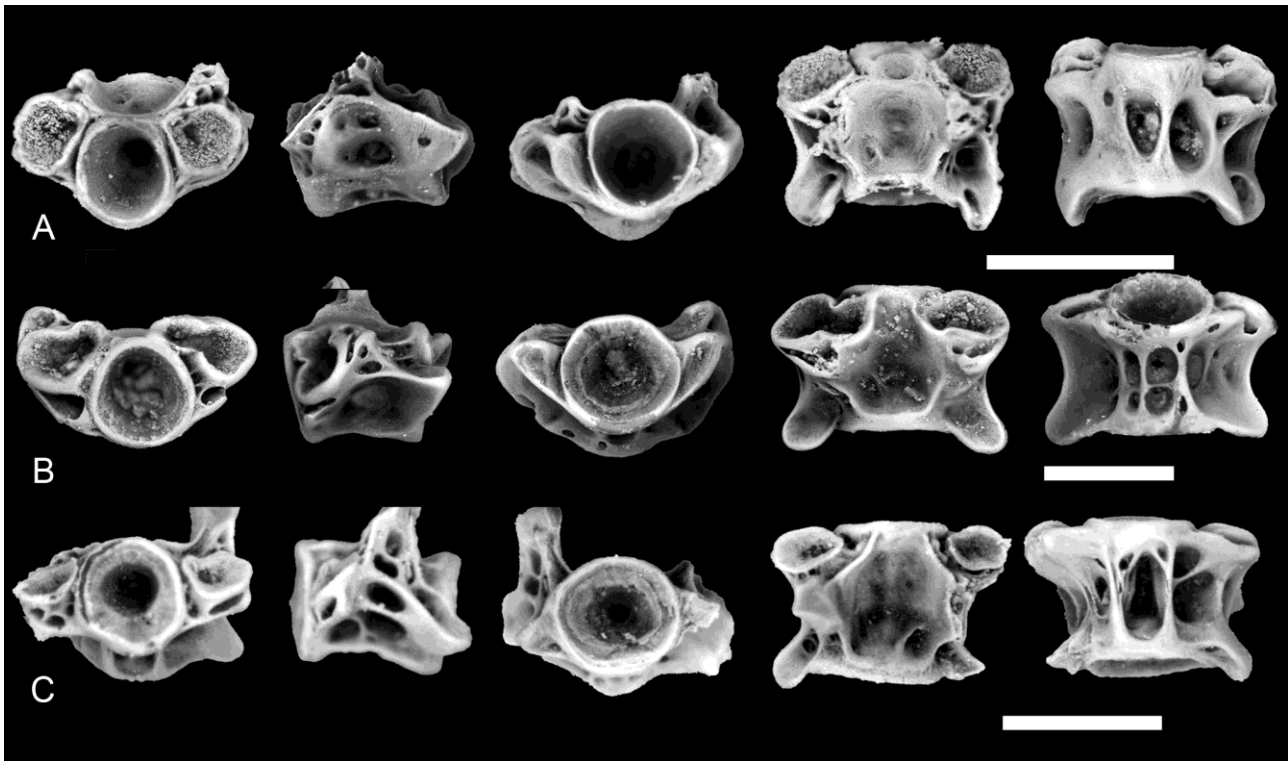


FIGURE 21. Acanthomorph centrum morphotype AvF shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A)** first centrum, TMP 2014.010.0010, from locality L1115; **B)** first centrum, TMP 2014.010.0010, from locality L1115; **C)** TMP 1995.157.0063, first centrum from locality L1108. Scale bar equals 1 mm.

Centrum Morphotype U-1 Figure 22 A-C

Voucher Specimens.—From Onefour area: TMP 1993.116.0019, approximately 50 centra from L1115; TMP 2016.009.0014, two centra from locality JMC 700; TMP 2019.060.0197, five centra from locality JMC mammal site 2.

Remarks.—Teleost centrum morphotype U-1 are elongate, have a long, narrow, mid-dorsal pit that generally extends for the full length of the centrum. Neural arches are fused to the centrum. The neural arch

bases are long, extending nearly the full length of the centrum. Parapophyses are fused to the centrum. These are short, blunt laterally facing structures. Ventrally, a mid-ventral ridge separates two elongate pits. These pits are bordered laterally by a well-defined ridge.

