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TELEOST CENTRA FROM UPPERMOST JUDITH RIVER GROUP (DINOSAUR PARK FORMATION, CAMPANIAN) OF ALBERTA, CANADA

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ABSTRACT—The diversity and distribution of teleosts in the Dinosaur Park Formation of Alberta, Canada, is evaluated on the basis of precaudal centra. In order to avoid the erection of redundant taxa, and to include all teleost precaudal centra in a single system, a parataxonomic system is erected. Fifteen distinct basal groups, termed morphoseries, are described. Growth-related changes and serial variation along the column are taken into account in defining these groups, so each morphoseries is interpreted as representing a distinct, low-level taxon of teleost. One of the morphoseries could be identified as hiodontid and two as acanthomorph on the basis of derived character-states. This is the first Cretaceous record of hiodontids in North America. In addition, elopomorphs, clupeomorphs, salmoniforms, and osteoglossoforms are recognized on the basis of general similarity with the precaudal centra in extant members of these groups. Two teleosts of intermediate level of evolution, but of uncertain relationships, are also present. Differences in the stratigraphic distributions of the morphoseries allow two distinct assemblages of teleosts to be recognized in the formation. One is present in fluvial-dominated localities of the Dinosaur Park Formation, the second in a complex of mud-filled channels in the Lethbridge Coal Zone. The paleoecological complexity present in the formation, and the high level of diversity of teleosts in these beds, emphasizes the importance of including disarticulated remains in studies of the diversity and distribution of teleosts in the Cretaceous.

INTRODUCTION

WHILE STUDIES of vertebrate microfossil assemblages from the late Cretaceous have provided a good understanding of the diversity and distribution of many groups, teleost fishes remain poorly known. The presence of a diverse assemblage has been suspected on the basis of disarticulated remains preserved in such localities (Estes et al., 1969; Dodson, 1983; Rowe et al., 1992). Some tooth-bearing elements have been named (Estes, 1964, 1969; Wilson et al., 1992), but many distinctive elements remain undescribed (Brinkman, 1990). As part of a survey of the vertebrate microfossil localities from the mid-Campanian Judith River Group (Brinkman, 1990; Eberth and Brinkman, 1997; Brinkman et al., 1998), distinctive elements of teleosts were grouped together and their distribution tabulated. One of the most frequently encountered kinds of teleost element in vertebrate microfossil localities of the late Cretaceous is precaudal centra. While of limited use for taxonomic studies, these elements have proved useful in paleoecological studies of the Dinosaur Park Formation (Eberth and Brinkman, l997).

In this paper, teleost precaudal centra from the Dinosaur Park Formation are described. The primary objective of this study is to describe morphoseries of precaudal centra that represent monotypic groups and that can be used in paleoecological studies focused on diversity and distribution of vertebrates in the late Cretaceous. It is likely that at least some of the precaudal centra described here belong to taxa currently known only from tooth-bearing elements. However, in only a few cases could such associations be demonstrated by articulated material or by unique patterns of distribution. To avoid the erection of redundant taxa, a parataxonomic system is developed. This system is considered to be a temporary arrangement that will be superseded by the use of formal taxonomic names when additional information is available that will allow precaudal centra to be associated with diagnostic elements. Towards this end, a survey of vertebral morphology in extant teleosts was undertaken as part of this study. Features of potential taxonomic significance were identified that allow some precaudal centra to be placed in established taxonomic groups, although generally at a high taxonomic level. However, many of the distinctive kinds of teleost centra present in the Dinosaur Park Formation cannot be assigned to a higher level category with certainty, and thus can only be identified by their parataxonomic designation.

METHODS

This study is restricted to precaudal centra from microvertebrate sites in the Dinosaur Park Formation (Judith River Group) of Alberta, and is based on a sample of over three thousand specimens from more than forty localities that were screenwashed using underwater screenwashing techniques (Table 1). The study was restricted to precaudal centra in order to minimize the variation introduced by serial variation along the vertebral column. To ensure that ontogenetic variation, regional variation along the precaudal region of the column, and variation between individuals in a population will all be documented, only precaudal centra represented by large numbers of specimens are described. Also, by only describing precaudal centra that are represented by large numbers of specimens, only groups that are useful for paleoecological studies using quantitative approaches are defined. Stratigraphic and geographic distributions provide a test of the hypothesis that two distinct vertebral morphotypes are from different kinds of fish. Elements from a single kind of fish should show the same patterns of distribution, so if two distinctive elements have a different distribution pattern, they are more likely to be from different kinds of fish. Surface collected specimens were included in the material examined in documenting distributional patterns based on presence and absence, but only screenwashed samples were considered in distributional patterns based on relative abundance.

A parataxonomic system was developed to organize the teleost centra into groups. Three levels are used in this system. The most inclusive level, referred to as ''supergroup'' and designated by roman numeral, reflects grades of evolution of teleost centra. In some cases, the features used to distinguish centrum supergroups vary along the column, so precaudal centra from a single fish could be placed into separate supergroup categories. Where centra with characteristics of two distinct supergroup categories are bridged by a series of transitional morphologies, it is assumed that the centra are from a single kind of fish. The dominant morphology will be used to place the morphoseries in a supergroup. The intermediate level, referred to as ''group'' and indicated by capital letters, are defined by features that characterize monophyletic taxa of extant teleosts whenever possible. The basal level, referred to as ''morphoseries'' and indicated by an arabic number, includes precaudal centra that are interpreted as being from a single low-level taxon. Individual morphoseries are referred to by a combination of the roman numeral indicating the supergroup

TABLE 1—Numbers of specimens of teleost centrum morphoseries from the Dinosaur Park Formation, Alberta, Canada, from screenwashed samples of vertebrate microfossil localities.

Centrum morphoseries	Dinosaur Park, Fluvial localities	Manyberries area Fluvial localities	Manyberries area Mud-filled channels
IA-1	0	7	41
IA-2	0	2	20
IA-3	0	1	78
IB-1	156	48	34
IB-2	51	3	38
IC-1	0	0	83
IIA-1	1158	97	73
IIA-2	16	2	214
IIA-3	0	0	49
IIB-1	77	6	4
IIB-2	0	0	92
IIIA-1	41	23	47
IIIA-2	1	11	448
IIIB-1	263	79	223
IIIB-2	0	16	25

category, the capital letter indicating the group within that supergroup category, and the number indicating the morphoseries within the group. Thus for example, morphoseries 1 of group A in supergroup II will be referred to as morphoseries IIA-1.

The terminology used to describe the centra follows Goodrich (1958), and Rojo (1991) whenever possible. Teleost precaudal centra are formed by a centrum and two pairs of cartilages, one ventral (basiventrals) and one dorsal (basidorsals). The basidorsals form the neural arch. The neural arch is separate from the centra in primitive teleosts, and leaves distinct pits that are referred to as neural arch articular pits. In the derived condition, the neural arch is fused to the centrum. The basiventrals form distinct elements that articulate with the pleural ribs in primitive teleosts, and thus act as parapophyses. In primitive teleosts, they fit in a distinct pit referred to below as a parapophyseal articular pit. In some groups, they are often preserved in place, although they remain recognizable as distinct ossifications. In derived teleosts, the basiventrals are incorporated into the centrum and the parapophysis is part of the centrum. The condition of having separate neural arch and parapophyses is referred to as the autogenous condition. Typically the pleural ribs articulate with the parapophysis, although in some teleosts, such as hiodontids, the ribs articulate with the centrum posterior to the parapophysis. Where the rib articulates with the centrum posterior to the parapophysis, the articular surface is referred to as the rib articular pit. A pit is identified as a rib articular pit if it is in an appropriate position and has a consistent size and shape and is not subdivided by accessory struts or buttresses. Processes extending dorsally from the centrum may be present. When the processes articulate with adjacent centra by way of a distinct articular surface, they are referred to as zygapophyses. Processes that are dorsally or ventrally directed, paired, and do not have distinct articular surfaces for contacting some part of the adjacent vertebrae are referred to as parasagittal processes. Processes extending laterally from the centrum are referred to as parapophyses.

