A morphological study of vertebral centra in extant species of pike, *Esox* (Teleostei: Esociformes) with implications for Cretaceous taxa

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Abstract: Isolated centra of members of the Esocidae occur frequently in vertebrate microfossil localities of Late Cretaceous and early Paleocene age and are an important source of data on the early history of the family. However, morphological variation along the vertebral column can lead to incorrect interpretations of diversity if they are not recognized. To facilitate the use of centra for interpreting the diversity and distribution of esocids in Cretaceous vertebrate microfossil localities, the variation along the column in five extant species of esocids is described. Comparison with Cretaceous centra referred to the Esocidae allows identification of a series of features in which species of *Esox* differ from basal members of the family. These include the presence of a mid-ventral groove bordered by a pair of low bulges on centra in the anterior end of the column, and antero-lateral processes on the posterior abdominal and anterior caudal centra. These differences provide a basis for recognizing early occurrences of the genus *Esox* in the fossil record and thus will allow centra to be used to document the timing of origin of the genus.

Key words: centra, *Esox americanus, Esox lucius, Esox masquinongy, Esox niger, Esox reichertii,* variation

INTRODUCTION

Our understanding of the diversity and distribution of non-marine teleost fishes in the Late Cretaceous has been greatly enhanced by information from isolated elements recovered from vertebrate microfossil localities. Tooth bearing elements were emphasized in initial studies, and several taxa were named on the basis of dentaries and pharyngeal elements (Estes 1969a, b; Estes and Hiatt 1978; Wilson et al. 1992). More recently, it has been recognized that abdominal centra are also an important source of information on the diversity, distribution, and relative abundance of teleost fishes of this time (Brinkman and Neuman 2002; Neuman and Brinkman 2005; Brinkman et al. 2013, 2014, 2017). In part, this is because abdominal centra tend to be well represented in vertebrate microfossil localities compared to tooth-bearing elements, likely because their nodular shape is favored by taphonomic processes. Also, a wealth of morphological features is present that allows lower-level taxonomic groups to be recognized. However,

interpretations of the diversity of teleost assemblages based on isolated centra must take into account variation along the vertebral column, which can result in an inflation of the interpreted diversity of an assemblage if not recognized.
In this paper, variation along the column in extant species of *Esox* is described. Variation along the column of *Esox* is of particular interest because the earliest members of the family Esocidae in the Western Interior of North America, which are from the Late Cretaceous, are documented in part by isolated centra. Cretaceous members of the Esocidae were first recognized on the basis of dentaries and palatines that showed distinctive features of tooth implantation. Two genera, *Oldmanesox* and *Estesesox*, differing in the size and arrangement of teeth on the dentary, were recognized (Wilson et al. 1992). Subsequently, isolated centra from vertebrate microfossil localities were referred to the family by Brinkman and Neuman (2002). Since these centra are well represented in vertebrate microfossil assemblages, they provided data on the diversity and distribution

of the family in the Late Cretaceous that supplemented the data provided by the tooth-bearing elements (Brinkman et al. 2013, 2014).

The genus *Esox* first occurs in the late Paleocene Paskapoo Formation of Alberta where it is represented by articulated material of *E. tiemani*, a species that differs little from modern members of the group (Wilson 1980, 1984). However, details of centrum morphology are not visible in this specimen. Thus, interpretations of the affinities of the centra from the Cretaceous esocids must be based primarily on comparison with younger species of *Esox*, particularly the extant taxa.

Centra have long been recognized as being useful for distinguishing between species of the genus *Esox*. Crossman and Casselman (1969) and Casselman et al. (1986) showed that *E. lucius* and *E. masquinongy* differ in features of the abdominal centra. Later, Grande et al. (2004) incorporated features of the centra in a phylogenetic analysis of the Esocidae. Isolated centra have also helped document the history of the genus. For example, the presence of *Esox* in the Miocene Wood Mountain Formation was documented by centra that showed little difference from those of extant members of the genus (Divay and Murray 2013).

The data on variation in the structure of vertebral centra along the column of extant species of *Esox* presented here will provide a basis for identifying features of the abdominal centra that can distinguish the basal esocids of the Upper Cretaceous from members of the genus *Esox*. This will allow centra to be used to more fully to document the diversity and relationships of esocids in the fossil record.

METHODS

This study is based on material in collections of the University of Alberta Museum of Zoology, Royal Ontario Museum, and Canadian Museum of Nature. Particular attention was paid to *Esox lucius* since this species has the largest distribution, being circumpolar, of all the pikes (Scott and Crossman 1973). A large series of specimens was examined that included skeletal preparations in which the centra remained in articulation, as well as preparations in which the centra were isolated and neural arches and parapophyses were disarticulated. Specimen numbers are given below where relevant.

Measurements of centra in species other than *Esox americanus* were made with a Mitutoyo dial caliper. Measurements of centra in *Esox americanus* were made from photographs of an articulated vertebral column seen in ventral view.

For photographs of isolated centra of *E. lucius, E. niger,* and *E. americanus,* specimens were coated with ammonium chloride to emphasize relief.

Anatomical terminology: Anatomical terms used in the descriptions follow Courtemanche and Legrandre (1985). In addition, the following terms are used for description of specific features of the centra:

Neural arch articular pit: a pit present in centra with autogenous (unfused) neural arches in which the base of the neural arch articulates with the centrum. In *Esox*, this is a deep pit, paired, seen in dorsal view (Fig. 1A).

Parapophyseal articular pit: A pit in centra that receives the parapophysis. This is generally best visible in lateral view (Fig. 1B).

Mid ventral groove: an elongate depression on the ventral surface of the centrum. This groove may hold the dorsal aorta, which runs along the ventral surface of the abdominal region of the vertebral column (Fig. 1C).

Rounded ventral surface: The condition of having no distinct grooves, pits or ridges on the ventral surface of the centrum (Fig. 1D).

Mid-ventral pit: a deep opening on the ventral surface of the centrum (Fig. 1E). This differs from a mid-ventral groove in that the pits in successive centra are separated by the raised
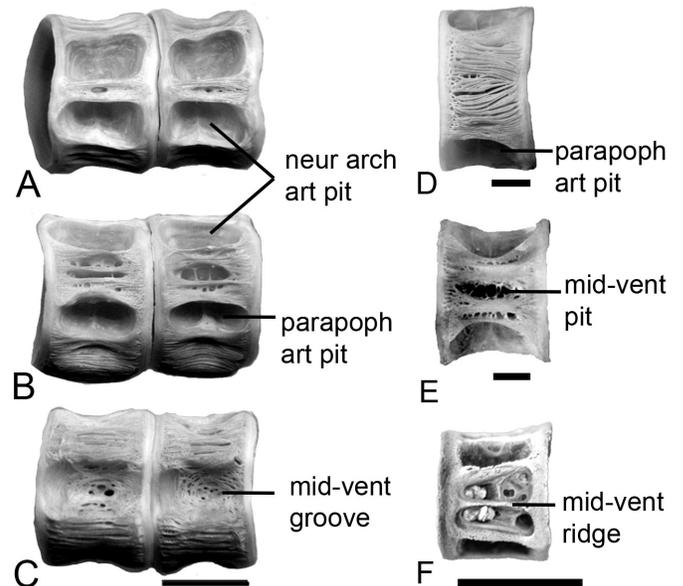
Figure 1. Esocid centra illustrating the morphological terms used in the text. A–C, mid-abdominal centra of *Esox lucius,* specimen ROM R2197, shown in A, dorsal, B, left lateral, and C, ventral views. Scale bar equals 5 mm. D, Cretaceous esocid centrum morphotype NvC (see Brinkman et al. 2014). Scale bar equals 1 mm. E, centrum number 25 of *Esox lucius,* UAMZ F8552, in ventral view, showing the condition of a mid-ventral pit. Scale bar equals 1 mm. F, Cretaceous esocid centrum, TMP 1995.177.0057, showing the condition of a mid-ventral ridge. Scale bar equals 1 mm. Anterior towards the left. Abbreviations: neur arch art pit, neural arch articular pit; parapoph art pit, parapophyseal articular pit; mid-vent groove, mid-ventral groove; mid-vent pit, mid-ventral pit; mid-vent ridge, mid-ventral ridge.

ends of the centrum. In some esocid centra, a mid-ventral pit may be developed at the base of a mid-ventral groove.

Mid-ventral ridge: a sagittal ridge at the middle of the centrum seen in ventral view (Fig. 1F).

Institutional Abbreviations: CMNFI, Canadian Museum of Nature, Fish collections; ROM, Royal Ontario Museum: UAMZ, University of Alberta Museum of Zoology; UCMP, University of California Museum of Paleontology.

DESCRIPTION

Variation along the vertebral column of *Esox (Esox) lucius*

Specimens studied: UAMZ F9079 (total length not available, estimated standard length is 51 cm), UAMZ F9077 (total length not available, estimated standard length is 39 cm) and UAMZ F9078 (length not available): three skeletons with centra in articulation and neural arches and parapophyses in place. UAMZ F9102 (total length not available, estimated standard length is 47 cm): complete skeleton with centra disarticulated and separated from the neural arches and parapophyses. ROM R8545 (total length is 52.5 cm, standard length not available): skeleton with first centrum still attached to the basioccipital; remainder of vertebral column held together by a thread through the neural arch so the order of the centra is maintained in the prepared specimen. ROM R2197 (total length is 66 cm, standard length not available) and CMNFI 1977-0217.1 (total length not available, standard length is 75 cm): two specimens in which the vertebrae are disarticulated and separated from the parapophyses and neural arches.

Description: In a sample of 76 specimens of *E. lucius* studied by Grande et al. (2004) the total number of abdominal centra in the vertebral column varies from 39 to 44. Among the specimens studied here, 44 abdominal centra are present in specimen UAMZ F8552 (Figs. 2, 3) and 41 abdominal centra are present in ROM R8545 (Tab. 1). Neural arches and parapophyses of the abdominal centra are autogenous except for the last abdominal centrum, which has fused parapophyses. In the caudal series, neural and haemal arches are fused to the centrum except for the last seven centra (Fig. 3L–N). Centra are nearly circular in end view throughout the abdominal region (Figs. 2, 3). The anterior and mid-region abdominal centra are rectangular when seen in dorsal view except for the posterior-most few centra, which, like the caudal centra, have concave sides (Fig. 3G).

Proportions: Measurements of the centra in one individual of *E. lucius* are given in Table 1, and a graph showing the change in the length of the centrum relative to its width is shown in Figure 4. The first centrum is relatively short, its length being about 60% of its width. The following four centra show a rapid increase in the relative length of the centra, so that by centrum 6 the length is 74% of its width. Posterior to this, the abdominal centra show a gradual increase in relative length along the column with the posterior-most abdominal centrum having a length that is 85% of its width. The first seven caudal centra show a further increase in length relative to width, and by centrum 54, the length is consistently equal to or exceeds the width.