Distribution.—Centrum morphotype U-1 is only present in localities on the Onefour area of Alberta where it occurs in the Onefour Mud-filled Channel Complex.

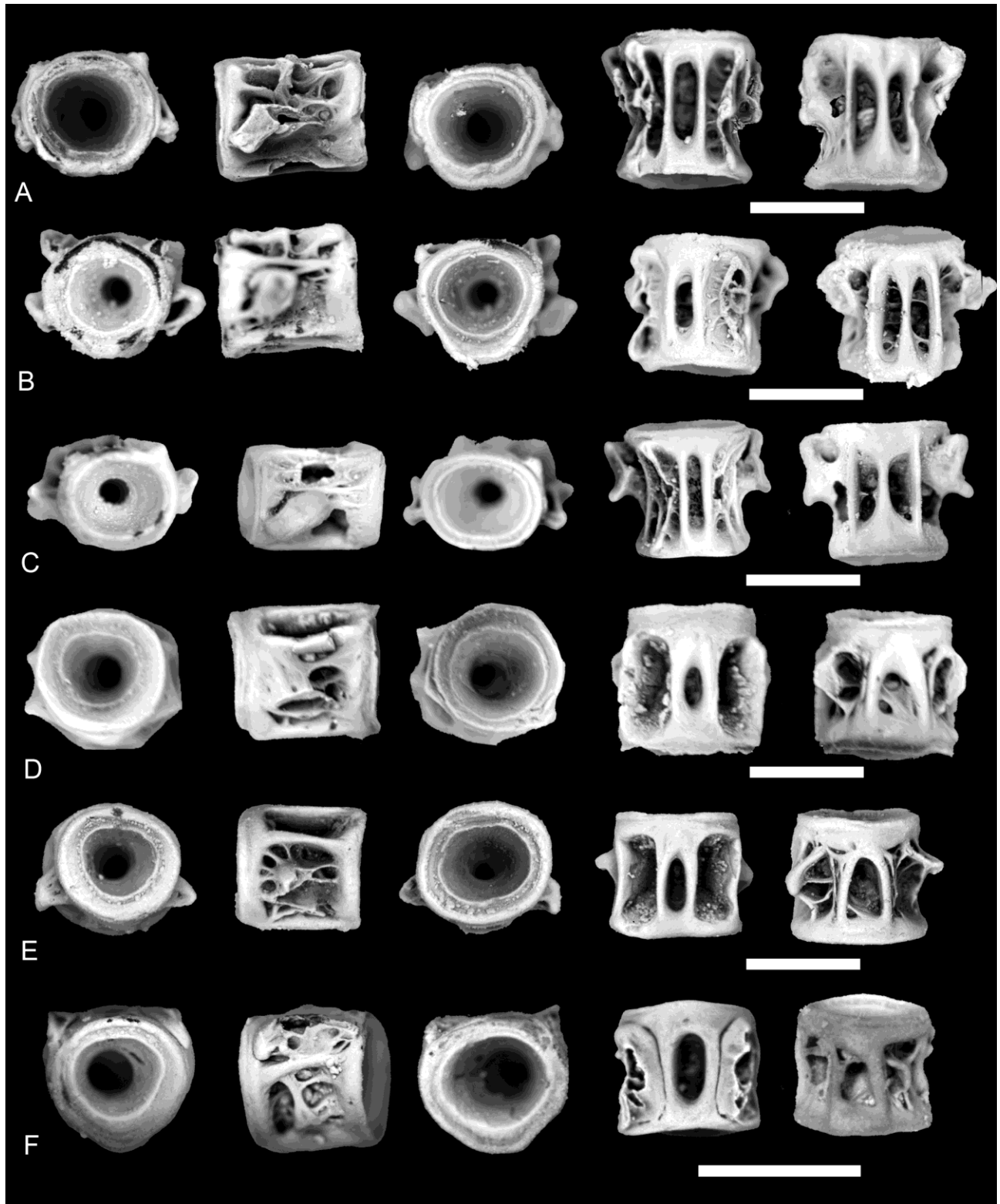


FIGURE 22. Teleost centrum morphotypes U-1 and U-2 shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. **A-C)** Teleost centrum morphotypes U-1. **A**, TMP 2016.009.0014; **B-C**, both included in TMP 1993.116.0019. **D-F)** Teleost centrum morphotype U-2. **D**, TMP 2016.009.0017; **E**, TMP 2016.9.0117, **F**, TMP 2008.025.0019. Scale bar equals 1 mm.