The list of specimens includes only the better-preserved material observed. In the specimen lists, the specimen number is followed by the locality name in brackets, and this is followed by the number of centra included in that specimen number.

Institutional acronyms: TMP: Royal Tyrrell Museum of Palaeontology; ROM: Royal Ontario Museum.

LOCALITIES SAMPLED

The Judith River Group of southeastern Alberta was subdivided into three units by Eberth and Hamblin (1993), the Foremost Formation, Oldman Formation, and Dinosaur Park Formation. This study is restricted to material from the Dinosaur Park Formation. The Dinosaur Park Formation includes deposits of a high-sinuosity, fluvial system capped by the Lethbridge Coal Zone, a series of coal-bearing beds transitional between the fluvial beds of the Dinosaur Park Formation and the overlying marine Bearpaw Formation system (Eberth and Hamblin, 1993). Material was collected from three areas: Dinosaur Provincial Park, an extensive area of badlands along the Red Deer River about 30 km S.E. of Brooks, Alberta; an area along the South Saskatchewan River about 50 km N.E. of Medicine Hat, Alberta, and an area south of Manyberries, Alberta. While a few elements were collected from the surface in these areas, most of the material described here was recovered by underwater screenwashing vertebrate microfossil localities. Fifteen localities in Dinosaur Park Formation were sampled. These are BB 98, 32, 51, 86; 97, 104, 117, 78, 25, 106, 102, 54, 108, 94, and 75. The stratigraphic position and environment of deposition of these localities were described by Eberth (1990). They are all preserved in fluvial beds below the Lethbridge Coal Zone. Fourteen microvertebrate sites were sampled in the area south of Manyberries. These are: L1104, 1107, 1108, 1101, 1102, 1103, 1105, 1106, 1109, 1110, 1111, 1112, 1113, and 1114. These localities were described by Eberth and Brinkman (1997). Three localities are preserved in the fluvial beds below the Lethbridge Coal Zone (L1104, 1107, and 1108), and ten from within the Lethbridge Coal Zone (L1101, 1102, 1103, 1105, 1106, 1109, 1110, 1111, 1112, and 1113). The Lethbridge Coal Zone localities all occur in a mud-filled channel complex deposited in the turbidity-maximum zone of an estuarine system (Eberth and Brinkman, 1997). Although all the localities in this complex are strongly influenced by tidal backwater effects, there is no evidence from microfossils or invertebrates for high salinity. Thus, the centra described here are all interpreted as belonging to freshwater fish.

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII (sensu Nelson, 1994)
Division TELEOSTEI (sensu Arratia, 1997)
Supergroup I

Description.—Precaudal centra with autogenous neural arches (not fused to the centrum) and parapophyses.

Discussion.—Neural arches and parapophyses are primitively autogenous on abdominal vertebrae and remain so in most lower euteleosteans (Johnson and Patterson, 1996). Among extant teleosts, the conditions of neural arches and parapophyses both autogenous is present as a primitive character within the elopomorphs (Bardack, 1965, 1970; Forey, 1973), salmoniforms (Ford, 1937), ostariophysans (Forey, 1973), and clupeomorphs (Ford, 1937), although Poyato-Ariza (1990) believed this is an advanced character for ostariophysans. Precaudal centra of extant members of these orders can be differentiated on the basis of proportions of the centra, patterns of development of pits for the neural arch and parapophyses and development of processes from the centra. These features are used to distinguish three groups within Supergroup I.

Group IA

Description.—Precaudal centra short, plate-like; neural arch articular pits and parapophyseal articular pits widely separated from one another; sides of centrum between the neural arch and parapophyseal articular pits covered by many antero-posteriorly oriented fibers of bone extending between the edges of the centrum.

Discussion.—The combination of features here listed as characteristic of teleost centrum group IA are present in the extant elopids *Elops* and *Megalops* (Forey, 1973, p. 25) and the extinct