Dorsal surface: Throughout the abdominal series the neural arch articular pits are close together and separated by either a narrow bar of bone or two closely-spaced ridges with a narrow opening between them (Figs. 2, 3). The articular pits are subdivided into anterior and posterior portions by a low vertical ridge mid-way along the lateral surface of the pit. The neural arch articular pits of the first centrum are oval in shape and about as wide as they are long (Fig. 2A). By centrum 10, the pits become narrow and elongate with a slightly wider anterior end (Fig. 3A). The difference in width of the anterior and posterior end of the pits is accentuated in the more posterior centra and towards the end of the abdominal series the neural arch articular pits are lachryform (Fig. 3F, G). In the centra with lachryform neural arch articular pits, the broader end reaches the anterior end of the centrum while the narrow posterior tip is separated from the posterior end of the centrum by a short space, and a dorsal process is present on the centrum behind the neural arch articular pit. This process shows little variation in size along the posterior end of the abdominal series. A posterodorsal process behind the neural arch articular pit is also present on the anterior centra of the caudal series (Fig. 3H–J).

Lateral surface: Parapophyseal articular pits are absent on the first abdominal centrum, although a shallow depression is present in the corresponding position on this centrum, and in UAMZ F9078 a parapophysis is preserved in articulation with the centrum in this depression. On centrum 2, deep parapophyseal articular pits are located low down on the side of the centrum (Fig. 2B). These are approximately equal in size to the pits of the more posterior centra. On centra 3 through 5 the parapophyseal pits shift progressively dorsally to reach the middle of the side of the centrum. At its highest point on these centra, the parapophyseal pit is separated from the neural arch articular pit by a broad surface about equal in size to the height of the parapophyseal pit (Fig. 2E). The parapophyses remain in this relatively high position on the following three centra, then gradually shift to a more ventral position, and by centrum 30 the parapophyseal pits are located close to the ventral edge of the centrum (Fig. 3E). Farther posteriorly along the column, the space between the left and right parapophyses on a single centrum becomes constricted by

a medial shift in the position of the pits, such that in the posterior abdominals the space between the parapophyses is only slightly greater than the space between the neural arch articular pits (Fig. 3G). As a result, the posterior abdominal centra differ little in morphology from the anterior caudal centra. The shape of the parapophyseal articular pits changes from an oval shape in the anterior centra (Fig. 2B–D) to elongate in the mid-abdominal region (Fig. 3). However, the pits continue to extend the full length of the centrum throughout the abdominal series. As with the neural arch articular pits, the parapophyseal articular pits are divided into an anterior and posterior portion. However, in contrast with the neural arch articular pits, ridges are present on both the lateral and medial walls of the parapophyseal pits.

As noted by Casselman et al. (1986), the lateral surface of the centra in *Esox lucius* are strongly striated. No secondary pits are present on the lateral side of the first centrum (Fig. 2A) but are typically present between the parapophyseal and neural arch articular pits on centra 2 through 4. However, the morphology of these pits is variable. In UAMZ F8552 a distinct pit is only present on the third centrum (Fig. 2C), but in ROM R8545, the second through fourth centra have a large, round pit between the parapophyseal and neural arch pits. Posterior to centrum 4, the sides of the centra between the parapophyseal pits and the neural arch articular pits are formed by a coarse network of bone with variably arranged elongate, narrow pits. Distinct secondary pits are also present ventral to the parapophyseal articular pits in the anterior and middle regions of the abdominal series. These pits first
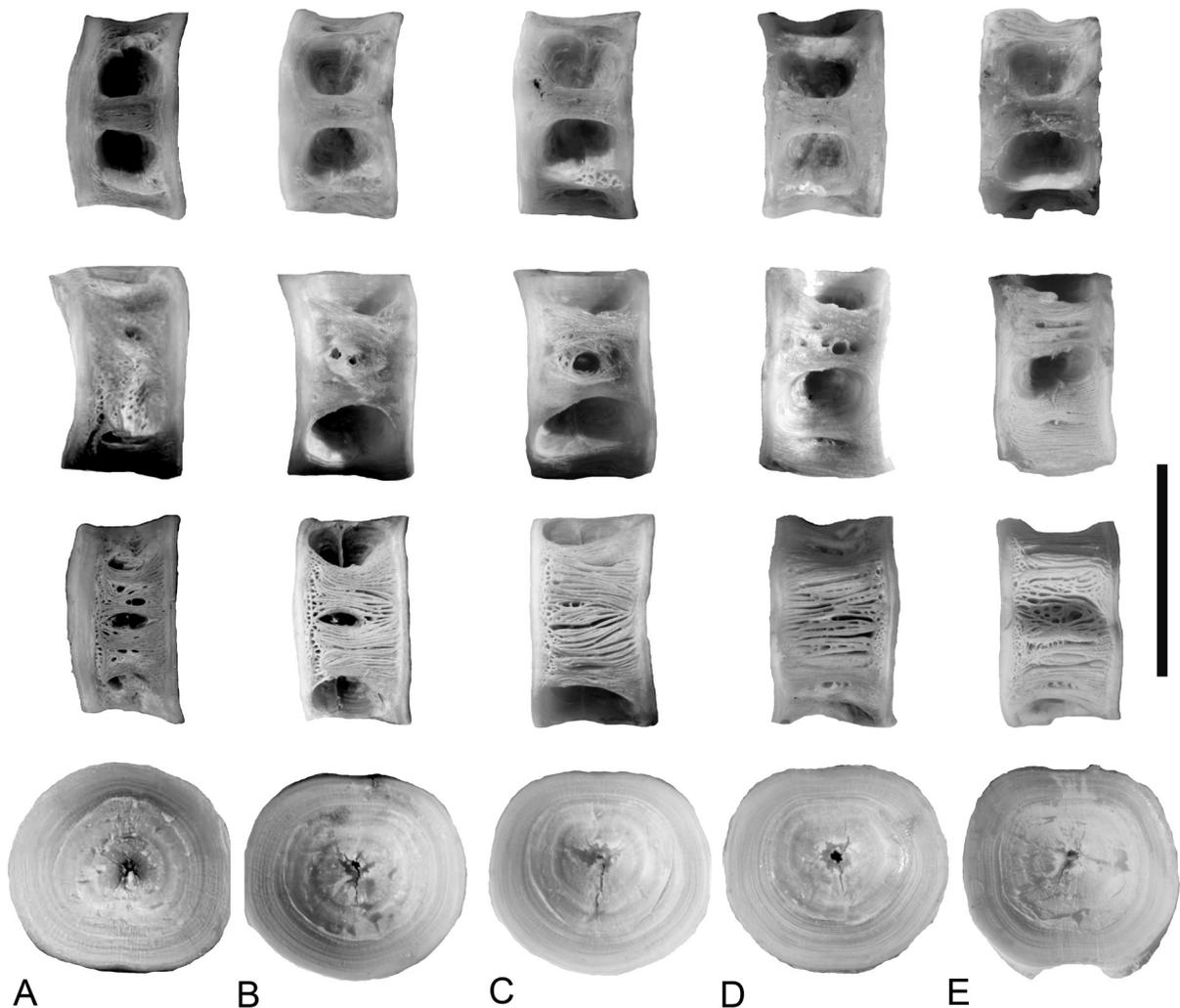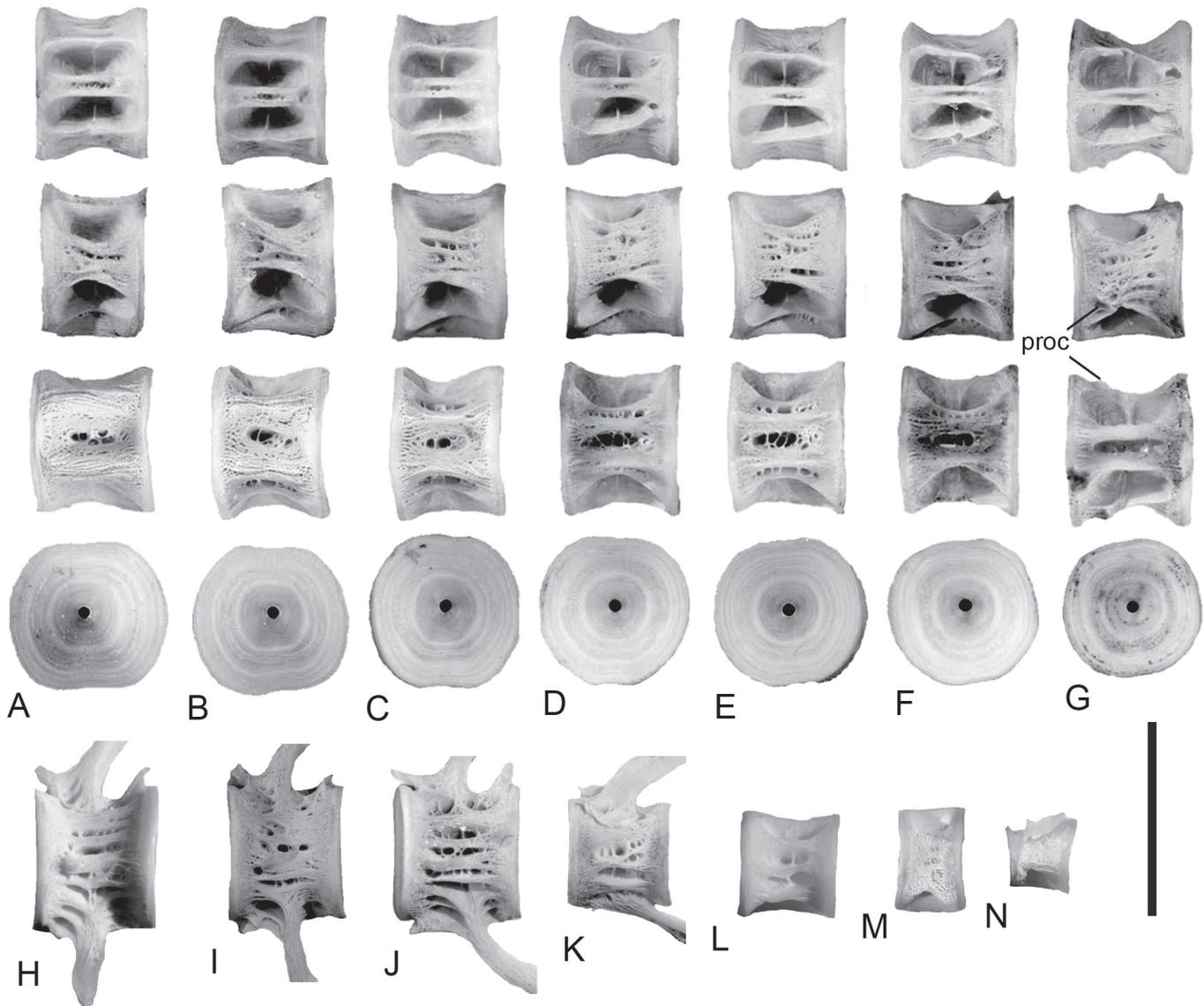

Figure 2. Centra 1 through 5 of *E. lucius*, UAMZ F8552, shown in (from top to bottom) dorsal, left lateral, ventral and posterior views. Anterior towards the left for all except posterior views. A, centrum 1; B, centrum 2; C, centrum 3; D, centrum 4; E, centrum 5. Scale bar equals five mm.

appear as a small, slit-like opening ventral to the parapophyseal articular pits on centrum 4 (Fig. 2D), and become large, elongate openings in the middle of the abdominal series. As the parapophyseal pits shift to a ventro-medial position in the posterior portion of the vertebral column, these pits become constricted and, in UAMZ F8552, they are lost by centrum 35 (Fig. 3F).