Teleost Centrum Morphotype U-2
Figure 22 D-F

Voucher Specimens.—From Onefour Mud-filled Channels: TMP 1993.116.0018, approximately 40 centra from locality L1115; TMP 2008.025.0019, two centra from JMC Stake Site; TMP 2016.009.0017, ten centra from locality JMC 700; TMP 2019.060.0198, approximately 20 centra from JMC Mammal site 2.

From Dinosaur Provincial Park: TMP 2016.011.0005, approximately 30 centra from locality 2371 (Wolf Coulee MV site); TMP 2019.060.0189, one centrum from BB 104.

Remarks.—Teleost centrum morphotype U-2 vary from subequal in width and length (Fig 21F) to longer than wide (Figure 22D). Neural arches are autogenous and neural arch articular pits are large, oval-shaped openings similar to those of esocids. A mid-dorsal pit is present between the neural arch articular pits. The ventral surface of the centrum is formed by a U-shaped ridge. In contrast to the esocid centra described above, a mid-ventral ridge is absent. Parapophyses which are fused to the centrum, are short, ventro-laterally directed processes.

Centrum morphotype U-2 has similarities to morphotype U-1 but is treated as a distinct morphotype because the ventral surface appears to be fundamentally different in that a mid-ventral ridge is present in morphotype U-1 but not U-2. Teleost centrum U-2 is similar to the esocid centrum from the Milk River Formation illustrated by Brinkman et al. (2017a:fig 15 A-D) in the presence of a U-shaped ventral ridge. These two centrum morphotypes differ primarily in that in the Milk River specimens a mid-ventral ridge is present, whereas this is absent in centrum morphotype U-2. Also, parapophyses are autogenous in the Milk River esocids, although generally preserved in place, but fused to the centrum in morphotype U-2.

Distribution.—Teleost centrum morphotype U-2 occurs in both Dinosaur Provincial Park and the Onefour area of southern Alberta. This differs from centrum morphotype U-1, which only occurs in the Onefour area, further supporting the conclusion that these are from different kinds of fish.

Teleost Centrum Morphotype U-4
Figure 23 A-C

Genus et sp. indet. type U-4, Brinkman et al., 2013:221, fig. 20.23

Genus and species indet. U-4, Brinkman et al., 2014:259-260, fig. 10A-B

Voucher Specimens.—TMP 2015.60.25, twelve specimens from BB 105; TMP 2017.011.0004, two centra from locality L2370; TMP 1987.02800.96, one specimen from BB 105; TMP 1995.181.0075, one centrum from BB 104; TMP 2004.104.0076, one centrum from Marie's Site, DPP; TMP 2015.060.0026, one centrum from L411, DPP.

Remarks.—The teleost represented by centra that are small, simple spools with deep neural arch and parapophyseal pits and a shallowly excavated to nearly flat anterior surface were referred to as teleost type U-4 by Brinkman et al. (2013). These centra are wider than high and shorter than wide. Neural arch articular pits are sub-triangular in shape, with the medial corners of opposite pits located near the midline. Generally, the neural arch articular pits are separated by a relatively wide solid bar of bone (Figure 23A-B), although a pit may be present (Figure 23C). Parapophyseal articular pits are large, oval pits about equal in size to the neural arch articular pits. The surface of the centrum between the neural arch and parapophyseal pits is generally pierced by one or two small foramina of moderate size. A mid-ventral pit is generally present, although this pit varies in size.

Distribution.—Centrum morphotype U-4 has been recovered only from localities in the fluvial beds of the Dinosaur Park Formation, and appears to be most frequently encountered in localities low in the formation. It is widely distributed in other Late Cretaceous assemblages of the Western Interior, occurring in the Turonian to late Campanian of Utah, the late Santonian Milk River Formation of Alberta, and the late Maastrichtian Hell Creek Formation of Montana (Brinkman et al., 2013, 2014, 2017a, b)

Teleost Centrum Morphotype BvB
Figure 24

Voucher Specimens.—TMP 1995.180.0058, two centra from BB 107; TMP 1986.172.0022, one centrum from BB 103; TMP 2019.060.0192, four centra, from BB 105; TMP 2019.060.0200, one centrum from Ken's site.