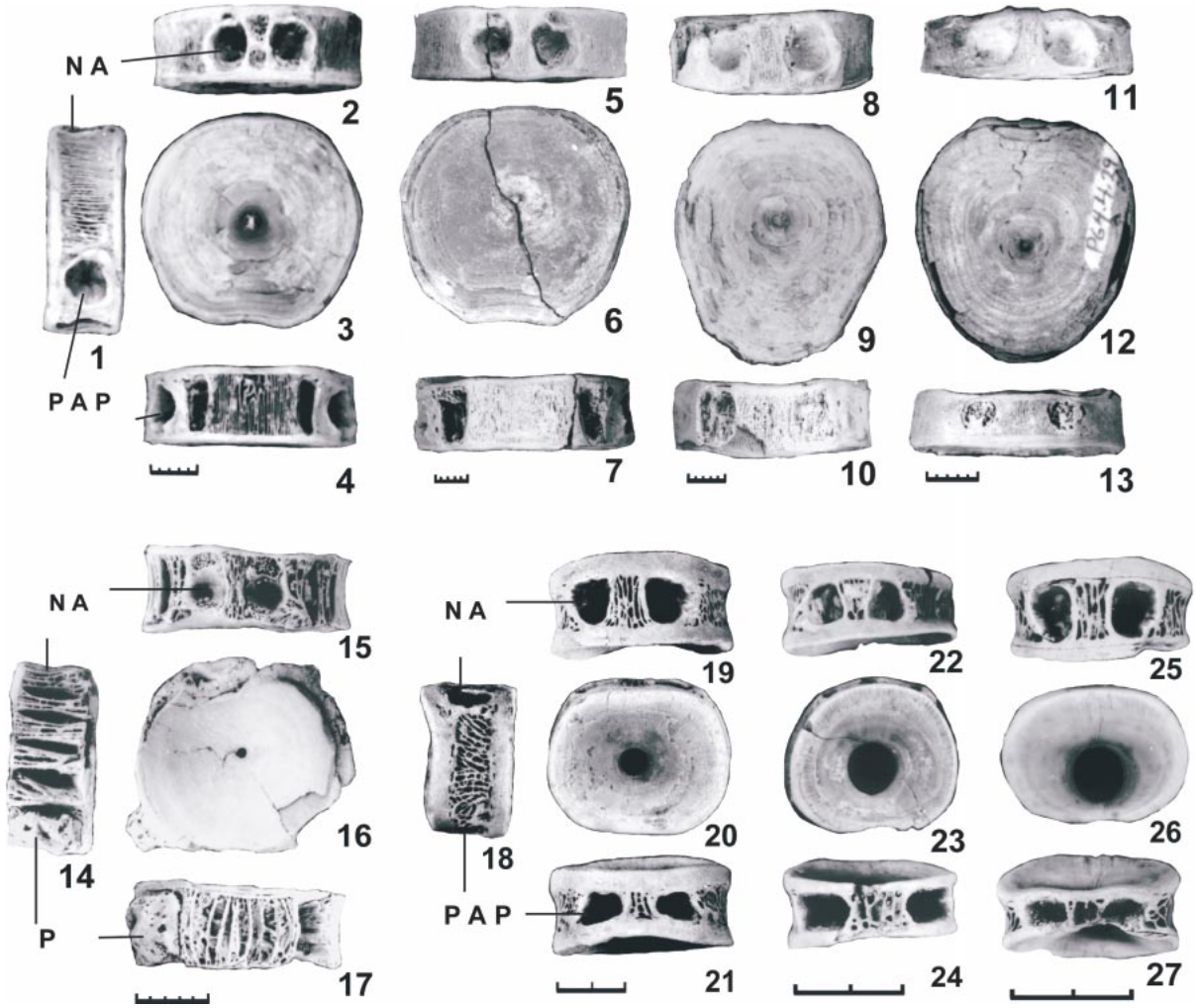

FIGURE *1*—Teleost centra of Group IA. *1–13*: morphoseries IA-1. *1–4*, specimen TMP 84.187.3, anterior precaudal centrum, in: *1*, lateral; *2*, dorsal; *3*, anterior; and *4*, ventral views. *5–7*, specimen TMP 93.36.232, anterior precaudal centrum, in: *5*, dorsal; *6*, anterior; and *7*, ventral views. *8–10*, specimen TMP 86.36.12, posterior precaudal centrum in: *8*, dorsal; *9*, anterior; and *10*, ventral views. *11–13*, specimen TMP 64.14.23, posterior precaudal centrum in: *11*, dorsal; *12*, anterior; and *13*, ventral views. *14–17*: morphoseries IA-2, specimen TMP 93.93.56, in: *14*, lateral; *15*, dorsal; *16*, anterior; and *17*, ventral views. *18–27*: Morphoseries IA-3. *18–21*, specimen TMP 97.19.11, in: *18*, lateral; *19*, dorsal; *20*, anterior; and *21*, ventral views. *22–24*, specimen TMP 97.19.13 in: *22*, dorsal; *23*, anterior; and *24*, ventral views. *25–27*, specimen 93.93.57 in: *25*, dorsal; *26*, anterior; and *27*, ventral views. Abbreviations: N A, neural arch articular pit; P, parapophysis; P A P, parapophyseal articular pit. Scale bars for *1–17* equal five mm, scale bar for *18–27* equals two mm.

elopid *Bananogmius* (Stewart, 1900, pl. 65), the primitive anguilliform *Brannerion* (Blum, 1991, p. 236), and the pachyrhizodontid *Rhacolepis* (Forey, 1977, p. 159; Maisey, 1991, p. 256). This combination of features has not been observed outside the Elopomorpha. Thus the centra included in this group are likely from members of the Elopomorpha.

A high diversity of group IA centra is present in the Dinosaur Park Formation, with three distinct morphoseries being recognizable. This is consistent with the high diversity of elopomorphs previously reported from this formation. Three elopomorph genera have been recognized in the Dinosaur Park Formation. One of these, *Paratarpon*, is represented by a postcranial skeleton from the Manyberries area of southern Alberta (Bardack, 1970) and an undescribed specimen in the Royal Ontario Museum collected from Dinosaur Provincial Park (specimen ROM 26290). The other two, *Coriops* and *Paralbula*, are represented by tooth-bearing elements.

Morphoseries IA-1
Figure 1.1–1.13

Material examined.—Surface collected centra from Dinosaur Provincial Park and area: TMP 93.36.262, one; TMP 84.187.3, one; TMP 86.36.12, one; TMP 84.187.3, one; TMP 66.15.22, one.

Description.—Precaudal centra much shorter than high; neural arch and parapophyseal articular pits shallow; fibers running between ends of the centrum fine, evenly spaced. Two distinct shapes present, representing regional variation along the column.

Anterior precaudal centra (Fig. 1.1–1.7) round, neural arch articular pits located close together (Fig. 1.2, 1.5); parapophyseal articular pits round, lined with smooth bone, located at the ventrolateral edge of the centrum (Fig. 1.1, 1.4), occasionally with parapophysis preserved in place; second pit of uncertain function present ventral to parapophyseal articular pit (Fig. 1.4), this pit narrow, rectangular, deeper than parapophyseal pits.

Posterior precaudal centra (Fig. 1.8–1.13) oval in shape, taller

than wide, without rectangular opening ventral to parapophyseal articular pit; parapophyseal articular pits located close together at ventral edge of centrum (Fig. 1.10, 1.13).

Discussion.—Morphoseries IA-1 centra can be identified as from *Paratarpon* on the basis of size and the narrow, plate-like proportions of the centra (Bardack, 1970). A distinctive feature of the anterior precaudal centra, not visible in the articulated specimens, is the presence of a slit-like pit ventral to the parapophyseal articular pit (Fig. 1.4). The function of this secondary pit is uncertain. In *Amia*, a slit-like pit on the ventral surface of the centrum supports cartilaginous haemal processes that lie on either side of the aorta (Goodrich, 1958), although these are located close to one another, rather than being widely separated as in teleost centrum morphoseries IA-1.

Morphoseries IA-2
Figure 1.14–1.17

Material examined.—TMP 93.93.124 (L1101), one; TMP 93.91.38 (L1101), two; TMP 93.93.119 (L1101), three; TMP 94.23.32 (L1102), two; TMP 93.93.56 (L1104), two; TMP 93.93.125 (L1105), three; TMP 90.48.58 (L1106), two; TMP 93.93.19 (L1101), five; TMP 93.93.44 (L1113), one; TMP 90.67.45 (L1113), one, TMP 93.116.65 (L1115), two.

Description.—Precaudal centra (TMP 93.93.56) with fibers extending between ends of centra grouped together into bundles (Fig. 1.14), the bundles being separated from one another by a distance about equal to the thickness of each bundle; neural arch and parapopyseal articular pits deep (Fig. 1.15, 1.17), without a second pit ventral to the parapophyseal articular pit (Fig. 1.17).

Discussion.—Morphoseries IA-2 is distinguished from morphoseries IA-1 by the bundles of fibers extending between the ends of the centrum and the presence of deep neural arch and rib articular pits. The proportions of the centra of morphoseries IA-2 and pattern of fibers of bone extending between the ends of the centra match those of elopiforms. However, the presence of deep pits for the neural arch and parapophyses is unusual since shallow pits are characteristic of the group (Forey, 1973).

The largest centrum of morphoseries IA-2, which is 1.2 cm high, is approximately equal in size to the smallest specimens of *Paratarpon*. Centra of morphoseries IA-2 have only been collected in localities of the Lethbridge Coal Zone of the Manyberries area, where the teeth of *Paralbula* are particularly abundant. Thus, it is possible that this morphoseries is from *Paralbula*, although no direct association demonstrates this.

Morphoseries IA-3
Figure 1.18–1.27

Material examined.—TMP 93.93.49 (L1101), one; TMP 93.93.57 (L1101), six; 93.91.37 (L1101), three; TMP 97.19.11 (L1101), one; TMP 97.19.13 (L1101), one; TMP 97.19.12 (L1102), one; TMP 93.93.50 (L1103), one; TMP 93.93.58 (L1105), two; TMP 90.48.14 (L1106), one; TMP 93.93.46 (L1110), three; TMP 93.93.47 (L1112), one; TMP 93.93.122 (L1112), two; TMP 90.67.19 (L1113), one.

