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Teleost centrum and jaw elements from the Upper Cretaceous Nemegt Formation (Campanian–Maastrichtian) of Mongolia and a re-identification of the fish centrum found with the theropod *Raptorex kreigsteini*

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Abstract

Isolated centra and a premaxilla of a teleost from the Upper Cretaceous Nemegt Formation (Late Campanian–Early Maastrichtian) of Mongolia are described and aligned with the hiodontids and the Late Cretaceous teleost *Coriops* from North America. The atlas of the Nemegt taxon has an anterior articular surface with the dorsal half being subdivided into two flat articulator surfaces as in those of the hiodontids. In more posterior abdominal centra, the centrum is strongly constricted at the notochord foramen, the rib loosely articulates in a facet on the lateral wall of the centrum posterior to the parapophysis as in hiodontids, and parapophyses are fused to the centrum. Neural arch articular facets are small and round. Distinct mid-dorsal foramina are absent or small and poorly developed. A single stout premaxilla is relatively straight and has a low rounded dorsal margin on the posterior end. There are two rows of strong conical teeth and the tooth bases of the lateral row protrude laterally. The Nemegt centra are then used to re-identify a teleost centrum associated with the Asian theropod, *Raptorex kreigsteini*. Initially the fish centrum found with *R. kreigsteini* was assigned to *Lycoptera*. The stratigraphic range of Lycopteridae, ~120–135 Ma, was used to infer an age of deposition for the basal taxon *Raptorex*. Subsequently this centrum was re-identified as a clupeomorph centrum. However, centra of *Lycoptera* are mainly comprised of the chordacentrum surrounded by a very thin autocentrum, thus giving the appearance of being tubular with an unconstricted notochordal foramen; they are thin-walled, small (≤2 mm diameter), and may have a broad bar (presence depends on the species and ontogenetic development) extending the length of the centrum in lateral view. Parapophyses are not fused with the autocentrum and articulate with the centrum at large facets as in those of lower teleosts. Pleural ribs in *Lycoptera* articulate with the parapophyses. The fish centrum found with *R. kreigsteini* is of a higher teleost with a well-developed autocentrum strongly constricting the notochord, thereby giving the centrum an amphicoelous shape. This centrum has several aspects in common with the Nemegt Formation teleost centra: poorly developed mid-dorsal foramen; shape and position of the facets, where the arch articulates, being circular and located near the anterior end of the centrum; presence of short, fused parapophyses at the ventro-lateral corner of the centrum; lateral surface of the centrum bearing a series of foramina of small to moderate size that are generally organized into rows. Thus we reject the hypotheses that the fish centrum found with *R. kreigsteini* has affinities with the Lycopteridae or the Clupeomorpha and reassign the centrum to the hiodontids. The morphological characteristics of the fish centrum found with *R. kreigsteini* suggest a Late Cretaceous hiodontid-like taxon and thus its co-occurrence with *Raptorex* suggests that dinosaur is an Upper Cretaceous theropod.

Introduction

Little is known of fishes from the fluvial beds of the Upper Cretaceous of Mongolia. Fish remains are present in some localities, often in great abundance, but as is typically the case for fluvial beds, are represented exclusively by isolated elements (NEUMAN & BRINKMAN 2005). While such material presents challenges, study of such material from the Upper Cretaceous of Alberta, Canada, shows that useful information regarding biology, distribution, diversity, and first occurrences of major groups can be obtained (BRINKMAN & NEUMAN 2002; NEWBREY et al. 2007, 2008, 2010). In this study, isolated centra and jaws from the Nemegt Formation of Mongolia are described and compared with similar elements from the Upper Cretaceous of North America. Specifically, we compared centra of a taxon from the Nemegt Formation to those of hiodontids and *Coriops* to test the idea of close taxonomic affinity. Our second goal was to examine an isolated centrum of uncertain locality referred to *Lycoptera* by SERENO et al. (2009) and the Ellimmichthyiformes by FOWLER et al. (2011), with the purpose of discussing its taxonomic affinity.

Materials and methods

Institutional abbreviations

FOBU, Fossil Butte National Monument, Kemmerer, Wyoming, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **MPC-KID**, Geological Institute, Academy of Sciences, Ulaan Baatar, Mongolia; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Alberta, Canada; **USNM**, Smithsonian Institution National Museum of Natural History, Washington DC, USA.

Fossil material examined

Ellimmichthyiformes: *Diplomystus dentatus* COPE, 1877, n = 34, Green River Formation, Eocene: LACM 133801, 54095; TMP 1986.224.0081, 1986.224.0084 (n = 2), 1986.224.0085, 1986.224.0086, 1986.224.0089, 1986.224.0091 (n = 2), 1986.224.0092, 1986.224.0135, 1989.124.0002; UALVP 226, 228, 2049, 17731, 20318, 20331, 21021, 21025, 21027, 21041, 21072, 21155, 22860, 52161, 21163, 52157, 52173, 52183, 52205, 52229; USNM 1707. *Horseshoeichthys* sp. NEWBREY et al. 2010, n = 10, Milk River (Santonian), Oldman and Dinosaur Park formations (Campanian): TMP 1986.010.0064, 1986.021.0063, 1986.038.0045, 1993.093.0097, 1993.093.0103, 1995.180.0031, 2001.045.0093; UALVP 48871, 48872, 48873.

Osteoglossomorpha, Lycopteridae: *Lycoptera davidi* (SAUVAGE, 1880), n = 55, Early Cretaceous: UALVP 44031 (n = 10); USNM 16616 (n = 20), 18199 (n = 8), 18268 (n = 17).

Hiodontiformes: *Coriops* ESTES, 1969, n = 74: TMP 1993.117.0007 (n = 27), 1995.006.0054 (n = 47) (BRINKMAN & NEUMAN 2002).

Hiodontidae: *Eohiodon woodruffi* WILSON, 1978, n = 2: FOBU 13276, UALVP 31948; hiodontid (n = 14): TMP 1986.037.0085, 1986.060.0032a, 1986.179.0006, 1986.198.0042, 1986.242.0068b, 1987.032.41, 1987.158.0029b,c, 1990.113.0057a, 1993.093.0094, 1995.147.0002, 1995.168.0047, 1995.182.0034 (BRINKMAN & NEUMAN 2002, specimens from NEWBREY et al. 2007).