Remarks.—The centra included in teleost centrum morphotype BvB vary between shorter than wide (Figure 24A) to longer than wide (Figure 24E), likely as a result of variation along the vertebral column. The neural arches are autogenous although they are often preserved in place (Figure 24C-E). In the anterior-most centra, the neural arch pits are separated by a narrow bar (Figure 24A); in more posterior centra a mid-dorsal pit is present. Parapophyses are autogenous but often preserved in place. The parapophyseal pit is broadly exposed both laterally and ventrally. The space

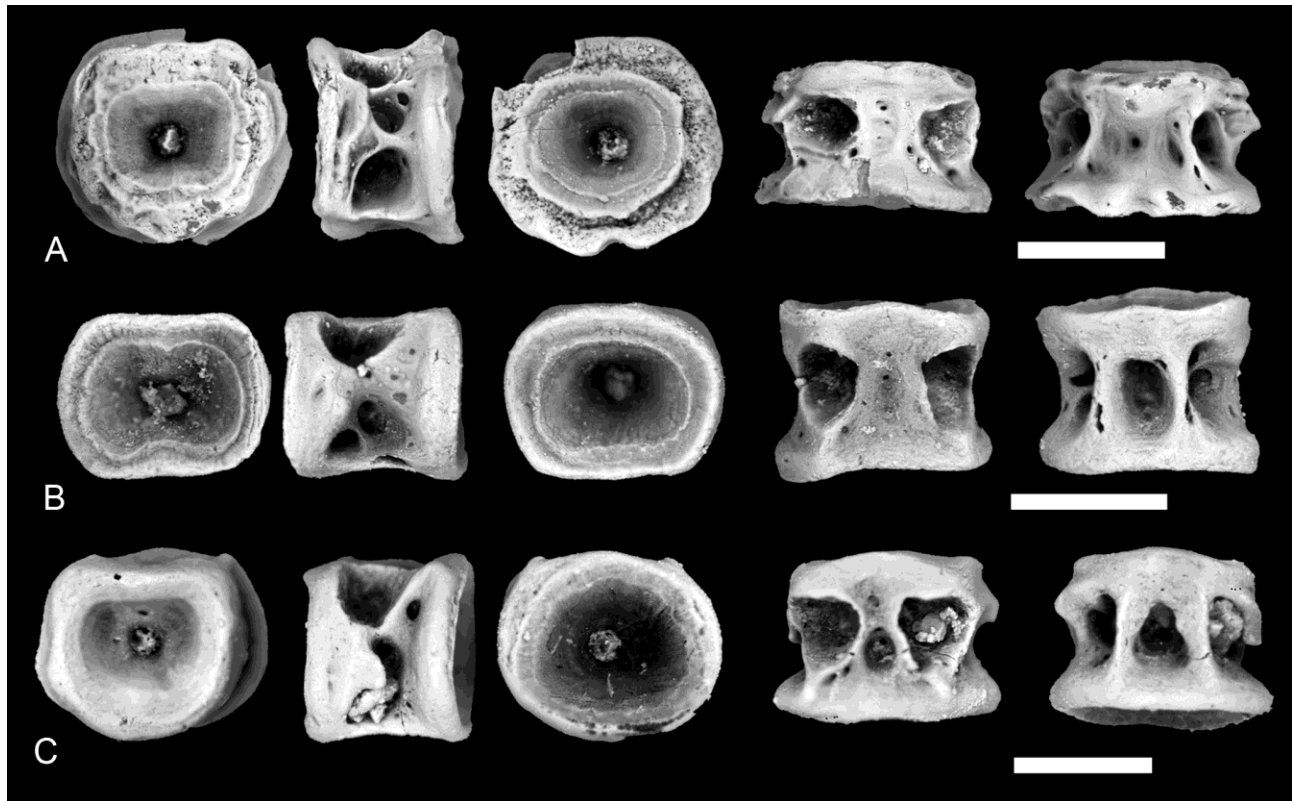


FIGURE 23. Teleost centrum morphotype U-4 shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. A-C) Teleost centrum morphotypes U-4. A: TMP 2015.060.0025; B: TMP 2017.0011.004; C: TMP 2015.060.0025. Figure 22C from Brinkman et al. (2017a:fig. 22F). Scale bar equals 1 mm.

between the parapophyses is formed by two strong ridges with smaller ridges passing between these.