Description.—Centra subtriangular to oval (Fig. 1.20) in end view, wider than high; fibers extending between the ends of the centra connected by cross bars, forming a series of small foramina arranged in rows (Fig. 1.18); neural arch articular pits (Fig. 1.19, 1.22, 1.25) and parapophyseal articular pits (Fig. 1.21, 1.24, 1.27) deep.

Discussion.—The centra of morphoseries IA-3 are distinct in their oval shape in end view and in the presence of cross bars between the fibers of bone. Most of the available examples are similar to the posterior-precaudal centra of morphoseries IA-1 in that the parapophyseal pits are typically located almost as close together as are the neural arch articular pits. However, in morphoseries IA-1, the centra are taller than wide, while in morphoseries IA-3 they are wider than tall. A few specimens are more nearly sub-triangular in shape and have parapophyseal pits more widely separated than the neural arch articular pits (e.g., TMP 97.19.13), and thus are similar to the anterior precaudal centra of morphoseries IA-1. However, a rectangular pit ventral to the parapophyseal articular pit like that present in the anterior precaudal centra of morphoseries IA-1 is absent.

All available specimens of morphoseries IA-3 are of small size, the largest being about 5 mm high. A growth series is present, with the smallest centra having a wide notocordal canal (Fig. 1.26) that becomes greatly restricted in the larger centra (Fig. 1.20). In the smallest specimens, the centra are wedge-shaped in lateral view with the dorsal edge of the centra wider than the ventral end. The dorsal and ventral edges of the centra are more nearly equal in width in the larger specimens. The mature morphology within this centrum morphoseries demonstrates that these centra are not an early stage of development of the much larger centrum morphoseries.

It is not known what kind of jaw elements is associated with morphoseries IA-3. *Coriops* can be excluded because the distribution of the diagnostic *Coriops* tooth-bearing elements is different from the distribution of morphoseries IA-3. Morphoseries IA-3 occurs exclusively in the mud-filled channels of the Manyberries area, where *Coriops* elements, although present, are rare. The centra are too small to be associated with tooth-plates of *Paralbula*. Thus morphoseries IA-3 indicates the presence of a previously unrecognized elopomorph in this assemblage.

Group IB

Description.—precaudal centra with neural arch and parapophyseal articular pits located close to one another, centrum without parasagittal processes extending dorsally from the posterior end of the centrum.

Discussion.—Teleost group IB centra are similar to group IA centra in that the neural arches and parapophyses are autogenous and in that parasagittal processes from the centrum are absent, but differ in that the centra are less distinctly plate-like and in that the neural arch and rib articular pits are located relatively closer to one another. Among extant teleosts, these features are only observed in the Salmoniformes. We follow traditional definitions of the Salmoniformes as a group including both the Salmonoidea and Esocoidea because the precaudal centra in these two groups are indistinguishable. However, we realize that this may be a paraphyletic grouping of primitive neoteleosts. Clupeomorphs, and some ostariophysans also have centra with autogenous neural arches and paraphophyses and with proportions similar to those of Salmoniformes, but in both clupeomorphs and ostariophysans, parasagittal processes extend dorsally from the posterior end of the centrum.

Morphoseries IB-1
Figure 2.1–2.14

Material examined.—TMP 86.199.27 (BB 97), one; TMP 86.60.33 (BB 54), six; TMP 86.45.85 (BB 54), two; TMP 86.43.82 (BB 54), one; TMP 86.44.16 (BB 54), one; TMP 86.21.66 (BB 54), two; TMP 86.45.65 (BB 54), two; TMP 86.19.65 (BB 54), one; TMP 86.60.31 (BB 54), four; TMP 86.193.8 (BB 104), one; TMP 86.242.67 (BB 104), one; TMP 87.19.40 (BB 104), three; TMP 86.198.22 (BB 104), one; TMP 86.43.80 (BB 86), one; TMP 86.43.53 (BB 86), one; TMP 86.23.87 (BB 86), three; TMP 86.6.50 (BB 31), one; TMP 86.4.37 (BB 31), one; TMP 86.53.12 (BB 102), one; TMP 86.8.83 (BB 102), one; TMP 2000.6.2 (South Saskatchewan River), six. TMP 90.43.64 (L1107), one; TMP 93.93.7 (L1108), four; TMP 89.1.60