Methods

Centra were described using the terminology of SCHULTZE & ARRATIA (1989), ARRATIA et al. (2001), and HILTON (2002). Comparisons of size among centra were made in two ways: absolute diameter of abdominal vertebral centra and diameter of those centra plotted against standard length (SL, distance from anterior tip of head to posterior tip of the second ural centrum). Means, standard errors (SE), and a 99 % confidence interval (CI) were calculated for each taxon. An Analysis of Variance (ANOVA) with Bonferroni post-hoc tests was used to determine if there were significant differences between centrum diameters of *Lycoptera* and other taxa examined. Statistical tests were performed with SYSTAT (2004) and alpha was set at 0.05 unless otherwise specified.

The *Raptorex*-associated teleost centrum (SERENO et al. 2009: fig. S8) was compared to the 99 % prediction interval (PI) of the relationship between SL and centrum diameter for *Lycoptera*. A single centrum was randomly selected from each fish for inclusion in the dataset. Height of vertebral centra and SL of *Lycoptera* taxa were measured using a digital caliper (mm) for each taxon. Plotting centrum diameter by SL provides a relative growth trajectory to check for an asymptote in size, reducing the possibility of making a Type I error. A quadratic least squares regression was used to describe the relationship between SL and centrum diameter of *Lycoptera*. Diameters of centra were also measured directly from specimens in the UALVP and USNM collections and from published images of *L. fuxinensis* (ZHANG 2002: fig. 1A,C) and *L. davidi* (ZHANG 2002: fig. 2A). In all, the diameters of 46 centra were measured from *L. davidi* and three centra (n = 2 diameters associated with SL data) of *L. fuxinensis* from ZHANG (2002).

Systematic paleontology

Class Actinopterygii COPE, 1887
Teleostei MÜLLER, 1845
Order Hiodontiformes TAVERNE, 1979

Family Hiodontidae CUVIER & VALENCIENNES, 1846

Fig. 1A–F

Material: MPC-KID 2006.002-01, -02, -03, -04, -05, -06.

Localities and strata: Ulan Khushu locality, Nemegt Formation, Gobi Desert, Mongolia.

Age: Late Campanian–Early Maastrichtian.

Description of Nemegt fossils

Centra. Morphological variation along the vertebral column was documented by a series of 130 centra from a single locality. Position in the vertebral column was estimated from comparison with extant teleosts, particularly clupeomorphs and osteoglossomorphs. Five centra illustrated in Figure 1 document the major features of the abdominal column.

The autocentra are large in diameter and originated from dysospondylous type vertebrae. Length is typically shorter than or equal to width. The notochord is strongly constricted giving the centrum an amphicoelous shape. Articular facets, where the neural arch articulates, are small and round. Distinct mid-dorsal foramina are absent or poorly developed. Parapophyses are fused to the centrum and they occur laterally as nearly transverse processes on anterior abdominal centra, but their orientation shifts to a more ventrolateral position in posterior abdominal centra. Anterior parapophyses are robust and distally curve ventrolaterally. Ventrolateral parapophyses are directed ventrolaterally.

Atlas centra (Fig. 1A) are short and small and are distinguished by the presence of an anterior articular surface. The dorsal half of this is like the atlas of hiodontids in being subdivided into two flat articular surfaces. However, in contrast with the hiodontid atlas, a corresponding pair of articular surfaces is not present ventrally. Transverse processes are absent and the neural arch articular facets are located towards the posterior end of the centrum.

Anterior abdominal centra (Fig. 1B,C) are shorter than long and have long, laterally directed parapophyses. The rib loosely articulates in a facet on the lateral wall of the centrum. The facet is immediately posterior to the parapophysis and the parapophysis probably provides additional support along the anterolateral edge of the pleural rib. The neural arch articular facets are located in the middle of the centrum and are separated by a solid bar of bone. The ventral surface of the centrum has one to three elongate fossae.

Mid-abdominal centra (Fig. 1D) have reduced parapophyses that slope ventrolaterally. As in more anterior abdominal centra, the rib loosely articulates in a facet on the lateral wall of the centrum just posterior to the parapophysis. The parapophysis in mid-abdominal centra probably also provides additional support to the pleural rib. Neural arch articular facets are located in the middle of the centrum and are separated by a single bar of bone, although slightly larger foramina anticipate the presence of mid-dorsal foramina present in more posterior centra. The ventral surface of the centrum has a single elongate mid-ventral foramen. The centrum is relatively longer than the anterior abdominal centra.

Transitional abdominal centra (Fig. 1E) have greatly reduced parapophyses that are distally incomplete and located at the ventrolateral corner of the centrum. The neural arch articular facets are located towards the anterior end of the centrum. Mid-dorsal fossae are present anterior and posterior to the neural arch articular facets. The lateral surface of the centrum between the parapophysis and neural arch articular facets is covered with multiple foramina of small to moderate size. The ventral surface of the centrum has a single elongate mid-ventral fossa. As with the mid-abdominal centra, the posterior abdominal centra are sub-equal in length and width.