Distribution.—Centra of morphotype BvB are rare and have only been observed in fluvial beds of the Belly River Group.

DISCUSSION

Based on the centra described above, a minimum of 25 taxa of teleost fishes are present in the Belly River Group. This is higher than both the temporally equivalent Kaiparowits Formation of Utah, which includes a minimum of 19 teleosts (Brinkman et al. 2013), and the younger Hell Creek Formation of Montana, which contains a minimum of 16 taxa (Brinkman et al. 2014).

In part, the high diversity of teleosts in the Belly River Group can be attributed to the diversity of the environments of deposition that were sampled. Of particular note is the difference in the composition of teleost assemblages preserved in the Onefour Mud-filled Channel Complex of southeastern Alberta and the fluvial beds of Dinosaur Provincial Park. This difference in the teleost assemblages was first recognized by

Eberth and Brinkman (1997). Because the Onefour Mud-filled Channel Complex is unusual in preserving a parautochthonous assemblage in a quiet water setting, it was assumed that these differences were a result of the different habitats being sampled and that this difference was associated with stratigraphic position. However, the possibility that the differences were a result of latitudinal differences cannot be discounted. With the much larger sample sizes resulting from subsequent collecting efforts, the paleoecological significance of the faunal differences recognized by Eberth and Brinkman (1997) can be reconsidered.

Taxa that are restricted to the Onefour Mud-filled Channel complex include the small elopomorph, *Clupeiformes* sp. indet., the acanthomorph represented by centrum type AvC, and the indeterminate teleosts represented by centrum morphotypes U-1. In addition, the characiform is present in most of the localities in the Onefour Mud-filled Channel complex but only two localities in Dinosaur Provincial Park, L2371 (Wolf Coulee) and Marie's Site. Significantly, both these sites are similar to the Onefour Mud-filled Channel localities in being deposited in fine-grained sediment (Table 1). Also, neither of these taxa or the taxa restricted to the