Anterior caudal centra typically have four or five stout ridges, sub-equal in size, extending between the anterior and posterior edges on the lateral surface of the centrum with irregular elongate spaces between them (Fig. 3H–J). In the more posterior caudal centra, the number of ridges is reduced, and towards the end of the column, only a single ridge extends between the ends of the centrum (Fig. 3M). The ural centra are smooth walled (Fig. 3M, N).

A short, rounded lateral process is present near the anterior end of the centrum on the side of the posterior abdominal and anterior caudal centra (Fig. 3G). In specimen UAMZ F9078, this process first develops on centrum 36 and extends onto the anterior caudal centra (Fig. 3H).

Figure 3. Representative centra from the vertebral column of *E. lucius*, UAMZ F8552, showing changes through the vertebral column. A–G, abdominal centra shown in (from top to bottom) dorsal, left lateral, ventral and posterior views. A, centrum 10; B, centrum 15; C, centrum 20; D, centrum 25; E, centrum 30; F, centrum 35; G, centrum 40. H, centrum 43, the posteriormost abdominal centrum, shown in left lateral view. I–L, caudal centra in left lateral view; I, centrum 45; J, centrum 50; K, centrum 55; L, centrum 56. M–N, ural centra in left lateral view; M, centrum 60; N, centrum 62. Anterior to left in all except posterior views. Abbreviations: proc, antero-lateral process. Scale bar equals 5 mm.

Table 1. Measurements of centra of five species of *Esox*. *Esox masquinongy* and *E. niger* are represented by disarticulated skeletons; the exact position of the centra posterior to centrum five is uncertain, so these are subdivided into regions. Abbreviations: C#, centrum position. All measurements are given in milimetres.

Esox lucius UAMZ F9078			*Esox musquinongy* CMN 77-311			*Esox reicherti* ROM R2243			*Esox niger* ROM R1607			*Esox americanus* ROM R8967		
C#	length	width	C#	length	width	C#	length	width	C#	length	width	C#	length	width
1	4.4	7.6	1	5.5	12.5	1	5.1	8.5	1	3.3	5.7	1	1.1	2.2
2	4.4	7.2	2	6.7	12.1	2	5.1	8.2	2	3.9	5.5	2	2.0	2.5
3	4.5	7.5	3	6.8	12.0	3	5.1	8.4	3	3.9	5.7	3	2.2	2.5
4	4.9	7.6	4	6.9	12.4	4	5.4	8.3		4.4	5.7	4	2.4	2.4
5	4.8	7.2	5	7.4	12.3	5	5.9	8.3		4.5	5.8	5	2.3	2.4
6	5.3	7.2		7.8	11.6	6	5.9	8.2		4.7	5.9	6	2.4	2.4
7	4.9	7.1		7.4	11.6	7	5.9	8.5		4.8	5.9	7	2.4	2.3
8	5.3	7.0		7.5	12.1	8	6.0	8.5		4.8	5.9	8	2.2	2.4
9	5.1	7.2		7.4	11.7	9	6.4	8.5		4.8	5.9	9	2.2	2.4
10	5.4	7.0		7.5	11.7	10	6.2	8.6		5.0	5.9	10	2.4	2.3
11	5.3	7.3		7.4	11.5	11	6.4	8.5		4.7	6.2	11	2.3	2.3
12	5.5	7.2		7.3	12.2	12	6.5	8.5		4.7	5.8	12	2.3	2.3
13	5.2	7.4		7.9	12.3	13	6.7	8.6		4.7	5.8	13	2.4	2.3
14	5.3	7.3		7.4	12.1	14	6.7	8.5		4.7	5.8	14	2.3	2.3
15	5.2	7.0		7.8	11.9	15	6.5	8.5		4.7	5.8	15	2.3	2.3
16	5.2	7.3		7.5	12.4	16	6.5	8.5		4.8	5.7	16	2.3	2.2
17	5.2	7.3		7.9	11.4	17	6.5	8.4		4.8	5.7	17	2.3	2.3
18	5.2	7.5		7.5	11.4	18	6.5	8.5		4.7	5.5	18	2.4	2.4
19	5.2	7.6		7.5	11.6	19	6.5	8.4		4.7	5.5	19	2.4	2.2
20	5.1	7.3		7.5	12.3	20	6.5	8.5		4.7	5.5	20	2.3	2.2
21	5.2	7.4		7.8	12.0	21	6.4	8.4		4.8	5.6	21	2.3	2.2
22	5.2	7.5		7.7	11.9	22	6.5	8.5		5.0	5.3	22	2.4	2.2
23	5.2	7.4		7.7	12.4	23	6.4	8.5		4.9	5.5	23	2.4	2.3
24	5.0	7.5		7.6	11.7	24	6.4	8.4		4.9	5.2	24	2.4	2.2
25	5.1	7.5		7.9	12.1	25	6.4	8.4		5.0	5.2	25	2.4	2.1
26	5.2	7.4		7.7	11.7	26	6.4	8.4		4.9	5.0	26	2.6	2.1
27	5.2	7.3		7.6	12.0	27	6.2	8.4		4.8	4.8	27	2.6	2.1
8	5.1	7.4		7.7	11.8	28	6.2	8.3		4.9	4.9	28	2.5	2.2
29	5.2	7.2		8.0	11.4	29	6.2	8.5		4.9	4.8	29	2.5	2.0
30	5.2	7.2		7.8	11.7	30	6.5	8.4		4.9	4.7	30	2.5	2.1
31	5.4	7.0		7.8	11.9	31	6.5	8.4		5.0	4.8	31	2.4	1.9
32	5.4	7.0		7.6	12.0	32	6.5	8.3		4.9	4.7	32	2.3	2.0
33	5.5	6.9		7.7	11.5	33	6.5	8.1		4.9	4.7	33	2.5	1.9
34	5.4	6.9		7.7	12.0	34	6.3	8.2		4.9	4.6	34	2.5	1.9
35	5.3	6.7		7.8	12.2	35	6.4	8.1		5.3	4.2	35	2.4	1.9
36	5.4	7.0		7.8	11.5	36	6.4	8.0		5.0	5.4	36	2.5	2.0

Region labels (vertical):
- *Esox lucius*: "anterior abdominal group 1" (C# ~8–16), "anterior abdominal group 2" (C# ~20–29), "mid-abdominal group 1" (C# ~31–36)
- *Esox musquinongy*: "anterior abdominal group 1" (upper rows), "anterior abdominal group 2" (middle rows), "mid-abdominal group 1" (lower rows)
- *Esox niger*: "anterior abdominal" (upper), "mid-abdominal" (middle), "posterior abdominal" (lower), "caudal" (last rows)

Table 1 continued.

Esox lucius UAMZ F9078			*Esox musquinongy* CMN 77-311			*Esox reicherti* ROM R2243			*Esox niger* ROM R1607			*Esox americanus* ROM R8967		
C#	length	width		length	width	C#	length	width		length	width	C#	length	width
37	5.4	6.9	mid-abdominal group 2	7.7	11.1	37	6.4	8.0	caudal	5.4	5.3	37	2.4	1.9
38	5.6	6.8		7.9	11.6	38	6.4	8.0		3.6	3.4	38	2.5	2.0
39	5.4	6.7		8.0	11.8	39	6.4	8.0		5.0	4.7	39	2.5	1.9
40	5.5	6.7		7.8	11.9	40	6.4	7.9		5.0	4.6	40	2.4	1.9
41	5.4	6.5		7.9	11.4	41	6.4	7.9		4.9	4.5	41	2.5	1.9
42	5.5	6.5	posterior abdominal	7.8	11.2	42	6.4	7.8		3.2	2.9	42	2.5	1.7
43	5.4	6.4		7.8	11.3	43	6.4	7.9		4.9	4.3	43	–	–
44	5.4	6.4		7.6	10.0	44	6.2	7.6		4.2	3.6	44	–	–
45	5.5	6.3		7.1	11.1	45	6.5	7.4		5.3	4.5	45	–	–
46	5.5	6.1		7.2	11.1	46	6.5	7.2		4.8	4.0	46	–	–
47	5.5	6.1		7.2	10.9	47	6.5	7.1		5.4	4.5	47	–	–
48	5.3	5.9		7.2	10.5	48	6.5	7.0		4.5	3.6	48	–	–
49	5.3	5.9		7.2	10.5	49	6.5	7.0		5.4	4.2	49	–	–
50	5.6	5.9	anterior caudal	7.5	10.3	50	6.5	7.0				50	–	–
51	5.6	5.6		7.4	10.5	51	6.5	6.8				51	–	–
52	5.0	5.4		7.5	10.1	52	6.5	6.7						
53	5.0	5.1		7.5	10.2	53	6.5	6.7						
54	5.0	5.1		7.2	10.5	54	6.4	6.5						
55	5.0	4.5	mid-caudal	7.4	9.7	55	6.2	6.0						
56	5.0	4.0		7.3	9.5	56	6.1	5.4						
57	4.6	3.4		7.1	9.6	57	6.1	5.2						
58	4.2	3.2	posterior caudal	7.0	8.9	58	5.6	5.0						
59	3.9	2.8		6.6	8.1	59	5.5	4.9						
60	3.6	0		5.9	7.8	60	5.0	–						
61				6.0	6.0									

Ventral surface: As noted by Casselman et al. (1986), a distinctive feature of *Esox lucius* is the presence of a deep, mid-ventral groove for the aortic artery on the abdominal centra. However, this groove does not extend the full length of the vertebral column; the anterior four centra have a rounded ventral surface lacking the groove. On centrum 5, a shallow mid-ventral depression is present bordered by low but distinct rounded bulges (Fig. 2E). These bulges are larger, and the mid-ventral groove is more distinct, on the centra immediately following. On centrum 15, the bulges become medio-laterally compressed and take on the appearance of ventrally-directed flanges bordering the mid-ventral groove (Fig. 3B). On centra 22–29, these flanges are reduced to form the lateral edge of a concave surface extending between the parapophyseal articular pits of each centrum (Fig. 3D). As the parapophyseal pits shift to a more ventro-medial position, the width of this surface becomes compressed, and by centrum 38 the space between the parapophyseal pits is a narrow surface formed by two lateral ridges bordering a shallow mid-ventral groove (Fig. 3G).