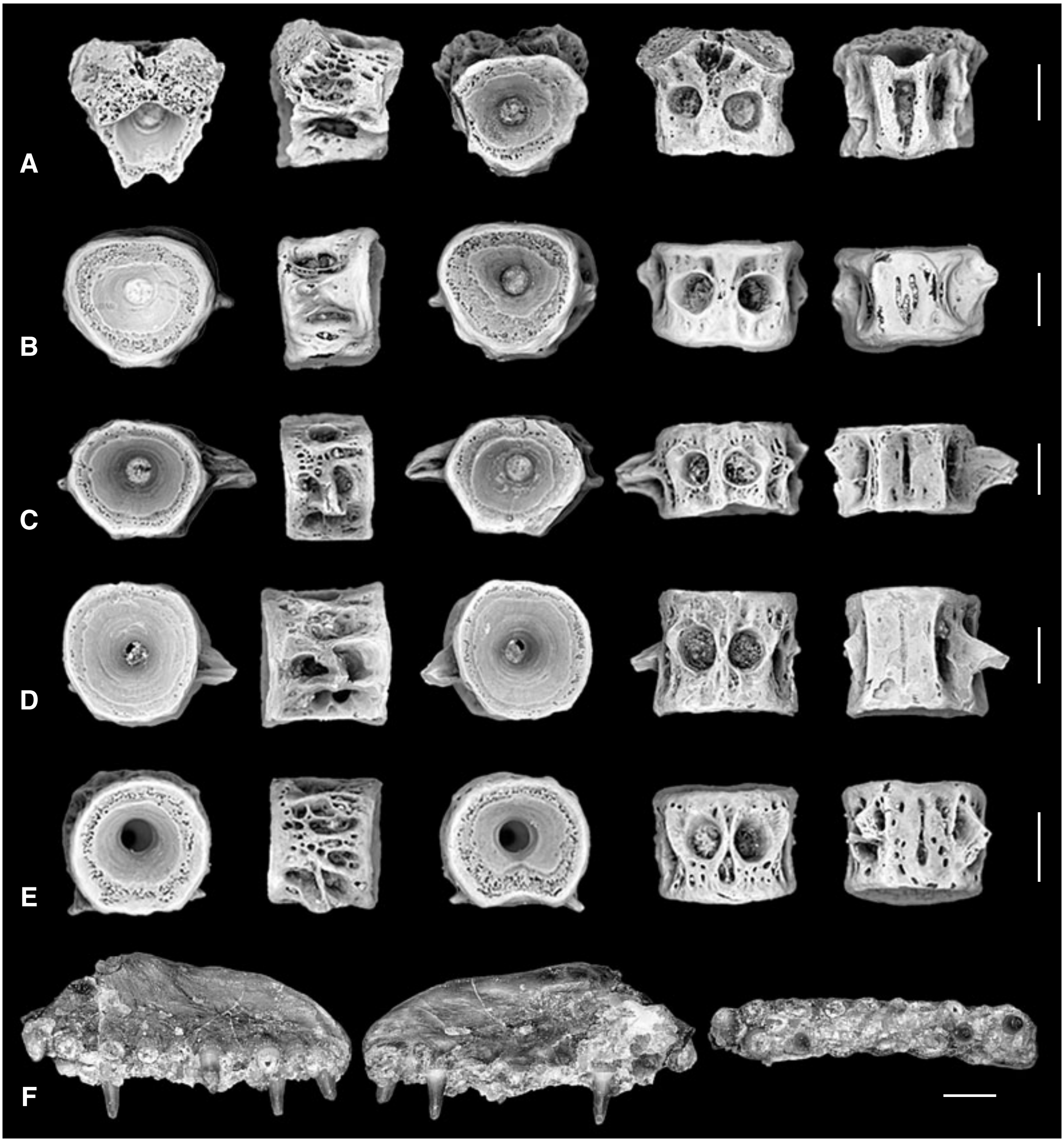

Fig. 1.
Centra and a premaxilla from the Nemegt Formation, Mongolia. Centra (**A**–**E**) are depicted from left to right in five views: anterior, left lateral, posterior, dorsal, and ventral. **A,** atlas (MPC-KID 2006.002-01). **B**–**C**, anterior dorsal, precaudal centra (MPC-KID 2006.002-02, -03); **D,** mid-dorsal precaudal centrum (MPC-KID 2006.002-04). **E,** posterior dorsal precaudal centrum (MPC-KID 2006.002-05). **F,** left premaxilla (MPC-KID 2006.002-06) in three views: labial, lingual, and occlusal. Scale bars: A–E = 2 mm; F = 1 mm.

Premaxilla. Jaw elements are represented by a partial right premaxilla (Fig. 1F). The premaxilla is stout, with a low rounded dorsal margin on the posterior end (Fig. 1F: labial view). The anterodorsal margin is slightly raised. The lingual face is slightly concave (Fig. 1F: lingual view). The premaxilla is relatively straight and bears two rows of strong conical teeth (Fig. 1F: occlusal view). The anterior teeth are more robust than the posterior teeth. Tooth bases of teeth in the labial row protrude laterally (Fig. 1F: labial view).