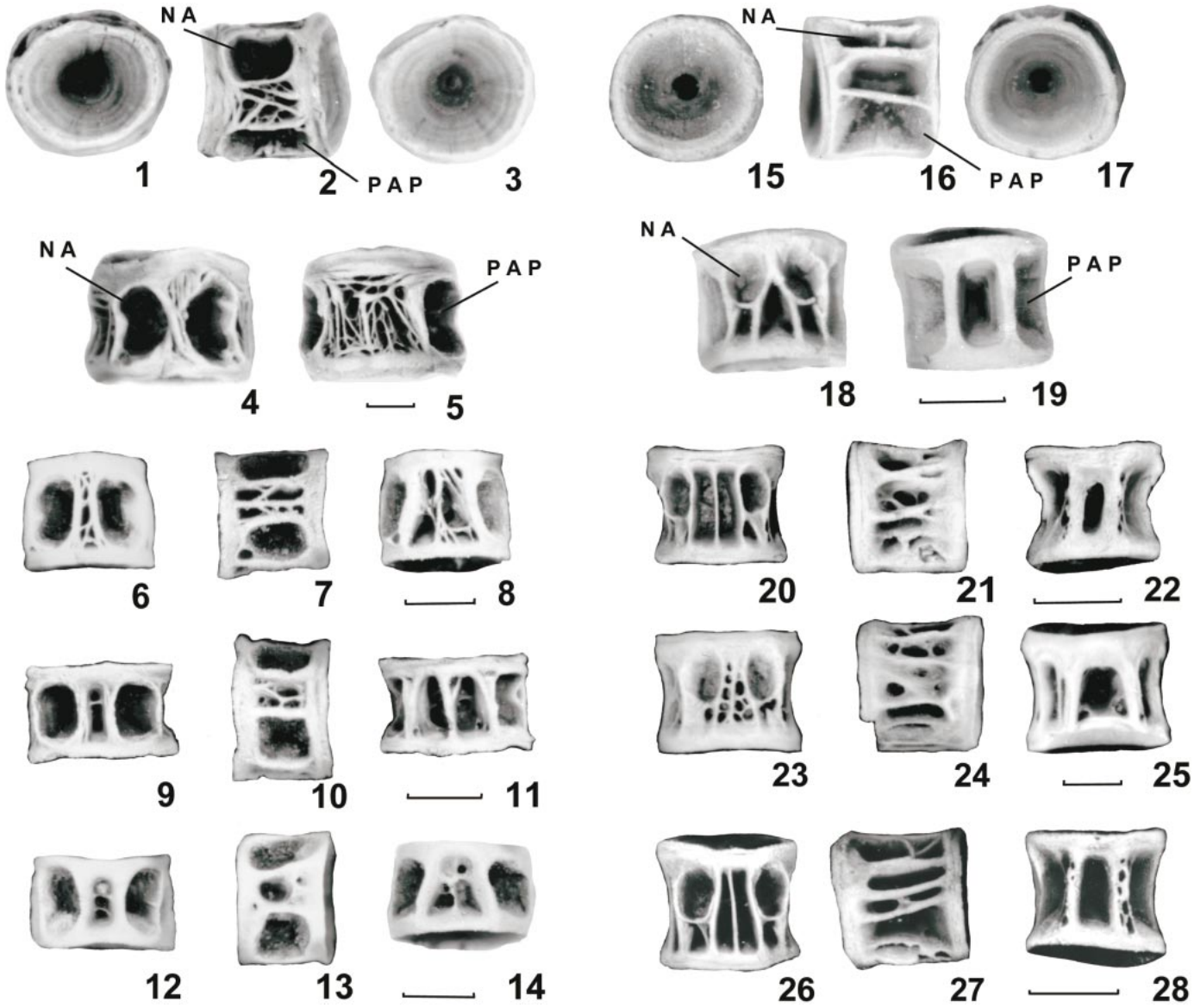

FIGURE 2—Teleost centra of morphoseries 1B-1 and 1B-2. *1–14*, morphoseries IB-1. *1–5*, specimen TMP 86.4.37 in: *1*, anterior, *2*, lateral, *3*, posterior, *4*, dorsal and *5*, ventral views. *6–8*, specimen TMP 86.45.85 in *6*, dorsal; *7*, lateral, and *8*, ventral views. *9–11*, specimen TMP 86.193.8 in: *9*, dorsal; *10*, lateral, and *11*, ventral views. *12–14*, specimen TMP 87.4.14 in *12*, dorsal; *13*, lateral; and *14*, ventral views. *15–28*, Teleost centrum morphoseries IB-2. *15–19*, specimen TMP 93.91.21 in: *15*, anterior; *16*, lateral; *17*, posterior; *18*, dorsal; and *19*, ventral views. *20–22*, specimen TMP 93.93.16 in: *20*, dorsal; *21*, lateral; and *22*, ventral views. *23–25*, specimen TMP TMP 86.21.63 in: *23*, dorsal; *24*, lateral; and *25*, ventral views. *26–28*, specimen 93.93.25 in: *26*, dorsal; *27*, lateral; and *28*, ventral views. Abbreviations: N A, neural arch articular pit; P A P, parapophyseal articular pit. Scale bars are one mm.

(L1105), three; TMP 93.93.2 (L1105), three; TMP 93.93.1 (L1105), one; TMP 93.93.4 (L1101), twelve; TMP 93.93.3 (L1102), one; TMP 93.93.5 (L1111), six; TMP 93.93.6 (L1112), one; TMP 93.93.8 (L1104), two.

Description.—Precaudal centra subequal in length and width (Fig. 2.1–2.8), or shorter than high (Fig. 2.9–2.14); neural arch articular pits (Fig. 2.4, 2.6, 2.9, 2.12) and parapophysis articular pits (Fig. 2.5, 2.8, 2.11, 2.14) deep, elongate, rectangular to oval in shape and subequal in size; neural arch pits closer to one another than to parapophysis articular pits (Fig. 2.2, 2.7, 2.10, 2.13); parapophysis articular pits extending well down the side of centrum so broadly visible ventrally; parapophyses often preserved in position in the parapophyseal articular pits; small centra with single deep fossa between neural arch pits (Fig. 2.9, 2.12), and between the neural articular pits and parapophyseal articular pits (Fig. 2.13), larger centra with accessory interconnecting ridges (Fig. 2.2, 2.7, 2.10), ridges between neural arch articular pits coalesce to form a single bar of bone in large centra (Fig. 2.4); ventral surface of centrum between the parapophyseal articular pits generally covered by a network of bone fibers, fibers longitudinally arranged or radiating laterally and posteriorly from the anterior edge and with a distinct mid-ventral ridge present (Fig. 2.5), although smaller specimens with shallow fossa on either side of a mid-ventral ridge (Fig. 2.11, 2.14) or with few fibers developed crossing the fossa on either side of the mid-ventral ridge (Fig. 2.8).

Discussion.—Morphoseries IB-1 centra are comparable to extant salmoniform centra in the relative size of the neural arch and

parapophyseal articular pits. Among extant esocoids, the umbrid genera *Dallia* and *Umbra* have centra similar to those of morphoseries IB-1 in the presence of a mid-ventral ridge and a ventral network of bone. The variation present in morphoseries IB-1 is largely size related, so is assumed to be a reflection of change during development, although a taxonomic component may be present. The relative abundance, size-frequency distribution, and stratigraphic and geographic distribution of morphoseries IB-1 corresponds to the esocoids *Estesesox* and *Oldmanesox*, so it is likely that the morphoseries includes centra from one or both of these teleosts.

Morphoseries IB-2
Figure 2.15–2.28

Material examined.—TMP 86.219.41 (BB 51), one; TMP 86.7.70 (BB 98), one; TMP 86.38.45 (BB 86), one; TMP 86.10.64 (BB 86), one; TMP 86.23.73 (BB 86), two; TMP 86.185.24 (BB 104), one; TMP 86.45.89 (BB 54), one; TMP 86.21.63 (BB 54), one; TMP 87.4.17 (BB 54), two; TMP 86.33.50 (BB 31), two; TMP 90.48.60 (L1106), three; TMP 93.93.22 (L1105), four; TMP 93.93.23 (L1105), four; TMP 93.91.23 (L1101), two; TMP 93.93.19 (L1101), three. TMP 93.93.18 (L1108), one; TMP 93.92.21 (L1102), one; TMP 93.93.15 (L1113), one; TMP 93.93.16 (L1109), one; TMP 93.93.21 (L1110), four; TMP 93.93.17 (L1111), six; TMP 93.93.20 (L1112), eight.

Description.—Precaudal centra sub-circular in end view (Fig. 2.15, 2.17) or deeper than wide; length of centrum slightly less than width; neural arch articular pits circular (Fig. 2.18, 2.20, 2.23, 2.26), less than half length of the centrum, located close to the anterior edge of centrum, of variable depth, bordered laterally by a parasagittal ridge that extends from the anterior to the posterior edge of the centrum, bordered medially by a parasagittal ridge that originates from the medial edge of the neural arch pit and extends to the posterior edge of the centrum; deep fossa present posterior to the neural arch articular pit between these parasagittal ridges; deep fossa present dorsally between the median parasagittal ridges (Fig. 2.18), subdivided by a mid-dorsal ridge in about one third of centra (Fig. 2.20, 2.26), occasionally further subdivided by variously developed crossbars and buttresses (Fig. 2.23), when present mid-dorsal ridge is less robust than either of the parasagittal ridges; mid-dorsal fossa extends anteriorly to separate the neural arch pits in about half the available centra (Fig. 2.20, 2.23, 2.26); presence of parapophysis articular pits variable, when present parapophyseal articular pits elongate, rectangular, located low on centrum (Fig. 2.16, 2.27); deep mid-ventral fossa present between parapophysis articular pits (Fig. 2.19, 2.22, 2.25, 2.28); lateral surface of the centrum between the parapophysis articular pit and the neural arch pit variously developed, may be a single, rectangular fossa (Fig. 2.16), subdivided by a longitudinal bar of bone (Fig. 2.27), or crossed by a course network of bone buttresses (Fig. 2.21, 2.24).