In addition to the aortic groove, mid-ventral pits are variably developed on the abdominal centra. A distinct mid-ventral pit is consistently present on the first two centra (Fig. 2A, B). The third centrum has a rounded ventral surface covered by a network of bone (Fig. 2C). Posterior to this, mid-ventral pits vary in size. In ROM R8545, mid-ventral pits are present on centrum 5 through 14. On the more posterior centra, the mid-ventral pits, when present, are typically small openings at the base of the mid-ventral groove. In UAMZ F8552, pits are present throughout the middle and posterior portions of the abdominal series (Fig. 3). In the middle of the abdominal series, these are typically round (Fig. 3A–C), while in the posterior part of the abdominal series, these are typically elongate (Fig. 3D–G).

Variation along the vertebral column of *Esox (Esox) masquinongy*

Specimens studied: CMNFI 1978-0202.1: (total length is 813 mm, standard length not available), skeleton with vertebrae disarticulated and neural arches not attached to centra. CMNFI 1977-0311-1 (total length is 826 mm, standard length is 718 mm), skeleton with vertebrae disarticulated, and parapophyses and neural arches not attached to centra. ROM R8971 (length not available): skeleton of juvenile individual with vertebral column in articulation.

Description: Material of *Esox masquinongy* examined is represented both by skeletons in which the centra are disarticulated (CMNFI 1978-0202.1, CMNFI 1977-0311-1) and by a skeleton in which the centra are preserved in articulation (ROM R 8971). Although the exact position of the centra in the fully disarticulated skeletons is unknown, except for those more distinctive ones at the anterior and posterior ends of the abdominal and caudal series, they could be placed in approximate position by comparison with the articulated specimen, ROM R8971.

In a sample of 86 specimens of *E. masquinongy* studied by Grande et al. (2004), the total number of abdominal centra in the vertebral column varies from 45 through 48. Specimen CMNFI 1977-0311-1 has 47 abdominal centra, but there are only 43 abdominal centra present in ROM R8971. However, in this latter specimen, three ribs articulate with the third centrum and two ribs articulate with the fourth, indicating these two centra are in reality a fusion of more than one centrum. If these are instead counted as fused centra (a fusion of three resulting in centrum 3, and a fusion of two resulting in centrum 4), a total of 46 precaudal centra would have been present, which better fits the expected number for this species.

Neural arches and parapophyses of the abdominal centra are autogenous except for those associated with the posterior end of the series. In ROM R8971, both parapophyses and neural arches are fused to the last four abdominal centra.

Proportions: Proportional changes along the vertebral column of *E. masquinongy* are similar to those of *E. lucius* in that the anterior centrum is short relative to its width, and length relative to width increases rapidly to the fifth centrum then shows only a slight change through the remainder of the abdominal series. However, the proportions are different in this species, in that the length is consistently shorter than in the equivalent regions of the vertebral column of *E. lucius* (Fig. 4). The length of the first centrum is only 44 % of its width. The average length of the anterior abdominals (centra 6–16) is 63% of width, and the average length of the posterior four abdominals (centra 44–47) is 68% of width. Caudal centra show only a small increase in relative length; the three caudals with the greatest relative length have an average length of 76% width.

Dorsal surface: The neural arch articular pits of the abdominal centra are similar to those of *E. lucius* in that the pits are close together and separated by a narrow bar (Fig. 5A–G). Neural arch articular pits are relatively wider than those of *E. lucius*, likely reflecting the shorter relative length of the abdominal centra in *E. masquinongy*. Posterodorsal processes are present behind the neural arch articular pits of the last 13 centra of the abdominal series (Fig. 5F, G).

Lateral surface: The placement of the parapophyseal articular pits on the centra of *E. masquinongy* is similar to that of *E. lucius* in that the pits first appear in a ventral position (Fig. 5C), move rapidly to a position mid-way up the side of the centrum (Fig. 5D), and then gradually shift to a ventral and medial position so that the last few abdominal centra differ little from the anterior caudals in the placement of the parapophyseal articular pits (Fig. 5H).
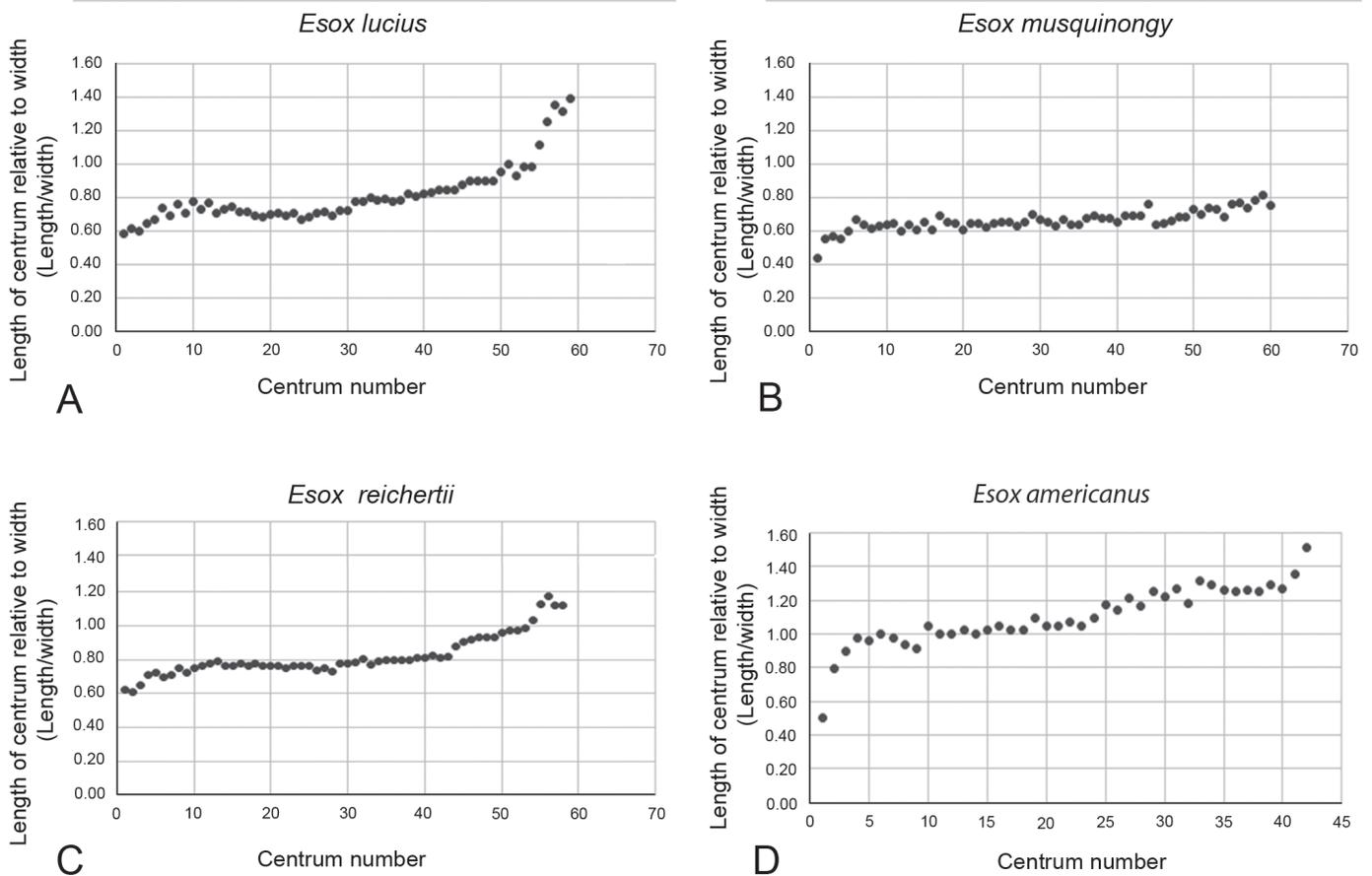
Figure 4. Graphs showing the change in length of centra relative to width along the vertebral column in four species of *Esox*. A) *Esox lucius*, UAMZ F9078. B) *Esox masquinongy*, CMNFI 1977-0311-1. C) *Esox recherti*, ROM R8294. D) *Esox americanus*, ROM R8967. Measurements given in Table 1.

However, in CMNFI 1977-0311-1, the first two centra are without distinct pits and the parapophyseal pit first develops on the third, rather than the second, centrum (Fig. 5A, B). The pits of centra 3 and 4 are oblique with the anterior end lower than the posterior end. By centrum 5, the pits become oriented horizontally and located mid-height on the lateral surface of the centrum. These pits remain in a relatively high position on the lateral surface through the following six centra, at which point they begin to shift to a ventral position. By centrum 20, the pits are located near the ventral edge of the centrum (Fig. 5F), and by centrum 27, the pits are located close to the midline and face primarily ventrally (Fig. 5G).

As reported by Casselman et al. (1986) the centra of *E. masquinongy* differ from those of *E. lucius* in having only slight striations on the side and ventral surface of the centrum. However, this feature is likely related to growth, because in ROM R8971, which has mid-abdominal centra with a length of 4 mm, small foramina become more frequent on the lateral surfaces of the posterior abdominal centra beginning at centrum 20. In CMNFI 1977-0311-1, which has

mid abdominal centra with a length of 7.7 mm and thus is from a much larger individual, the sides of the centrum remain smooth until the last two abdominal centra, in which small pits first occur (Fig. 5N). The sides of the anterior and mid-caudal centra are formed by coarsely woven bone fibers (Fig. 5I–K). A small lateral process is present on the last ten abdominal and first eight caudal centra.

In contrast with *E. lucius* and species of *Esox* described below, accessory pits are absent on the lateral surface of the centrum below the parapophyseal articular pit in *E. masquinongy*.