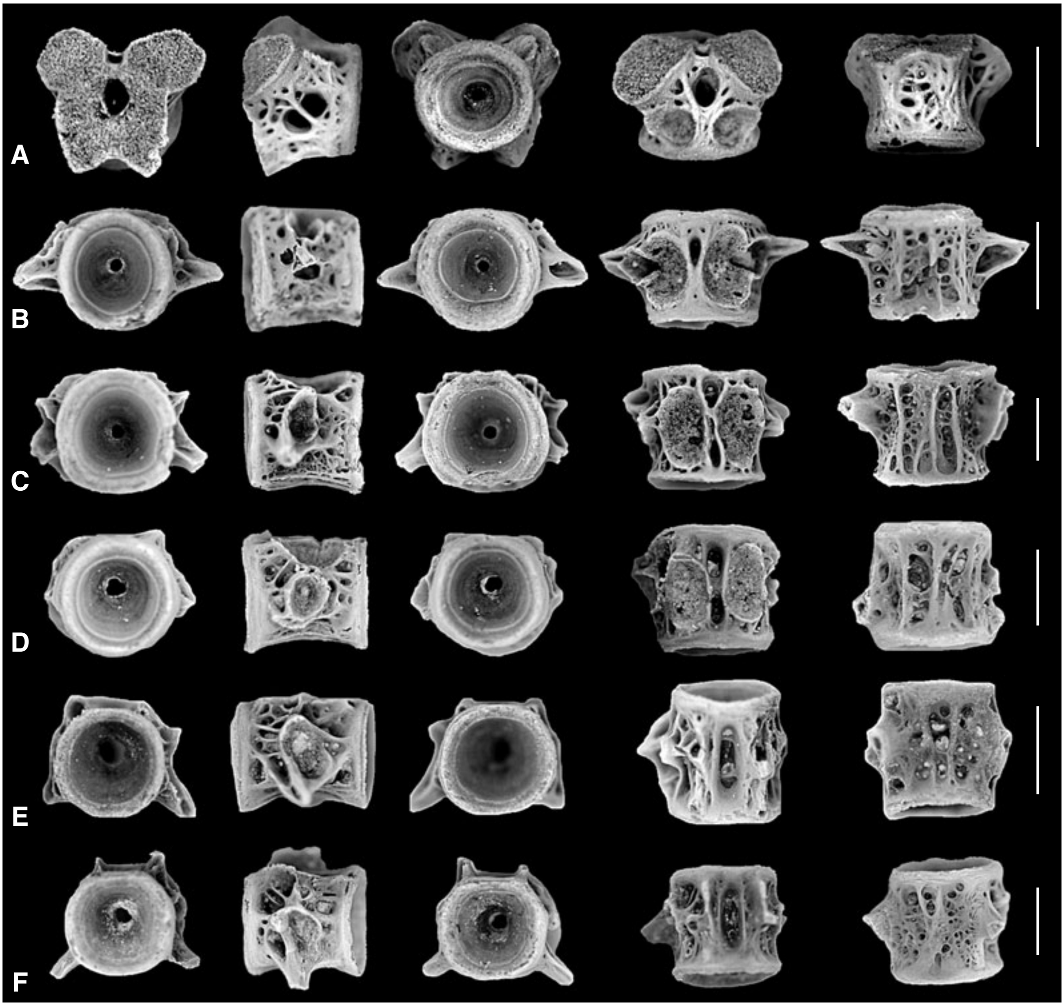

Fig. 2.
Centra of Hiodontidae from the Dinosaur Park Formation, Alberta, Canada. Centra are depicted from left to right in five views: anterior, left lateral, posterior, dorsal, and ventral. **A,** atlas (TMP 2005.012.0569). **B,** anterior precaudal centrum (TMP 1995.181.0034d). **C–D,** mid-precaudal centra TMP 1995.181.0034b, 2000.006.0003c). **E–F,** posterior precaudal centra (TMP 1995.181.0034a, 2000.006.0003a). Scale bars: A–F = 1 mm.

Comparisons

All the centra examined were consistent with a single type of teleost. This is interpreted as a hiodontid primarily because of the features of the atlas centrum. As in hiodontids, flat bipartite articular surfaces are present dorsally and the neural arch articular facets are small, circular, and located on the posterior half of the centrum (BRINKMAN & NEUMAN 2002). Similarities with the atlas of the hiodontids from the Late Cretaceous of North America (Fig. 2A) when seen in dorsal view are particularly striking. As well as being similar in the shape of the anterior articular surfaces and the size, shape, and position of the neural arch articular facets, the centra of these two taxa are also similar in the position of a small mid-dorsal fossa anterior to the neural arch articular facets.

The atlas centra of the Nemegt taxon lack a flat bipartite articular surface on the ventral half of the atlas centrum that is present in hiodontids from North America, including the Late Cretaceous taxon from the

Dinosaur Park Formation (Fig. 2A). Instead of such a surface, the ventral surface of the centrum forms a sharp edge. As well, rather than a flat ventral surface formed by a network of bone, the atlas centrum of the Nemegt taxon has a mid-ventral fossa separating a pair of robust rounded ridges extending anteroposteriorly.

The more posterior abdominal centrum is similar to those of hiodontids (HILTON 2002) in having long parapophyses with pleural ribs loosely articulated in deep facets directly on the lateral wall of the centrum posterior to the parapophyses. As in extant *Hiodon*, the parapophyses provide additional support for the pleural ribs. They differ in that the neural arch articular facets are relatively small and round throughout the length of the vertebral column, rather than being elongate oval neural arch articular facets that nearly extend the full length of the centrum as in Late Cretaceous hiodontids from North America (Fig. 2B–D) (BRINKMAN & NEUMAN 2002).

The Nemegt premaxilla is similar to premaxillae attributed to *Coriops* in having multiple rows of strong, conical teeth (Fig. 1F). In the Nemegt taxon, two rows of teeth are present, as is typically the case in the premaxilla of *Coriops* (Fig. 3F–G). HILTON (2002) reports that most specimens of extant *Hiodon* have one row of teeth but some may have two rows anteriorly. Both taxa have more robust teeth anteriorly and protruding tooth bases laterally. They differ in that the teeth of the labial tooth row of *Coriops* are located on the lateral surface of the premaxilla and those teeth are curved such that the crowns point ventrally. In the Nemegt taxon, both rows of teeth are located on the ventral surface of the premaxilla and the teeth of both rows are relatively straight in a ventral direction (Fig. 1F). Furthermore, the premaxilla of *Coriops* has a strong medial bend, while the Nemegt taxon is relatively straight. The premaxilla of the Nemegt teleost lacks an anterior ascending process as is also the case for Paleogene and extant hiodontids (LI & WILSON 1994, LI et al. 1997, HILTON 2002, HILTON 2003, HILTON & GRANDE 2008). In contrast, *Coriops*, *Lycoptera*, and other osteoglossomorphs have an ascending process on the premaxilla (MA 1987, HILTON 2003: fig. 17, HILTON & GRANDE 2008).

Taxonomic affinities of Nemegt Formation centra

The centra of the Nemegt taxon are similar to centra attributed to *Coriops* in the presence of long, laterally directed parapophyses with rib articular facets located on the lateral wall of the centrum posterior to the parapophyses (NEUMAN & BRINKMAN 2005: fig. 9.8D). Additional similarities with *Coriops* are suggested by similarities in the premaxilla of the Nemegt taxon and that of *Coriops* (Fig. 3F,G). Unfortunately, tooth-bearing elements of Late Cretaceous hiodontids from North America have not been identified, although the presence of multiple rows of large conical teeth is also consistent with the condition in extant members of *Hiodon* (HILTON 2002).

The centra of the Nemegt taxon are similar to hiodontid centra in the development of the anterior articular surface of the atlas and of the articular facets on the dorsal surface. The presence of similarities with both *Coriops* and hiodontids is consistent with the suggestion that *Coriops* is closely related to the Hiodontidae (BRINKMAN et al. in press). Thus the similarities of the atlas of the Nemegt taxon with hiodontids suggests that it is more closely related to that family than is *Coriops*, but the absence of fully developed quadratic articular surface on the atlas suggests that it is basal to other members of that family.