Discussion.—Morphoseries IB-2 centra are clearly distinct from the centra of morphoseries IB-1 in the structure of the neural arch articular pit (large in morphoseries IB-1, small and located anteriorly in morphoseries IB-2) and the structure of the ventral surface of the centrum (a network of bone fibers in morphoseries IB-1, a mid-ventral pit present in morphoseries IB-2). The degree to which the fossa between the parapophysis articular pit and the neural arch articular pit is filled in or crossed by fibers of bone appears to be related to the absence of a parapophyseal articular pit. Bone network along the side of the centra is most extensive in centra without distinct parapophyseal articular pits. The absence of a distinct parapophyseal articular pit in some specimens is likely a result of variation along the vertebral column, although it is uncertain which morphology is the more anterior in the column.

Morphoseries IB-2 centra conform to the salmoniform pattern in proportions and in having autogenous neural arch and parapophyses. The distinctive features of a small neural arch articular pit and a large mid-ventral pit are present in some extant salmoniforms, such as the genus *Thymallus*, but are also present in clupeomorphs and ostariophysans. Thus the identity of morphoseries IB-2 as from a salmoniform is tentative.

Group IC

Description.—Precaudal centra with neural arch articular pits short, generally less than half the length of the centrum, parasagittal processes extending dorsally posterior to the neural arch articular pits.

Discussion.—Centra included in group IC differ from those of group IB in the presence of parasagittal processes extending dorsally posterior to the neural arch articular pits. Among extant taxa, these features are present in both clupeopmorphs and some ostariophysans. The extant clupeomorphs examined (*Alosa*, *Clupea*, *Dorosoma*, and *Brevoortia*), share the presence of a neural arch base that is a small, circular opening restricted to the anterior half of the centrum, and dorsal processes posterior to the neural arch base. Most ostariophysans have neural arches fused to the centrum, but some, such as *Chanos*, retain the primitive condition of having autogenous neural arches and parapophyses at least anterior to the dorsal fin (Poyato-Ariza, 1996). In *Chanos* the neural arch articular pits are like those of clupeomorphs in being restricted to the anterior end of the centrum, but differ in that they are are confluent with each other through most of the precaudal region. Also, in ostariophysans with autogenous parapophyses, the rib articular pits are larger relative to the size of the centrum compared with clupeomorphs.

Morphoseries IC-1
Figure 3.1–3.12

Material examined.—TMP 89.1.58 (L1105), eighteen; TMP 93.93.12 (L1105), seven; TMP 93.93.10 (L1105), eleven; TMP 90.48.17 (L1106), two; TMP 90.48.17, (L1106), five; TMP 90.67.33 (L1113), three; TMP 93.93.9 (L1103), five; TMP 93.93.14 (L1103), four; TMP 93.93.11 (L1101), three; TMP 93.91.36 (L1101), one; TMP 93.92.31 (L1102), two; TMP 93.93.13 L1102), twelve.

Description.—Precaudal centra with neural arch articular pits (Fig. 3.1, 3.5, 3.9) small, subcircular, deep, located near the anterior end of the centrum; a single mid-dorsal ridge and one pair of parasagittal ridges extend posteriorly from neural arch articular pits, mid-dorsal ridge more strongly developed than parasagittal ridge; parasagittal ridges with dorsally extending flanges near their posterior ends; rib articular pit (Fig. 3.2, 3.6, 3.10) about half the length of centrum, floored by a sharp-edged ridge that extends between the two ends of the centrum, short buttresses running dorsally from posterior end of rib articular surface to ventral edge of neural arch pit; posterior half of centrum smooth, cone-shaped in lateral view; mid-ventral fossa present (Fig. 3.3, 3.7, 3.11), bordered by ventral parasagittal ridges which may be subdued (Fig. 3.11) or strong (Fig. 3.3, 3.7); mid-ventral pit separated from the rib articular pit by a deep fossa equal to (Fig. 3.3) or wider than (Fig. 3.7) mid-ventral pit.

Posterior precaudal centra (Fig. 3.9–3.12) elongate, only slightly wider than high, with rib articular pit and neural arch articular pits shorter than half the length of the centrum.

Anterior-precaudal centra short, oval in end view, wider than high (Fig. 3.1–3.4); neural arch and rib articular pits relatively larger than in posterior precaudal centra, occasionally longer than half the length of the centrum. Transition zone between posterior precaudal and anterior precaudal centra represented by centra of intermediate proportions (Fig. 3.5–3.8).

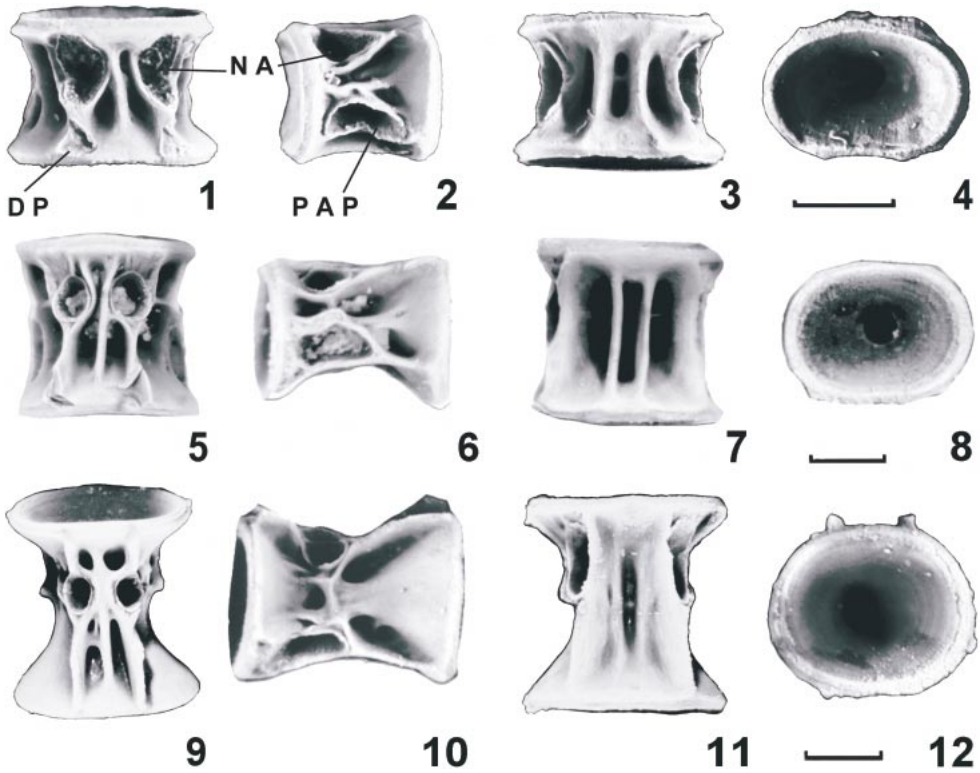

FIGURE *3*—Teleost centra of morphoseries IC-1. *1–4*, specimen TMP 89.1.58, in *1*, dorsal; *2*, lateral; *3*, ventral; *4*, anterior views. *5–8*, specimen TMP 90.67.33 in: *5*, dorsal, *6*, lateral, *7*, ventral, and *8* anterior views. *9–12*, specimen TMP 89.1.58 in: *9*, dorsal; *10*, lateral; *11*, ventral; and *12*, posterior views. Abbreviations: D P, dorsal process; N A, neural arch articular pit; P A P, parapophyseal articular pit. Scale bar is one mm.