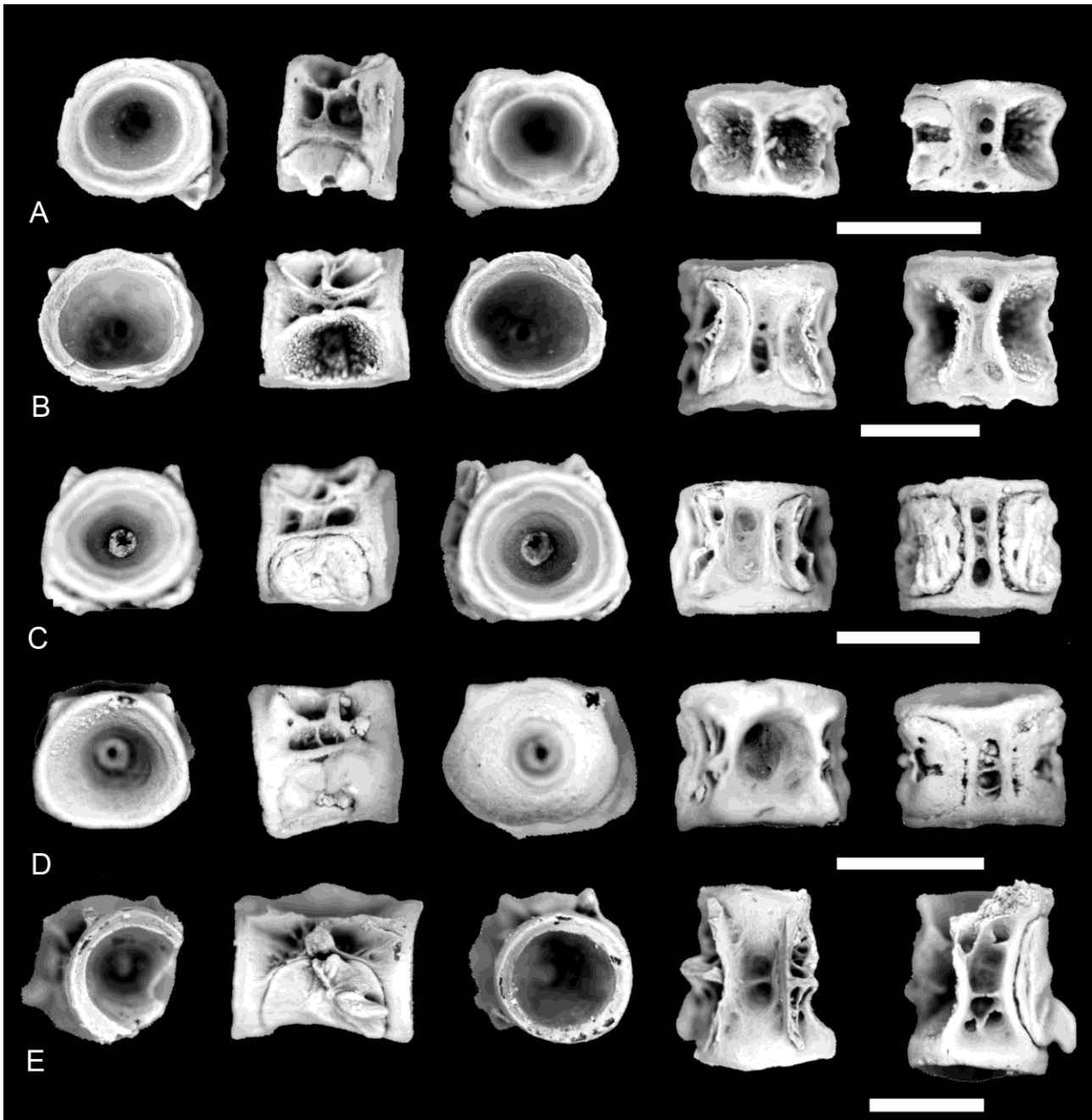


FIGURE 24. Teleost centrum morphotype BvB shown in, from left to right, anterior, left lateral, posterior, dorsal and ventral views. A) TMP 1995.180.0058; B) TMP 1995.180.0058; C) TMP 1995.180.0058; D) TMP 1995.180.0058; E) TMP 1995.180.0058. Scale bar equals 1 mm.

Mud-filled Channel Complex are present in either of the localities preserved in fluvial deposits present in the Onefour area, localities L1108 and L1104. This supports the conclusion that the faunal differences are related to the difference in environment of deposition, rather than latitude.

The taxa recognized on the basis of centra include at least three elopomorphs, four osteoglossomorphs,

four clupeomorphs, four ostariophysans, one esocid, five acanthomorphs, and four teleosts of uncertain relationships. All occur in fully non-marine environments of deposition (Eberth, 2005) so are assumed to be members of fresh-water aquatic communities of the late Campanian.

The presence of members of the Elopiformes in non-marine assemblages of the Late Cretaceous is

unexpected because extant members are marine and the fossil record appears to indicate that this was the case for other fossil members of the group. The large-bodied taxon *Paratarpon* is not known outside of the Belly River Group in the Western Interior of North America, but the small-bodied elopiform is present in Cenomanian to Santonian localities of Utah and Southern Alberta (Brinkman 2013, 2017a). However, it is absent in the Hell Creek Formation so does not appear to extend into the Maastrichtian.

The high abundance and diversity of osteoglossomorphs appears to be a characteristic feature of non-marine teleost assemblages from the Campanian and Maastrichtian of the Western Interior as they are also abundant and diverse in the Kaiparowits and Hell Creek formations. At least one additional osteoglossomorph is present in the Belly River Group because *Cretophareodus*, an osteoglossomorph from the Dinosaur Park Formation represented by an articulated skeleton (Li, 1996), is not represented by isolated centra. One possible explanation for this is that the centra of *Cretophareodus* do not differ significantly from those referred to *Coriops*. As mentioned above, the centrum morphotype here referred to *Coriops* is also present in the late Paleocene osteoglossomorph *Lopadichthys* (Murray et al., 2018) and *Phareodus* (Divay and Murray, 2016). Thus this centrum morphotype is likely present in a larger group of related taxa and *Cretophareodus* may be one of these.