Since hiodontids are relatively basal osteoglossomorphs (WILSON & MURRAY 2008), which are in turn sister to the Clupeocephala (sensu ARRATIA 2010a), comparison with that group is warranted. Two ellimmichthyiform clupeomorphs were examined from the Cretaceous Sorbinichthyidae, *Horseshoeichthys armaserratus*, and the Eocene Paraclupeidae, *Diplomystus dentatus*. Descriptions and figured centra from *H. armaserratus* and *D. dentatus* are provided by NEWBREY et al. (2010). These centra are strongly amphicoelous and robust (Fig. 4A–E). Two anteriorly placed neural arch articular facets generally occur on the anterior half of the centrum (FOBU 11661, TMP 1993.091.0021; BRINKMAN & NEUMAN 2002: fig. 2). The neural arch articular facets may or may not be separated by the large mid-dorsal fossa that occurs primarily on the posterior half of the centrum (TMP 1993.091.0021, 1986.021.0063; BRINKMAN & NEUMAN 2002: fig. 2; Fig. 4D). In *H. armaserratus*, as in the Nemegt taxon, the neural arch articular facets are circular and are small relative to the length of the centrum (Fig. 4D). This is also the case in the more posterior abdominal centra of *Diplomystus dentatus*. The mid-dorsal fossa may or may not be subdivided into two lateral halves. Separate single or double fossae follow each of the neural arch articular facets in dorsal view (TMP 1993.091.0021; BRINKMAN & NEUMAN 2002: fig. 2). Laterally, the parapophyseal articular facets occur on the lower half of the centrum (Fig. 4B). Dorsal to the parapophyseal articular facet

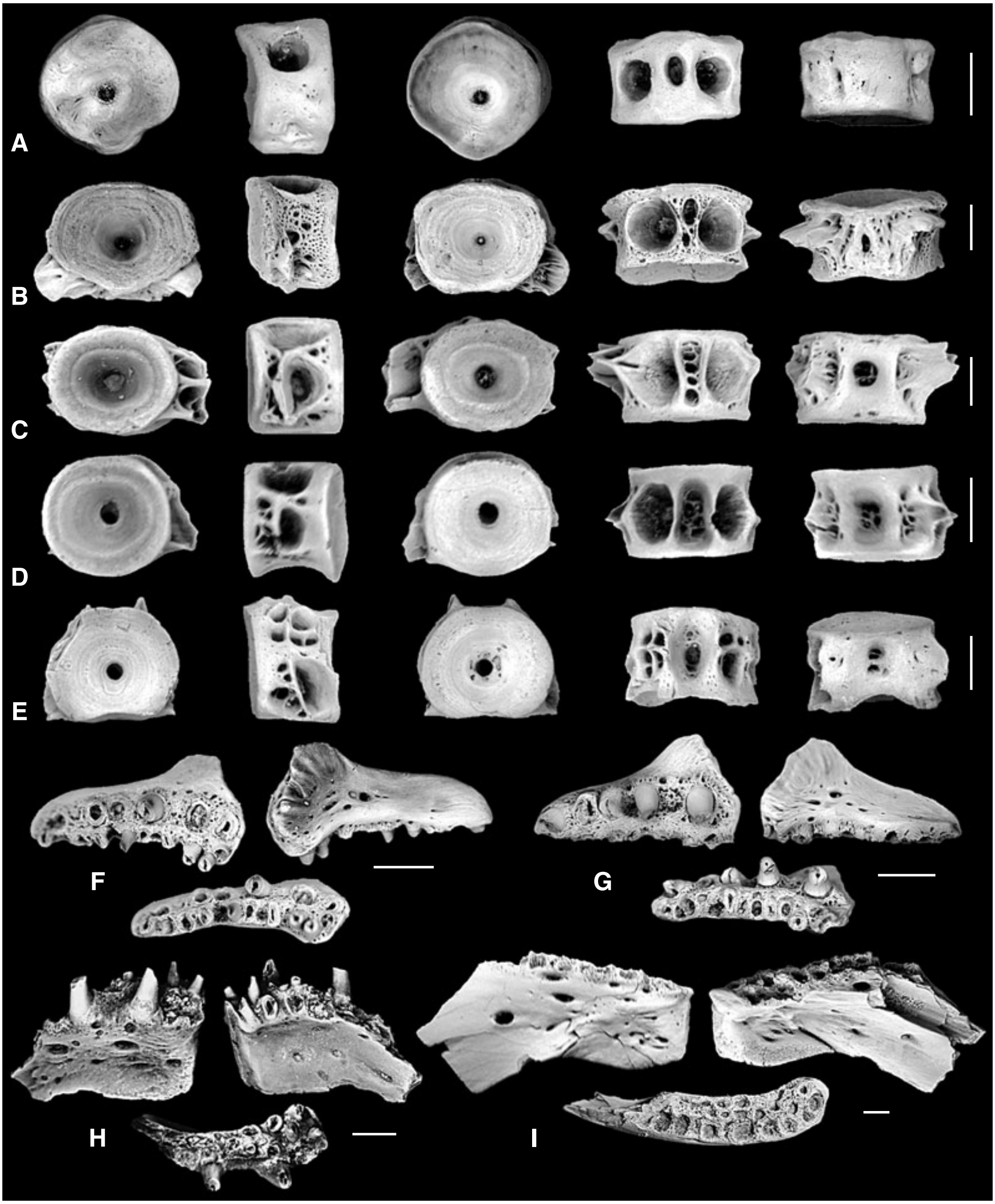

Fig. 3.
Centra, premaxillae, and dentaries of *Coriops* from the Dinosaur Park Formation, Alberta, Canada. Centra (**A**–**E**) are depicted from left to right in five views: anterior, left lateral, posterior, dorsal, and ventral. Right premaxillae (**F**–**G**) are depicted left to right and top to bottom in three views lateral, medial, and occlusial. Right dentaries (**H**–**I**) are depicted left to right and top to bottom in three views: lateral, medial, and occlusial. **A,** anterior precaudal centrum (TMP 1986.044.0043a). **B**–**D**, mid-precaudal centra (TMP 1995.177.0067b, 1995.177.0067a, 1987.004.0018a). **E,** posterior precaudal centrum (TMP 1990.115.0046a). **F,** premaxilla (TMP 2000.006.0028a). **G,** premaxilla (TMP 1990.033.0064a). **H,** dentary (TMP 1986.043.0033); dentary (TMP 1990.119.0035a). Scale bars: A, B, E–I = 2 mm; C, D = 1 mm.