Ventral surface: A striking difference between the centra of *E. masquinongy* and *E. lucius* is the absence of a mid-ventral groove in the centra of *E. masquinongy*. As described by Casselman et al. (1986), the aortic artery has shifted away from the midline, and a shallow groove is present on the side of the centrum for this artery. The ventral surface of the centrum is similar to the lateral surface in that it has a smooth surface formed by a fine network of bone. This surface texture is present throughout the abdominal series in both juvenile and adult specimens.
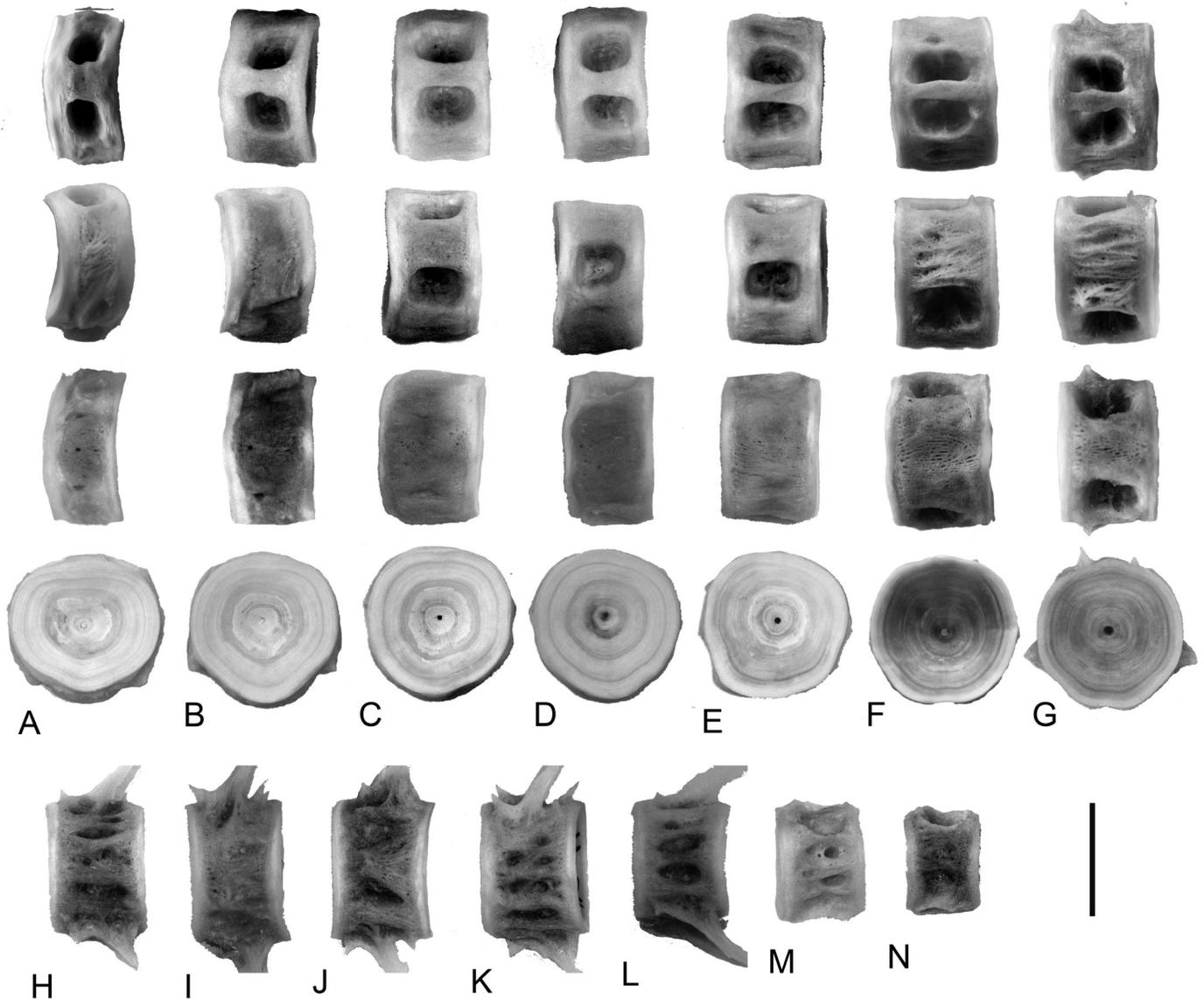
Figure 5. Representative centra from the vertebral column of *E. masquinongy* showing changes through the vertebral column. A–H, abdominal centra shown in (from top to bottom) dorsal, left lateral, ventral and posterior views. A, centrum 1; B, centrum 2; C, centrum 3; D, centrum 4; E, anterior abdominal centrum; F, mid-abdominal centrum; G, posterior abdominal centrum; H, posterior-most abdominal centrum in left lateral view. I–L, caudal centra in left lateral view; I, anterior caudal centrum; J, anterior caudal centrum; K, mid-caudal centrum; L, posterior caudal centrum. M–N, ural centra in lateral view. Anterior towards the left in all except posterior views. Specimen CMNFI 1977-0311.1. Scale bar equals one cm.

Variation along the vertebral column of *Esox (Esox) reichertii*

Specimen studied: ROM R8294 (length not available): skeleton with vertebral column in articulation.

Description: The single skeleton of *E. reichertii*, ROM R 8294, that was available for this study included a complete articulated vertebral column (Fig. 6). Forty-five abdominal vertebral centra are present, which is within the range of 44 to 47 abdominal centra reported by Grande et al. (2004) based on their study of five specimens. Neural arches of the abdominal centra are autogenous except for the last two in the series, and parapophyses are autogenous except for the last three centra in the series.

Proportions: The pattern of changes in proportion of the centra is similar to that of *E. lucius* in that the first centrum is relatively short (length about 60% of width; Tab. 1; Fig. 4C). Relative length increases over the following six centra to reach 70% of width, then gradually increases to 80% of width by the end of the abdominal series. In the mid-caudal region, the relative length of the centra becomes equal to the width.

Dorsal surface: *E. reichertii* is similar to *E. lucius* in that the neural arch pits are located close to one another and are separated by two closely spaced ridges. However, it differs from *E. lucius* in that the neural arch articular pits of *E. reichertii* extend the full length of the centrum throughout the length of the abdominal series and a posterodorsal process is absent on the posterior abdominal centra.

Lateral surface: In ROM 8294, a small parapophyseal pit is present on the right lateral surface of the first centrum but not on the left side. Because of this asymmetry, this is assumed to be an individual variant rather than a typical feature of the species. The change in position of the parapophyseal articular pit throughout the vertebral column (Fig. 2A) is similar to that of *E. lucius*. In both, the parapophy-
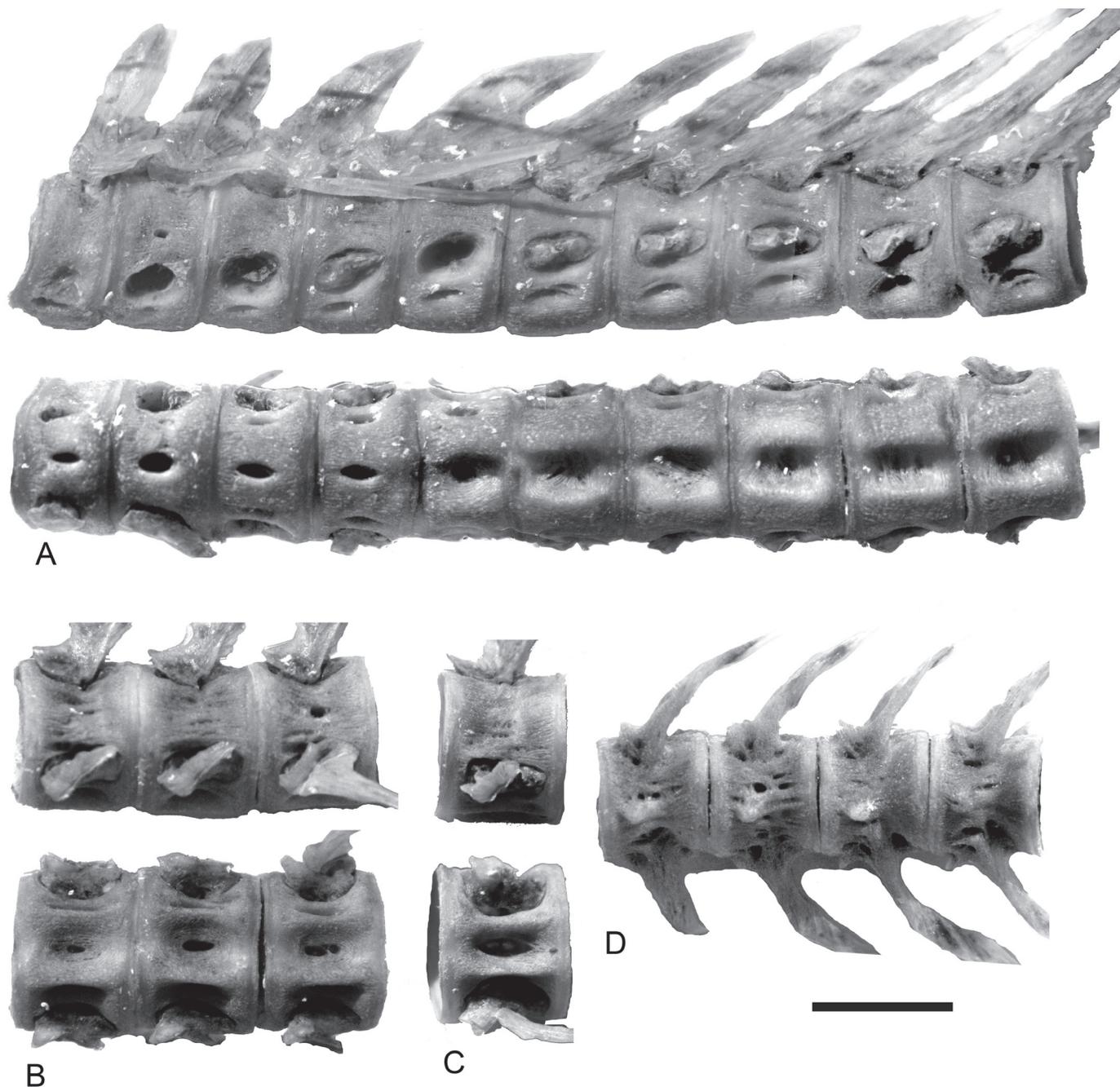
Figure 6. Representative centra from the vertebral column of *E. reichertii* , ROM R8294, showing changes in structure of the centra through the vertebral column. A, centra 1 through 10 in articulation, shown in left lateral and ventral views. B, mid-abdominal centra shown in left lateral and ventral views. C, posterior abdominal centra shown in left lateral and ventral views. D, anterior caudal centra shown in lateral view. Anterior towards the left. Scale bar equals one cm.

seal pit of the second centrum is located low on the lateral surface of the centrum and over the course of the following three vertebrae this shifts to a more dorsal position, eventually reaching a position at midheight of the centrum (Fig. 5A). The pit remains in this relatively high position until centrum 14, when it begins to shift to a more ventral position. By centrum 21, it is located near the ventral edge of the centrum (Fig. 4B), and by centrum 30 the parapophyseal pits have moved to a more medial position and so face primarily ventrally (Fig. 4C).

As in *E. lucius*, large accessory pits are present below the parapophyseal pits in the anterior and middle portions of the vertebral column (Fig. 4A,B). The accessory pit first appears below the parapophyseal pit on centrum 2. It extends posteriorly through to centrum 33, at which point the ventromedial shift of the parapophyseal articular pits squeezes the accessory pit shut (Fig. 4C).