Discussion.—The centra of morphoseries IC-1 conform to the clupeomorph pattern in the presence of small, neural arch articular pits located close to the anterior end of the centrum, neural arch articular pits separated from one another, and parasagittal processes extending dorsally from the centrum posterior to the neural arch articular pits. Clupeomorph centra also frequently show a cone-like appearance of the posterior end of the centrum in lateral view as is seen in morphoseries IC-1. The centra differ from any of the extant clupeomorphs observed (*Alosa*, *Brevoortia*, *Clupea*, and *Dorosoma*) in having a mid-dorsal ridge and a mid-ventral fossa. The extant clupeids have a mid-dorsal fossa and a mid-ventral ridge.

The difference in proportions of the centra included in morphoseries IC-1 is striking, and is not matched in any of the extant clupeomorphs examined. It is assumed that this reflects variation along the column, rather than two distinct precaudal morphoseries of centra, because intermediate forms are present. As well, the two morphologies here identified as anterior and posterior precaudal centra have a similar, very restricted, distribution in the Dinosaur Park Formation. The identification of the short, oval centra as anterior is based on the tendency for posterior precaudal centra to approach the caudal centra in proportions.

Teleost Centrum Supergroup II

Description.—Precaudal centra with parapophysis fused to centrum, neural arch autogenous.

Discussion.—The presence of mid-anterior precaudal centra with an autogenous neural arch and well-developed parapophyses fused to the centrum is seen in osteoglossomorphs (e.g., *Phareodus*, *Osteoglossum*, and hiodontids) and appears to be typical for the members of the clade (Taverne, 1977, 1978, and 1979). This condition may be present as a variant along the anterior-most portion of the vertebral column of the gonorhychiform *Notogoneus*.

One osteoglossiform is known from the Dinosaur Park Formation on the basis of articulated material (Li, 1996), although centra are not preserved in this specimen. The centra of supergroup II from the Dinosaur Park Formation can be separated into two groups according to the relative depth of the neural arch articular pits.

Group IIA

Description.—Precaudal centra with deep neural arch articular pits.

Discussion.—In extant osteoglossomorphs, two patterns of neural arch articular pit morphology are present. In *Phareodus* and *Osteoglossum*, the neural arch articular pits are deep, while in hiodontids the neural arch articular pits are largely filled by bone. Both morphologies are present in the supergroup II centra from the Dinosaur Park Formation, and are used to subdivide supergroup II into two groups, with group IIA having a structure like that in *Osteoglossum*.

Morphoseries IIA-1
Figure 4.1–4.11

Material examined.—TMP 86.7.48 (BB98), nine; TMP 87.156.28 (BB 71), three; TMP 86.60.29 (BB 54), fifty-six; TMP 86.45.64 (BB 54), sixty-eight; TMP 86.23.35, (BB 86), twenty-five; TMP 86.171.41 (BB 103), twelve; TMP 87.99.11 (BB 75), seven; TMP 86.200.20 (BB 97), eight; TMP 86.213,16 (BB107), three; TMP 86.219,42 (BB 51), sixteen; TMP 95.145.1 (BB 51), thirty-nine; TMP 95.177.67 (BB 100), sixty-six; TMP 95.157.65 (L1108), thirty-three; TMP 2000.6.1 (South Sask. River, Tony's Site), six centra; TMP 93.117.7 (L1104), nineteen.