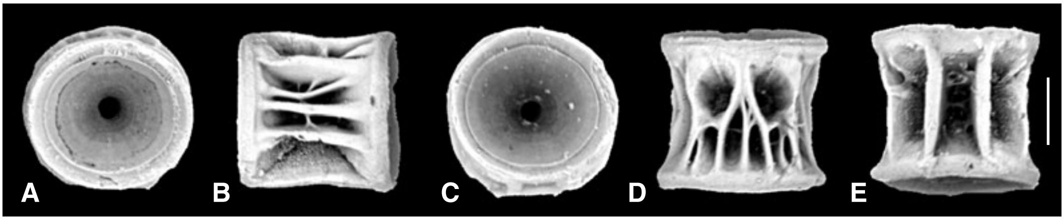

Fig. 4.
Centrum of Cretaceous ellimmichthyiform, *Horseshoeichthys* sp. from the Oldman Formation (Campanian) (TMP 1995.180.0039). **A,** anterior. **B,** lateral. **C,** posterior. **D,** dorsal. **E,** ventral views. Scale bar = 1 mm.

is a large, subdivided fossa that extends the full length of the centrum (TMP 1986.038.0045) or a series of small foramina arranged in an irregular manner (TMP 1986.021.0063). Thus, overall, the centra of the Nemegt hiodontid, as with hiodontids from the Upper Cretaceous of North America, are distinct from those of ellimmichthyiforms.

The fish centrum found with *Raptorex kreigsteini*

With this understanding of the centrum morphology of the Nemegt teleost, the affinities of a centrum found in association with a dinosaur described by SERENO et al. (2009) as *Raptorex kreigsteini* can be re-evaluated. This centrum was recovered with that theropod, but the age and stratigraphic description of this material is imprecisely known (SERENO et al. 2009, FOWLER et al. 2011). The possibility that it is from the Lower Cretaceous lake beds of Liaoning was rejected because of the absence of laminated, fine-grained sediment and conchostracans (SERENO et al. 2009). However, the presence of an unidentified clam and fish centrum identified as "cf. *Lycoptera*" was used to suggest that *Raptorex* was from the Lujiatun Beds of the Yixian Formation. Thus the age of *Raptorex* is based primarily on the identity of the fish centrum (SERENO et al. 2009: supp. info. figure 8, FOWLER et al. 2011). SERENO et al. (2009) inferred that the *Raptorex* locality was within the age range ~130 Ma (p. 419) to 125 Ma as stated in their figure 4A. Fossils of *Lycoptera* are known from Lower Cretaceous deposits (CHANG & MAIO 2004, ARRATIA 2010b) and range in age from 122–135 Ma (LI et al. 1994) or 120–133 Ma (CHEN & CHEN 1997, WANG et al. 1999: 8). Thus the identity of the centrum has profound implications for the stratigraphic age of *R. kreigsteini*. However, no description was given by SERENO et al. (2009) for the fish centrum found with *R. kreigsteini*, and there are no thorough descriptions of centra of *Lycoptera* in the published literature, so this identification has been questioned. FOWLER et al. (2011) rejected the hypothesis that the teleost centrum found with *Raptorex* was that of a lycopterid and suggested rather that it was related to an ellimmichthyiform; however, the analysis was preliminary pending a more thorough review such as that in this work (FOWLER et al. 2011). The analysis in FOWLER et al. (2011) bases its morphologic comparison mostly on the reported "large opening for the notochord" of *Lycoptera* (ZHANG 2002: 265), but lacks a detailed, specimen-based description to address the hypothesis that the fish centrum found with *Raptorex* is not of *Lycoptera.* To test the biostratigraphic conclusions of SERENO et al. (2009) and FOWLER et al. (2011), the identity of the *Raptorex* teleost centrum is re-evaluated by comparison to those of *Lycoptera*, the Nemegt teleost, and teleosts from North America that are thought to be broadly related to the Nemegt teleost, particularly hiodontids, *Coriops*, as well as the ellimmichthyiform *Horseshoeichthys*.

Description of the fish centrum found with *Raptorex kreigsteini*

The fish centrum found with *Raptorex kreigsteini* was illustrated with the dorsal, anterior, and right lateral surfaces visible in SERENO et al. (2009: fig. S8); the SERENO et al. image of the fish centrum was republished in FOWLER et al. (2011). The centrum is re-figured as a line drawing here for ease of comparison (Fig. 5A). This centrum originates from a dysopondylous vertebra and is rectangular in lateral view. The centrum displays two small, round neural arch articular facets in the anterior half (Fig. 5A). The centrum is strongly amphicoelous and the autocentrum is thick, thereby constricting the notochord. In the posterior half of the centrum, a single, mid-dorsal fossa narrows anteriorly and does not separate the neural arch articular facets. Two small fossae (i. e., extending anterior to posterior) occur behind the right neural arch articular facet (FOWLER et al. 2011). In lateral view and on the dorsal half of the centrum,

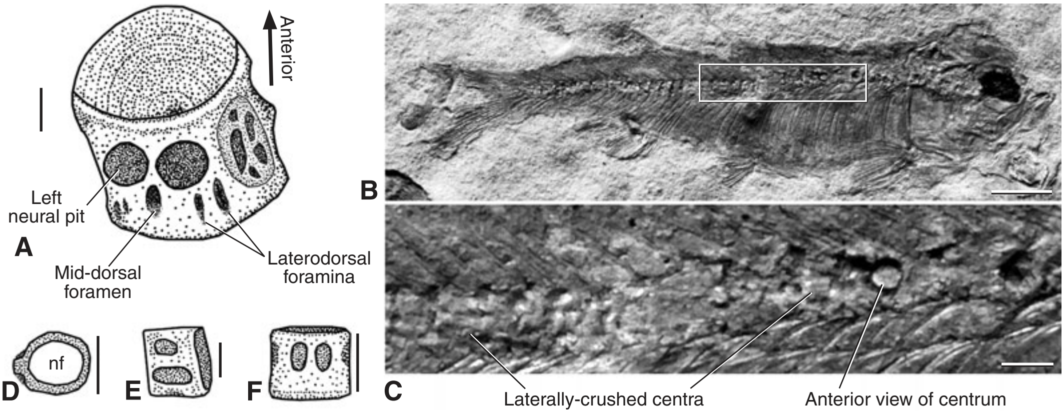

Fig. 5.
Centra of Cretaceous fishes. **A,** fish centrum found associated with *Raptorex kreigsteini* (SERENO et al. 2009: fig. S8). **B,** *Lycoptera davidi* (UALVP 44031), rectangle indicates area magnified in 'C'. **C,** precaudal and caudal centra of *L. davidi* (UALVP 44031). **D,** anterior view of *L. davidi* centrum naturally broken in transverse section through the anterior half. **E,** lateral view of a precaudal centrum of *L. fuxinensis* from ZHANG (2002: from fig. 1C). **F,** interpretation of dorsal view of *L. davidi* (UALVP 44031, USNM 18199). Scale bars: A, C, E; B = 5 mm; D, F = 0.5 mm. Abbreviations: **nf**, notochord foramen.

there are several small foramina separated by fine ridges of bone (Fig. 5A). The parapophyses are fused to the ventrolateral corners of the centrum. The diameter of the centrum is 4 mm (SERENO et al. 2009, FOWLER et al. 2011).