The lateral surface of the centrum above the parapophyseal pit is formed by a fine network of bone. Small accessory pits are irregularly developed on this surface. In the anterior half of the abdominal series, these rarely extend through a series of more than two centra. They become more numerous in the posterior half of the vertebral column (Fig. 4D), and in the caudal centra, they result in a series of ridges extending between the anterior and posterior ends of the centrum.

Posterolateral processes are present on the last ten abdominal and first seven caudal centra (Fig. 4D). As in *E. lucius*, these are short, blunt spines.

Ventral surface: As in *E. lucius*, centra 1 through 4 have a rounded ventral surface (Fig. 4A). Parasagittal bulges begin to develop on centrum 5 and are distinct by centrum 6. On centra 7 through 20, these appear as rounded bulges with a low wide depression between them. By about centrum 20, these become medio-laterally compressed and form ventrally directed flanges bordering a mid-ventral groove (Fig. 4B). A mid-ventral pit is present on centra 1 through 5. On the following 15 centra, the ventral surface is covered by a network of bone with irregular development of enlarged mid-ventral foramina towards the end of this series. Distinct mid-ventral pits reappear on centrum 21 and continue to be present to the end of the abdominal series (Fig. 4B, C).

Variation along the vertebral column of *Esox (Kenoza) niger*

Specimens studied: ROM R1607 (total length is 450 mm, standard length not available): skeleton with disarticulated vertebral column, parapophyses and neural arches remain attached to the centra.

Description: One skeleton with a fully disarticulated vertebral column was available for study. Thirty-four abdominal and 16 precaudal centra are present. This is within the range of 33 to 39 abdominal centra present in the species documented by Grande et al. (2002) based on a sample of 50 specimens.

Although the centra are fully disarticulated, the first three centra could be recognized on the basis of relative length and position of the parapophyseal pit (Fig. 7A–C). The more posterior abdominal centra could be identified as belonging to the anterior, mid-, and posterior abdominal regions based primarily on the position of the parapophyseal pits and the development of a lateral processes (Fig. 7D–F). Similarly, the caudal centra could be assigned to anterior, middle, and posterior regions (Fig. 7G–L).

Proportions: The variation of proportions of the centra in *E. niger* (Tab. 1) is similar to that of *E. lucius* and *E. reichertii* in that the length of the first centrum is approximately 60% of its width and there is a rapid increase in relative length seen over the following two centra. The average length of the anterior abdominal centra is 80% of width. The more posterior abdominal centra show a further increase in relative length, with the average length of the mid-series abdominal centra being 83% of width, and the average length of the posterior abdominal centra being 108% of width. Caudal centra show a further increase in relative length, with the length of the posterior caudal centra reaching 130% of width in some of the centra in the middle of the caudal series.

Dorsal surface: In dorsal view, the anterior abdominal centra of *E. niger* are similar to those of *E. lucius* in that the neural arch articular pits are located close to one another and are separated by two closely spaced ridges with the space between the ridges filled in by a network of bone.

Posterodorsal processes are present on the last 14 abdominal centra (Fig. 7F). These extend through the anterior and middle regions of the caudal series (Fig. 7G, H).

Lateral surface: The first centrum of *E. niger* is similar to that of *E. lucius* in lacking distinct parapophyseal pits (Fig. 7A). The lateral and ventral surfaces of the centrum are covered by a fine network of bony fibers. No secondary pits are present. A deep parapophyseal pit is present on the middle of the lateral surface of the second centrum (Fig. 7B). As in *E. lucius*, this shifts dorsally to a relatively high position on the side of the centrum by centrum 5, and remains in this position on the anterior centra of the abdominal series (Fig. 7C). In the mid-abdominal centra, this pit shifts to a more ventral position (Fig. 7D), and in the posterior abdominal centra, this is located at the ventral edge of the centrum in lateral view (Fig. 7E, F). Also, as in *E.lucius*, an accessory pit is present beneath the parapophyseal pit in the anterior and mid-abdominal centra (Fig. 7C, D). This pit is lost as a result of a medial shift in the position of the parapophyseal pit in the posterior abdominal centra (Fig. 7E, F).

The lateral surface of the anterior and mid- abdominal centra is formed by a fine network of bone (Fig. 7A–D). This becomes coarser in the posterior abdominal centra (Fig. 7E–G), and in the anterior caudal centra, the lateral surface becomes formed by narrow, elongate ridges extending between the anterior and posterior ends of the centrum (Fig. 7H, I). These elongate ridges are reduced in number towards the end of the caudal series (Fig. 7J, K) with the most posterior centra having smooth surfaces (Fig. 7I).
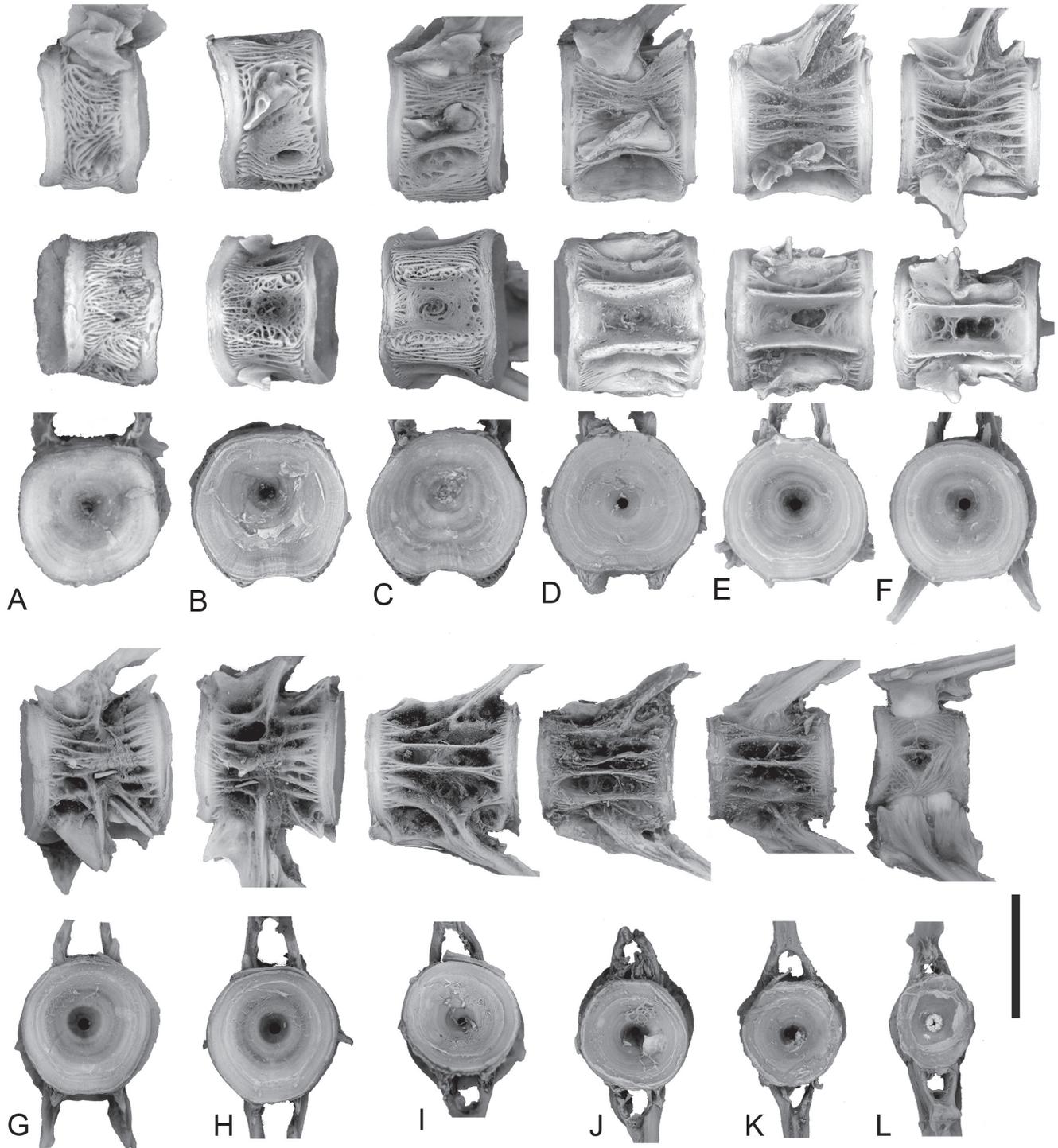
Figure 7. Representative centra from the vertebral column of *Esox niger*, ROM 1607, showing changes in structure of the centra through the vertebral column. A–F, abdominal centra shown in left lateral, ventral and end views; A, centrum 1; B, centrum 2; C, centrum 3; D, anterior abdominal centrum; E, mid-abdominal centrum; F, posterior abdominal centrum. G, posterior abdominal centrum shown in left lateral and posterior views. H–L, caudal centra shown in left lateral and posterior views. Anterior towards the left in all except posterior views. Scale bar equals 5 mm.

Ventral surface: In ventral view, the abdominal centra of *E. niger* differ from those of *E. lucius* in that the aortic groove extends further forward in the series, so that it is present on the ventral surface of the second centrum (Fig. 7B). As in *E. lucius*, this groove is bordered by bulges that are broad on the anterior abdominal centra (Fig. 7B, C), become compressed and ridge-like on the mid-abdominal centra (Fig. 7D, E), and are reduced on the posterior-most abdominal centra (Fig. 7F).

Variation along the vertebral column of *Esox (Kenoza) americanus*

Specimens studied: ROM R8967 (total length is 184 mm, standard length not available): articulated skeleton with neural arches, parapophyses, and ribs in place. ROM R8966 (total length not available, standard length 147 mm): partially articulated skeleton, with first abdominal and posterior caudal centra disarticulated. ROM R1736 (total length is 141 mm, standard length not available): disarticulated skeleton with parapophyses and neural arches separate from centra, anterior-most centra not present. Although this species contains two subspecies (*E. americanus americanus* and *E. americanus vermiculatus*), none of the skeletal specimens were identified to subspecies.

Description: Three skeletons were available for study. ROM R8967, the only one of these with a fully articulated vertebral column, had 35 abdominal centra and 16 caudal centra, which is within the range of 46 to 51 total centra reported by Grande et al. (2004) based on a sample of 23 specimens of *Esox americanus americanus*, and 46–54 total centra reported by Grande et al. (2004) based on a sample of 71 specimens of *Esox americanus vermiculatus*.

Proportions: The change in relative length of the centra along the vertebral column in *E. americanus* is similar to that in *E. lucius* in that the first centrum is relatively short, the length increases rapidly over the next few centra, then slowly increases through the remainder of the abdominal series (Tab. 1; Fig. 4D). However, it differs from *E. lucius* in that the abdominal centra are relatively longer in *E. americanus*. The mid-abdominal centra are about as long as they are wide. Relative length slowly increases through the remainder of the column, with the posterior abdominal centra having a length that is up to 125% of width.