The clupeomorphs present in the Belly River Group have a patchy distribution, generally being rare but sometimes occurring in abundance. In general, they are most abundant in localities deposited in fine-grained sediments, suggesting that they were ecologically restricted to quiet-water environments, which is consistent with their occurrences in lake environments elsewhere and their hypothesized schooling behaviour.

The diversity of ostariophysans is of interest because of the subsequent history of the group. The presence of *Notogoneus* has previously been documented in the late Campanian of the Western Interior of North America (Grande and Grande, 1999). However, a member of the Characiformes remains an anomaly given the apparent restriction of the group to the southern hemisphere through most of its history. Thus, the presence of centra that can be identified as being from the Weberian apparatus of this taxon is significant in adding to the evidence that these centra represent a member of the Ostariophysi, and therefore that the identification is correct.

Esocids first appear in the late Santonian Milk River Formation, where they are represented both by centra and tooth-bearing elements (Brinkman et al. 2017a), and extend to the late Maastrichtian (Brinkman et al. 2014). Within the Belly River Group two genera esocids have been recognized based on dentaries,

Oldmanesox and *Estesesox*. Although five discrete morphotypes of esocid centra can be recognized, these are likely a result of variation along the column rather than a reflection of taxonomic diversity.

The diversity of acanthomorphs is of particular interest given the subsequent history of the group. The first occurrences of acanthomorphs in non-marine assemblages of the Western Interior of North America are in the Coniacian (Brinkman et al., 2013). They are very rare in the Coniacian locality, but increase in abundance through the younger beds, so in the late Maastrichtian Hell Creek Formation they constitute on average 50% of the teleost centra present in a sample (Brinkman et al., 2017:fig. 23). They also increase in diversity. The high level of diversity of acanthomorphs in the Belly River Group is consistent with this general pattern. Five taxa are present in the Belly River Group in contrast to the late Santonian Milk River Formation of Alberta where a single acanthomorph morphotype was present (Brinkman et al. 2017a,b). The diversity of acanthomorphs in the Belly River Group is slightly greater than in the Hell Creek Formation of Montana, where four centrum morphotypes are present (Brinkman et al. 2014). However, based on dentaries, a greater number of higher-level groups of acanthomorphs is present in the Hell Creek Formation. All the acanthomorph dentaries from the Belly River Group can be included in the Percopsiformes (Neuman and Brinkman, 2005; Murray et al., 2019), and two of the centrum morphotypes recognized here, centrum morphotypes AvE and AvF, show features typical of percopsiforms. In addition to the Percopsiformes, two derived acanthomorphs were recognized in the Hell Creek Formation by Brinkman et al. (2014). One of these is the enigmatic *Platacodon*, represented by distinctive pharyngeal tooth-plates. The second is *Priscacara*, represented by dentaries and pharyngeal tooth-plates. Furthermore, the size range of centra present in the Hell Creek Formation is much greater. All the centra from the Belly River Group are of small size, with a diameter rarely exceeding 3 mm. In contrast, in the Hell Creek Formation, centra reaching 10 mm in diameter are present. This indicates that acanthomorphs were taking on new roles in the late Maastrichtian paleo-communities, possibly occupying higher positions in the food web.

The four centrum morphotypes from teleosts of uncertain relationships recognized here are all rare. One of these has an extensive stratigraphic range, extending from the Turonian to the late Maastrichtian. The remaining three are not known outside the Belly River Group.

SUMMARY

The diversity of centra of teleost fishes from the Belly River Group provides an understanding of the diversity of teleosts in the late Campanian of North America and a better understanding of the structure of non-marine aquatic paleocommunities. Differences in quiet water and fluvial paleocommunities are indicated by differences in the teleost assemblages preserved in fine-grained channel deposits and cross-bedded fluvial deposits. The composition of this late Campanian assemblage differs from that of the late Maastrichtian primarily in the absence of the two derived acanthomorphs, *Priscacara* and *Platacodon*, and the presence of a series of taxa shared with localities of similar or older age from southern Utah, but absent in the late Maastrichtian. In these features, the teleost assemblage of the Belly River Group and Kaiparowits Formation appears to document a distinct assemblage that is transitional between the earlier Santonian assemblages of Alberta and Utah and the late Maastrichtian assemblage of the Hell Creek Formation.

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