Description of centra of *Lycoptera*

The morphology of centra of *Lycoptera* sp. is distinct among fishes examined in this study (Fig. 5B–F). The centra originate from dysospondylous vertebrae and are thin-walled, being mainly comprised of the chordacentrum in small individuals and surrounded by a thin autocentrum in larger individuals. The centra are perforate being relatively unconstricted at the notochord foramen (UALVP 44031, USNM 16616). Strictly speaking, the notochordal foramen or the inside diameter of the chordacentra is no larger in diameter than, for example, those of the hiodontids or ellimmichthyiforms (M.G.N. pers. obs.); it is the walls of the autocentrum that are thinner than in other more advanced teleosts with well-developed autocentra. FOWLER et al. (2011) also correctly pointed out that centra of *Lycoptera* are tubular in appearance and cited ZHANG (2002) for noting the tubular appearance of the centra, but this is imprecise. ZHANG (2002) only stated that the opening for the notochord foramen is large, which is relative. Specifically, the notochordal foramen represents 71 % of total centrum diameter (Fig. 5B–F). An unconstricted notochord could also be present in young individuals, thereby giving the false perception that centra in the species are tubular in appearance. FOWLER et al. (2011) stated that individuals of *Lycoptera* generally range in size from 7 to 13 cm, and their centra are typically 1–2 mm long and cite MA (1987) and ZHANG (2002) for the information. However, MA (1987) does not address these points and only figures posterior caudal centra and ZHANG (2002) only states a range in size from 3.5 to 9 cm SL from a small sample (n = 8 complete specimens). GREENWOOD (1970) also noted the maximum recorded size of members of the family was <12 cm in length but did not address the presence or absence of adults. However, our results reveal the presence of a quantifiable "asymptote" in size of centra in longer individuals, thus confirming the existence of adults in the sample.

The centra of *Lycoptera davidi* and *L. fuxinensis* remain small (thin) throughout life in the material and taxa examined (n = 29) with no diameter exceeding 2 mm (Fig. 6A,B). An asymptote in size occurs at 1.6 mm centrum diameter and at 49 mm SL or greater for all *Lycoptera* taxa examined. In this study, the 99 % prediction interval calculated from the relationship between SL and centrum diameter of *Lycoptera* does not exceed 2.6 mm centrum diameter and a clear "asymptote" is present, suggesting adults are present in the sample and that autocentra stay small and thin, thereby maintaining a proportionally large chordacentrum (Fig. 6A,B).

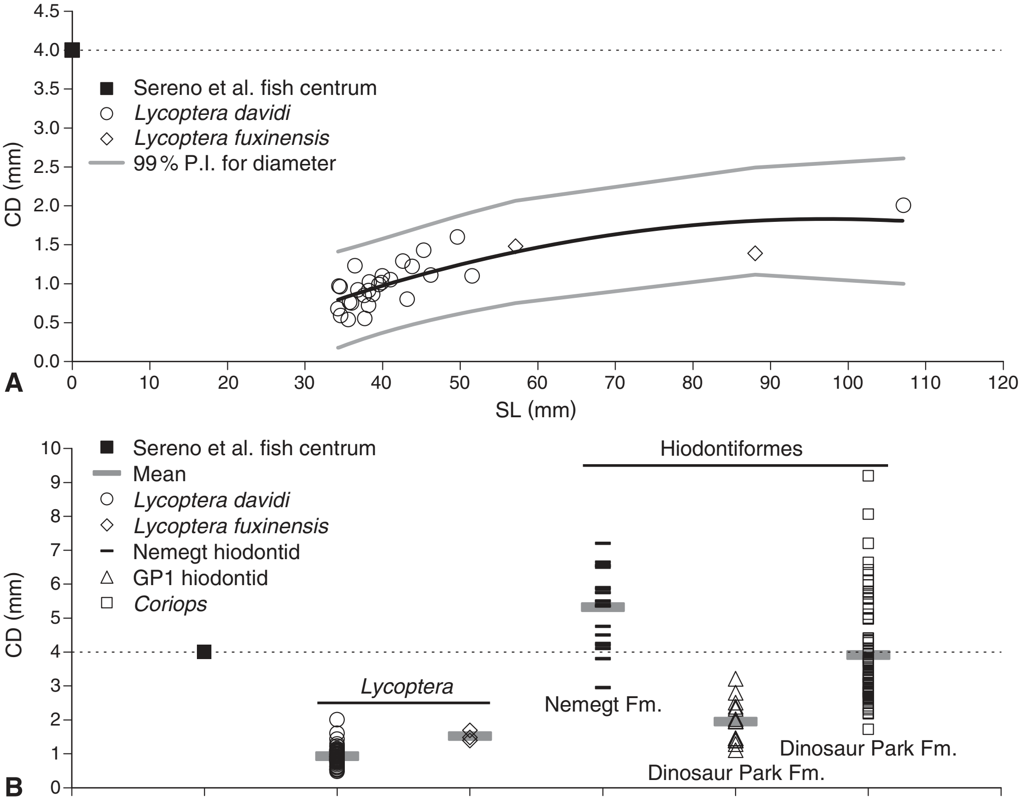

Fig. 6.
Centrum diameter (CD) and standard length (SL) of taxa of *Lycoptera* and hiodontiforms compared to the diameter of the fish centrum found with *Raptorex kreigsteini* and figured in SERENO et al. (2009: fig. S8). **A,** the relationship between SL and CD of two taxa of *Lycoptera*, solid black line represents a quadratic least squares regression ($R^2 = 0.591$, $P < 0.001$), solid gray lines represent 99 % prediction intervals (PI), broken line represents the diameter of the SERENO et al. (2009) fish centrum. **B,** centrum diameter of the SERENO et al. (2009) fish centrum compared to those of two taxa of *Lycoptera*, and three taxa of hiodontiforms: Nemegt Formation, Mongolia, a large hiodontid (NEWBREY et al. 2007: growth profile 1 [GP1]) from the Dinosaur Park Formation, Alberta Canada, and *Coriops* from the Dinosaur Park Formation, Alberta, Canada.