Dorsal surface: In dorsal view, *E. americanus* differs from other species of *Esox* in that the neural arch articular pits of the anterior-most centra are widely separated and a deep mid-dorsal pit is present between them (Fig. 8A). However, this configuration is reduced to a narrow bar formed by two closely spaced ridges by the sixth centrum (Fig. 8B–F). On the anterior abdominal centra, the neural arch extends the full length of the centrum (Fig. 8B), but towards the end of the column they are shorter in length and a posterodorsal process is present posterior to the pits (Fig. 8D–F).

Lateral surface: In lateral view, *E. americanus* is similar to *E. lucius* in that the first centrum is without a parapophyseal pit. The pit is present low on the second centrum, rapidly moves to a dorsal position (Fig. 8B), then gradually shifts to a ventral position (Fig. 8F). However, it differs from *E. lucius* in that the parapophyseal pit reaches a relatively higher position on the centrum. On centrum 3 through 8, the parapophyseal pits butt against the neural arch articular pits or are separated from the neural arch only by a narrow bar (Fig. 8B, C). Posterior to centrum 8, as the parapophyseal pit shifts to a more ventral position, the space between the two pits is formed by widely spaced ridges (Fig. 8D–F). On the caudal centra, these ridges tend to extend the whole distance between the anterior and posterior ends of the centrum (Fig. 8H–J).

E. americanus is similar to *E. lucius* in that a large accessory pit is present ventral to the parapophyseal articular pits on the anterior abdominal centra (Fig. 8B, C). This pit is found along the series up to centrum 18, at which point it is lost on more posterior centra as a result of the ventro-medial shift in the position of the parapophyseal articular pits.

Antero-lateral processes are present on the posterior abdominal centra (Fig. 8E, F), but their shape differs from that of other species of *Esox*. Rather than a short, cylindrical process or blunt nubbin of bone, the process in *E. americanus* has the shape of a triangular flange. On the posterior abdominal centra, this flange is restricted to the anterior half of the centrum, but on the caudal centra, the flange extends to the posterior end of the centrum.

Ventral surface: In ventral view, *E. americanus* differs from *Esox lucius* in that the anterior end of the ventral groove on the centra is bordered by ventrally directed flanges rather than rounded bulges. These ridges first develop on the second abdominal centra. They are slightly wider on centrum 2 through 5 than they are on the more posterior abdominal centra and have a rugose ventral surface. As the parapophyseal pits move to a more ventral position the ridges become closer together, until the ridge is reduced and lost as a distinct feature.

DISCUSSION

Centrum morphology of extant *Esox*: Based on this survey of centrum morphology along the vertebral column in five species of *Esox*, a generalized pattern of change along the vertebral column in the genus can be recognized. The first centrum is relatively short, a rapid increase in length is seen in the next two to three centra, and posterior to these, the centra show little change in proportions along the column or a slight increase in relative length. Also, a similar
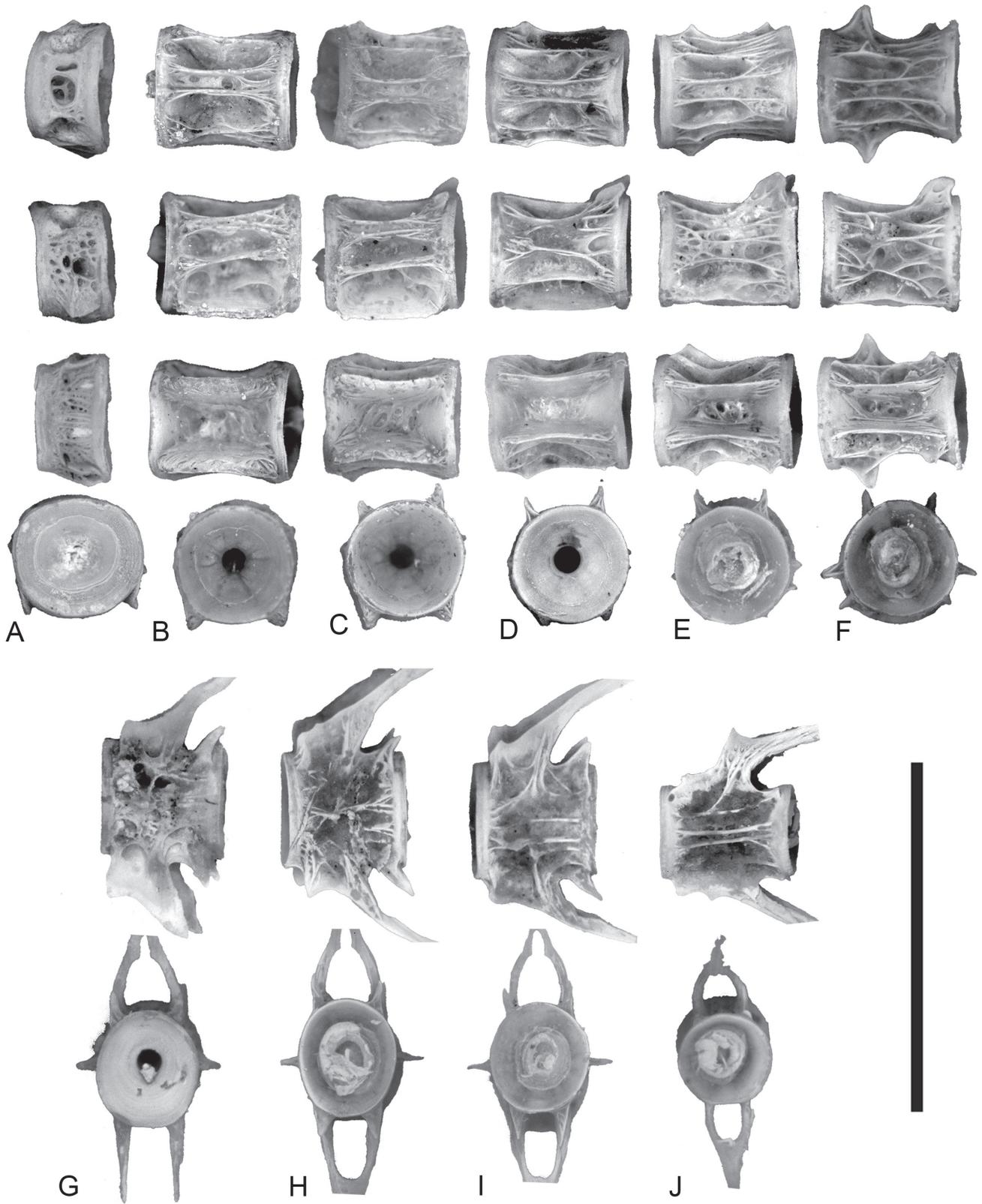
Figure 8. Representative centra from the vertebral column of *Esox americanus* showing changes in structure of the centra through the vertebral column. A–F, abdominal centra in dorsal, left lateral, ventral and end views; A, centrum 1; B and C, anterior abdominal centra; D, mid-abdominal centrum; E and F, posterior abdominal centra. G, posterior-most abdominal centrum in left lateral and posterior views. H–J, caudal centra in left lateral and posterior views. A, from specimen ROM R8966; B–J, from specimen ROM R1736. Anterior to left in all except end views. Scale bar equals 5 mm.

pattern in change in position of the parapophyseal articular pits through the abdominal series is seen. The first centrum is typically without parapophyseal pits. Large pits are present relatively low on the lateral surfaces of the second, or rarely third, centrum; these rapidly shift to a dorsal position, then more slowly shift to a ventral and medial position farther posteriorly in the vertebral column.

In addition to easily recognizing the first three centra, the approximate position of isolated centra from other parts of the abdominal region of the vertebral column can be recognized using the relative length of the centrum, presence/absence and position of the parapophyseal articular pits, and features of the ventral surface of the centrum. Posterior to the anterior-most three centra, the abdominal series can be divided into three regions: an anterior, middle, and posterior abdominal region. In the anterior region, a mid-ventral groove is present, bordered by either a pair of rounded bulges or ventrally directed flanges, and the parapophyseal articular pits are located on the lateral surfaces of the centrum. In the middle region, the parapophyseal pit is relatively low on the centrum and the ventral flanges are reduced. In the posterior region, the parapophyseal pit is in a more medial position and a lateral process is present on the side of the centrum. The changes along the column are gradational, so transitional morphologies are present, and within each of the regions isolated centra can be placed in relatively more anterior or posterior positions. The caudal centra show a similar subdivision into anterior, middle, and posterior caudal regions. In the anterior region, lateral processes are present on the side of the centrum. In the middle region, the side of the centrum is formed by a network of bone. In the posterior region, which is restricted to the ural centra and usually one or two immediately preceding centra, the sides of the centra are smooth.

The documentation of variation of centrum morphology in a single species based on position along the vertebral column now allows isolated centra of dissimilar morphology to be recognized as belonging to a single species. Additionally, the variation documented here among the various species of *Esox* might allow the identification of multiple species in a sample of isolated centra, which previously could not confidently be assigned to more than one species. Based on this new information, we are better able to assess a variety of pike material from the Upper Cretaceous deposits that previously was identified only to the family level.

Comparison with centra from the Upper Cretaceous referred to the Esocidae: Centra recovered from microvertebrate sites of Late Cretaceous age have been referred to the Esocidae based on a pattern of co-occurrence with tooth-bearing elements of *Estesesox* and *Oldmanesox*, a similar size-frequency distribution, and general similarities with the centra of extant esocids and