The autocentra of *Lycoptera* have neural arch articular facets that are very shallow and elongate but do not extend the full length of the centrum (USNM 18199, UALVP 44031). No large, central foramen (mid-dorsal) could be confirmed on the posterodorsal surface of examined centra of *Lycoptera* (Fig. 5F). Anteriorly, parapophyseal facets occur low on the centrum and ribs articulate on the parapophyses (ZHANG 2002: fig. 1C,D; USNM 18199; UALVP 44031). Parapophyseal facets extend most of length of the centrum in the material examined.

Chordacentra are often crushed in a lateral plane (Fig. 5B–C) and up-turned to expose an anterior or posterior view. This is especially common in specimens under 5 cm SL. The lateral faces of chordacentra are smooth in small (<5 cm SL) specimens similar to those of leptolepids (see ARRATIA & HIKUROA 2010: fig. 7c). In larger specimens, the lateral faces of the autocentrum have a prominent ridge that extends the full length of the centrum between the parapophyseal facet and a relatively large foramen (Fig. 5E). The large foramen is anteriorly placed on the upper half of the lateral wall of the centrum and extends 50–70 % the length of the centrum (see ZHANG 2002: fig. 1C,D).

Comparison of centra of *Lycoptera* to the fish centrum found with *Raptorex kreigsteini*

The fish centrum found with *Raptorex kreigsteini* differs from those of *Lycoptera* in being a well-developed autocentrum of a higher teleost. The autocentrum is large in diameter with thick walls, having deep amphicoelous ends (i.e., strongly constricting the notochord), fused parapophyses, and lacking a mid-horizontal bar in lateral view. The walls of the autocentrum of *Lycoptera* are very thin and the centrum stays small during ontogenetic development with the chordacentrum representing the majority of the centrum. Parapophyses are not fused to the centrum and pleural ribs articulate on the parapophyses as with other lower teleosts. The fish centrum found with *R. kreigsteini* is 33 % larger than the upper 99 % prediction interval of the centrum diameters of taxa of *Lycoptera* examined in this study ($n = 59$, $\bar{x} = 0.96 \pm 0.04$ SE mm diameter, Fig. 6A). This size difference adds further evidence that the fish centrum found with *R. kreigsteini* is not from any known species of *Lycoptera*. Thus, based on morphological and phylogenetic differences, we reject the hypothesis that the fish centrum found with *R. kreigsteini* is from a species of *Lycoptera*.

Comparison of centra of *Horseshoeichthys* to the fish centrum found with *Raptorex kreigsteini*

The fish centrum found with *Raptorex kreigsteini* is similar to mid-abdominal autocentra of the ellimmichthyiform *Horseshoeichthys* in the presence of small, circular neural arch articular facets located near the anterior end of the centrum, and based on this similarity, the fish centrum found with *R. kreigsteini* was tentatively attributed by FOWLER et al (2011) to the Ellimmichthyiformes. However, this feature is also present in the Nemegt teleost and not strongly indicative of a relationship. In other features, the fish centrum found with *R. kreigsteini* differs substantially from those of examined ellimmichthyiforms. These include the lack of prominent longitudinal ridges subdividing the lateral face and the presence of parapophyses fused to the centrum of Cretaceous forms. Thus, despite the similarity in the shape of the neural arch articular facets with that of some ellimmichthyiforms, we reject the hypothesis that the fish centrum found with *R. kreigsteini* is of an ellimmichthyiform.

Comparison of centra of Nemegt teleost to the fish centrum found with *Raptorex kreigsteini*

The fish centrum found with *Raptorex kreigsteini* is similar to the posterior precaudal centra of the Nemegt teleost (Fig. 1E) in proportions, shape and position of the neural arch articular facets, development of a series of small foramina on the side of the centrum, and presence of a short parapophysis at the ventrolateral corner of the centrum. In both types, the centrum is subequal in length and width. The neural arch articular facets are circular and located near the anterior end of the centrum. The lateral surface of the centrum bears a series of foramina, small to moderate in size, that are generally organized into rows. In both types, short, fused parapophyses are present on the ventrolateral corner of the centrum. Thus, based on morphological features that can be observed, the fish centrum found with *R. kreigsteini* is likely from the Nemegt taxon. To further test this identification, the fish centrum found with *R. kreigsteini* was compared in size with 25 centra of the Nemegt teleost and two taxa from North America, *Coriops* and the hiodontid from the Dinosaur Park Formation. The fish centrum found with *R. kreigsteini* plots outside the 99 % confidence interval for the Dinosaur Park Formation hiodontid ($n = 14$, $\bar{x} = 2.0 \pm 0.17$ SE mm diameter), but falls within the range of sizes of centra from the Nemegt Formation ($n = 25$, $\bar{x} = 5.3 \pm 0.20$ SE mm diameter) and *Coriops* ($n = 75$, $\bar{x} = 3.9 \pm 0.17$ SE mm diameter) from the Dinosaur Park Formation (Fig. 6B). Thus the size of the centrum is consistent with the hypothesis that the fish centrum found with *R. kreigsteini* is from the Nemegt teleost. Since centra like those of the Nemegt teleost are not known from outside the Nemegt Formation, this identification implies that *R. kreigsteini* is from the Upper Cretaceous and probably from the Nemegt Formation.

The conclusion that the fish centrum found with *R. kreigsteini* is from the Nemegt teleost can be further tested by examining features that are not currently visible in the SERENO et al. (2009) figure. These include the presence and position of a facet for a pleural rib on the wall of the centrum posterior to the parapophysis and the presence and shape of a mid-ventral fossa. In the Nemegt teleost, the rib articular facet is located posterior to the parapophysis and the surface of the centrum is flat and has a long narrow mid-ventral fossa. If the identification of the fish centrum found with *R. kreigsteini* as a posterior-precaudal centrum from the Nemegt teleost is correct, it would have these features.

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