salmoniforms (Brinkman et al. 2013, 2014). Comparison with the centra of *Esox* described above allows the recognition of a series of features in which the Cretaceous esocids differ from the extant species of *Esox*. In dorsal view, the Cretaceous esocid centra are similar to those of extant species of *Esox* in that the neural arch articular pits extend the full length of the centrum and are separated by a narrow bar of bone or two closely spaced ridges. This similarity increases our confidence that the fossil material does indeed belong to Esocidae.
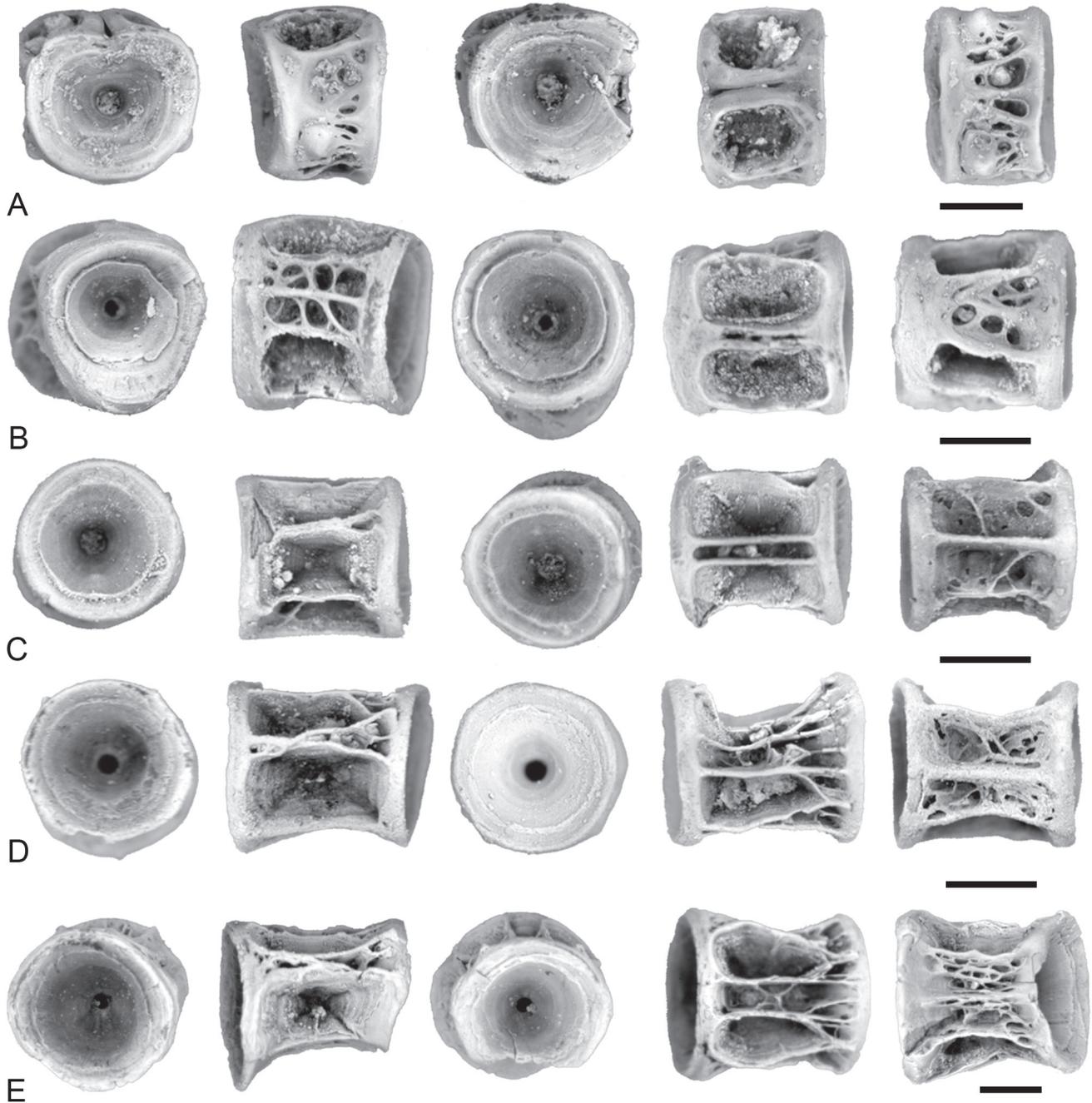
In lateral view, the Cretaceous esocid centra are similar to those of *Esox* in that the parapophyseal articular pits extend the full length of the centrum. They are similar to *E. americanus* and differ from the other extant species of *Esox* studied in that the parapophyseal pit closely approaches the neural arch articular pit. This differs from other species of *Esox* where a broad surface separates the parapophyseal articular pits from the neural arch articular pits. Also, a lateral process like that seen on the posterior abdominal centra of *Esox* is not present in the Cretaceous centra.

In ventral view, the Cretaceous esocid centra differ from those of extant species of *Esox* in the lack of a mid-ventral groove or pit. Instead, either a mid-ventral ridge is present or the centrum is covered by a network of bone extending between the anterior and posterior ends of the centrum. However, the shape of the ventral surface of the Cretaceous esocid centra is similar to the third centrum of *Esox lucius*, which has a smoothly rounded ventral surface without a mid-ventral pit. Based on these differences, we consider the Cretaceous esocid material to represent a different genus from *Esox*.

The variation along the column in extant species of *Esox* allows the taxonomic significance of the morphological variation in Cretaceous esocid centra to be evaluated. Three distinct morphotypes of centrum were recognized by Brinkman et al. (2104) in the upper Maastrichtian Hell Creek Formation based on differences in the lateral and ventral surfaces of the elements (Fig. 9). Although these were assumed to be taxomically distinct by Brinkman et al. (2014), some of the features in which they differ can be interpreted as a result of variation along the column. One of these is the variation in proportions. In extant species of *Esox*, the anterior-most abdominal centra are relatively short, and posterior abdominals become more elongate. Centrum morphotype NvC includes centra that are relatively shorter than wide (Fig. 9A) as well as centra that are about equal in length and width (Fig. 9B), while NvD includes centra that are longer than wide (Fig. 9D. E). This difference in proportions suggests that morphotype NvC includes centra from the anterior and middle regions of the abdominal series, and morphotype NvD includes centra from the posterior region of the series. Also, morphotype

NvD is similar to the posterior abdominal centra of extant species of *Esox* in that the neural arch articular pits are oval and a process extends dorsally posterior to these pits, adding support to the interpretation that these centra are from the posterior end of the abdominal series. The third morphotype present in the Hell Creek Formation, NvE (Fig. 9C) may be from an intermediate region of the vertebral column. Thus, based on a comparison with the pattern of variation along the column in extant species of *Esox*, the esocid centrum morphotypes present in the Hell Creek

Figure 9. Esocid centrum morphotypes from the Upper Cretaceous Hell Creek Formation. From left to right, in anterior, left lateral, posterior, dorsal and ventral views. A and B, centrum morphotype NvC. A, centrum morphotype NvC shorter than wide, interpreted as anterior-most abdominal centrum, specimen UCMP230743/V77130. B, centrum morphotype NvC subequal in length and width, interpreted as from the anterior or middle regions of the column, UCMP 230607/V73097. C, centrum morphotype NvE, interpreted as transitional from mid and posterior regions of the column, UCMP 191603/V99369. D and E, centrum morphotype NvD, interpreted as from the posterior region of the abdominal series. D, UCMP 230604/V73087; E, UCMP 230603/V73087. Anterior to left in all except anterior and posteror views. Scale bar equals one mm.

Formation are best interpreted as regional variants from the column of a single taxon.

The gap between the last occurrence of the Cretaceous esocids and the first occurrence of *Esox* in the late Paleocene suggests that the early and middle Paleocene was a critical period in the evolution of esocids. Isolated centra and other skeletal elements from this time period will be an important source of information on this early stage of esocid evolution, providing data on the timing of the origin of the genus *Esox* and changes in diversity across the Cretaceous/Paleogene boundary.

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LITERATURE CITED

Brinkman, D.B., and A.G. Neuman. 2002. Teleost centra from uppermost Judith River Group (Dinosaur Park Formation, Campanian) of Alberta, Canada. Journal of Paleontology 76: 138–155. DOI: 10.1017/S002233600001742X

Brinkman, D.B., A.G. Neuman, and J.D. Divay. 2017. Non-marine fishes from the late Santonian Milk River Formation of Alberta, Canada – evidence from vertebrate microfossil localities. Vertebrate Anatomy Morphology and Paleontology 3:7–46. DOI: 10.18435/B5PP41

Brinkman, D.B., M.G. Newbrey, A.G. Neuman, and J.G. Eaton. 2013. Freshwater Osteichthyes from the Cenomanian to late Campanian of Grand Staircase—Escalante National Monument, Utah. Pp. 195–236 in A.L. Titus and M.A. Loewen (eds). At the Top of the Grand Staircase: The Late Cretaceous of Southern Utah. Indiana University Press, Bloomingdale, Indiana.

Brinkman, D.B., M.G. Newbrey, and A.G. Neuman. 2014. Diversity and paleoecology of actinopterygian fish from vertebrate microfossil localities in the Maastrichtian Hell Creek Formation of Montana. Geological Society of America Special Papers 503:247–270. DOI: 10.1130/2014.2503(09)

Casselman, J.M., E.J. Crossman, P.E. Ihssen, J.D. Reist, and H.E. Booke. 1986. Identification of muskellunge northern pike and their hybrids. American Fisheries Society Special Publication 15:14–46.

Courtemanche, M. and V. Legendre. 1985. Os de poissons: nomenclature codifiée, noms anglais et français. Bibliothèque nationale du Québec, Montréal, Quebec.

Cuvier, G. 1817. Le Règne Animal Distribué d'aprés son Organisation Pour Servir de Base á L'histoire Naturelles des Animaux et D'introduction á L'anatomie Comparée. Les Reptiles, les Poissons, les Mollusques et les Annélides (1 ed.); P.F. Paris: Didot le jeune.

Crossman, E.J. and J.M. Crossman. 1969. Identification of northern pike and muskellunge from axial skeletons, scales, and epipleurals. Journal of the Fisheries Board of Canada 26:175–178.

Divay, J.D. and A.M. Murray. 2013. A mid-Miocene ichthyofauna from the Wood Mountain Formation, Saskatchewan, Canada. Journal of Vertebrate Paleontology 33:269–1291. DOI: 10.1080/02724634.2013.773334

Estes, R. 1969a. Studies on fossil phyllodont fishes: Interrelationships and evolution in the Phyllodontidae (Albuloidei). Copeia 1969:317–331. DOI: 10.2307/1442082

Estes, R. 1969b. Two new Late Cretaceous fishes from Montana and Wyoming. Breviora 335:1–15.

Estes, R., and R. Hiatt. 1978. Studies on fossil phylodont fishes; a new species of *Phyllodus* (Elopiformes, Albuloidea) from the Late Cretaceous of Montana. PaleoBios 28:1–10.

Grande, T., H. Laten, and J.A. López. 2004. Phylogenetic relationships of extant esocid species (Teleostei: Salmoniformes) based on morphological and molecular characters. Copeia, 2004:743–757. DOI: 10.1643/CG-04-007R1

Neuman, A.G., and D.B. Brinkman. 2005. Fishes of the fluvial beds. Pp. 167–185 in P.J. Currie and E.B. Koppelhus (eds.). Dinosaur Provincial Park, A Spectacular Ancient Ecosystem Revealed. Indiana University Press, Bloomington, Indiana.

Scott, W.B., and E.J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada, Ottawa, 966 pp.

Wilson, M.V.H. 1980. Oldest known *Esox* (Pisces: Esocidae), part of a new Paleocene teleost fauna from western Canada. Canadian Journal of Earth Sciences 17:307–312. DOI: 10.1139/e80-030

Wilson, M.V.H. 1984. Osteology of the Palaeocene teleost *Esox tiemani*. Palaeontology 27:597–608.

Wilson, M.V.H., D.B. Brinkman, and A.G. Neuman. 1992. Cretaceous Esocoidea (Teleostei): early radiation of the pikes in North American fresh waters. Journal of Paleontology 66:839–846. DOI: 10.1017/S0022336000020849