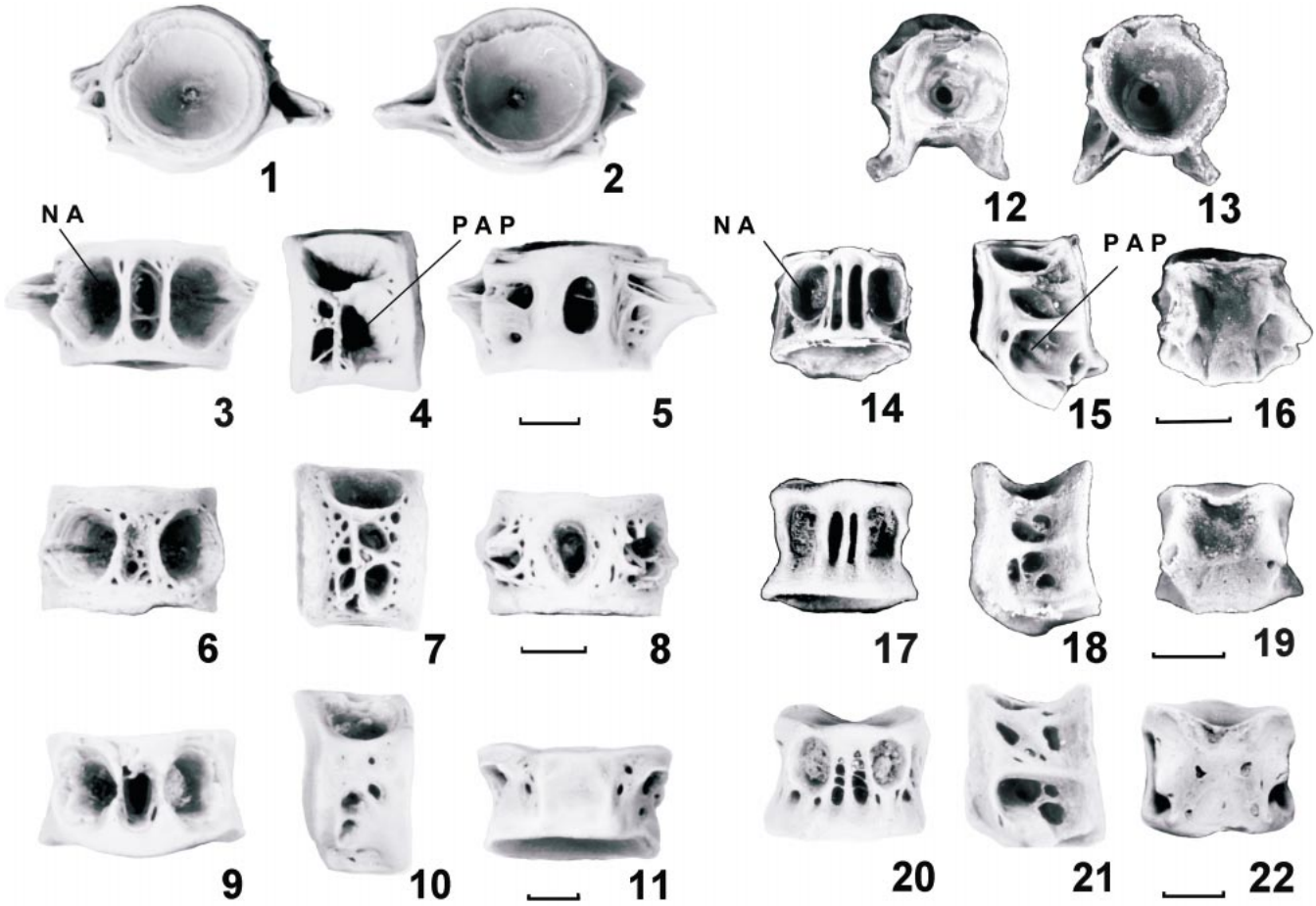

FIGURE 4—Teleost centra of morphoseries IIA-1 and IIA-2. *1–11*: morphoseries IIA-1. *1–5*, specimen TMP 2000.6.1, mid- precaudal centrum in: *1*, anterior; *2*, posterior; *3*, dorsal; *4*, lateral; and *5*, ventral views. *6–8*, specimen TMP 86.7.88, posterior precaudal centrum in: *6*, dorsal; *7*, lateral; and *8*, ventral views. *9–11*, specimen TMP 93.117.7, anterior precaudal centrum in: *9*, dorsal; *10*, lateral; and *11*, ventral views. *12–22*: morphoseries IIA-2. *12–16*, specimen TMP 93.93.97, precaudal centrum in: *12*, anterior; *13*, posterior, *14*, dorsal; *15*, lateral; and *16*, ventral views. *17–19*, specimen TMP 89.1.56 in: *17*, dorsal; *18*, lateral; and *19*, ventral views. *20–21*, specimen TMP 86.21.63, in *20*, dorsal; *21*, lateral; and *22*, ventral views. Abbreviations: N A, neural arch articular pit; P A P, parapophyseal articular pit. Scale bar equals one mm.

Description.—Precaudal centra amphicoelous, circular in end view (Fig. 4.1, 4.2), width equal to or greater than the length; neural arch articular pits (Fig. 4.3, 4.6, 4.9) oval, deep, extend the full length of the centrum; neural arch articular pits separated from each other by a single, deep mid-dorsal fossa; deep mid-ventral fossa generally present (Fig. 4.5, 4.8), bordered by strong parasagittal ridges. Three distinct regions of the column recognizable.

Mid-precaudal centra (Fig. 4.1–4.5) round in end view but slightly wider than high; parapophyses long, laterally directed; rib articular pits deep, circular, located posterior to parapophyses (Fig. 4.4), extending dorsally to reach the lateral edge of the neural arch pits; a pair of deep fossae present anterior to the parapophyses; parapophyses buttressed ventrally by short ridges that extend across a shallow fossa from the base of the transverse process to the parasagittal ridge bordering the mid-ventral fossa (Fig. 4.5).

Anterior-precaudal centra (Fig. 4.9–4.11) higher than wide; parapophyses short, ventro-laterally directed, located low on side of centrum (Fig. 4.10, 4.11); mid-ventral pit reduced in size or absent in about half the examples; where absent, ventral surface of centrum between parapophyses bulbous (Fig. 4.11); neural arch pit and parapophysis widely separated from each other, lateral surface of centrum between parapophysis and neural arch pit solid or with fossae and ridges variably developed (Fig. 4.10); distinct rib articular pit absent; usually a pair of deep fossae posterior to parapophysis although these variably subdivided; fossa absent anterior to parapophysis.

Posterior-precaudal centra (Fig. 4.6–4.8) circular in end view, with parapophysis sloping more strongly ventrally than in mid-precaudal centra and with sharp ridge extending from neural arch pit to tip of parapophysis (Fig. 4.7), distinct rib articular pits absent; pair of fossae present posterior to parapophysis.

Discussion.—The centra of morphoseries IIA-1 are the most common teleost precaudal centra in the Dinosaur Park Formation outside the Lethbridge Coal Zone localities with usually more that half the centra from a locality being from this morphoseries. The mid-precaudal centra are most numerous and are easily recognizable on the basis of the long, laterally directed parapophyses, well developed mid-dorsal and mid-ventral pits, and deep neural arch pits that are oval in shape and extend the full length of the centrum. A mid-precaudal centrum of morphoseries IIA-1 was illustrated by Brinkman (l990), as of teleost type ''D''. This designation was followed by Eberth and Brinkman (l997). Brinkman (l990) associated these centra with a distinctive type of jaw, as yet unnamed, on the basis of size-frequency distributions and a

similar pattern of relative abundance in twenty-five vertebrate microfossil localities. This association remains strongly supported with an increase in the number of the microvertebrate sites sampled.

The presence of autogenous neural arches and long laterally directed parapophyses in the mid-precaudal centra is similar to the condition in *Osteoglossum* (Taverne, 1977) and suggests that morphoseries IIA-1 centra are from a member of the Osteoglossomorpha. Deep circular pits posterior to the parapophyses are identified as rib articular pits from comparison with *Hiodon*, and suggest that, as in *Hiodon*, the rib articulated directly with the centrum. This contrasts with the condition in extant members of the Osteoglossiformes, where the ribs do not insert on the centrum but insert on a groove on the posterior face of the parapophyses (Taverne, 1977). This suggests that either the presence of an articulation of the rib with the centra posterior to the parapophysis is a primitive character in the Osteroglossomorpha, or within the group the affinities of the teleost represented by centra of morphoseries IIA-1 lie within the Hiodontiformes, rather than the Osteoglossiformes.

Morphoseries IIA-2
Figure 4.12–4.22

Material examined.—TMP 86.219.47 (BB 51), one; TMP 86.216.20 (BB 51), one; TMP 86.217.47 (BB 51), one; TMP 86.238.24 (BB 94), one; TMP 86.199.48 (BB 97), one; TMP 86.58.71 (BB 102), one; TMP 86.53.13 (BB 102), two; TMP 89.1.56 (L1105), fifty-four; TMP 93.93.103 (L1105), twenty; TMP 93.93.102 (L1105), thirty-eight; TMP 90.43.65 (L1107), one; TMP 90.48.22 (L1106), seventeen; TMP 93.92.20 (L1102), one; TMP 93.93.98 (L1102), three; TMP 93.93.101 (L1101), six; TMP 93.91.20 (L1101), eighteen; TMP 93.93.99 (L1101), five; TMP 93.93.108 (L1103), three; TMP 93.93.107 (L1103), one; TMP 93.93.96 (L1109), one; TMP 93.93.100 (L1109), one; TMP 93.93.104 (L1110), eight; TMP 93.93.97 (L1111), twenty; TMP 93.93.105 (L1112), ten; TMP 93.93.106 (L1112), five; TMP 90.67.26 (L1113), one.

Description.—Precaudal centra with deeply amphicoelous posterior end (Fig. 4.13), nearly flat or weakly amphicoelous anterior end (Fig. 4.12); neural arch articular pits (Fig. 4.14, 4.17, 4.20) deep, oval to circular in shape, generally located slightly closer to anterior edge and often truncated by anterior edge of centrum; pair of deep fossae separated by mid-dorsal ridge between neural arch articular pits; parapophyses short, ventro-laterally directed (Fig. 4.12, 13); ventral surface of centrum between parapophyses smooth and flat (Fig. 4.16, 4.19, 4.22), sloping posteriorly and ventrally from anterior end of centrum so posterior end relatively higher than anterior end; posterior end usually higher than wide, anterior end wider than high; lateral surface of centrum (Fig. 4.15, 4.18, 4.21) variably subdivided by antero-posteriorly oriented ridges, occasionally filling in lateral surface of centrum leaving only small circular fossa just dorsal to transverse process; distinct rib articular pits absent.

Discussion.—The centra of morphoseries IIA-2 are easily recognizable by the nearly flat anterior end, smooth ventral surface, short ventro-laterally directed parapophyses, anterior placement of the neural arch pits, and presence of a mid-dorsal ridge separating two parasagittal fossae between the neural arch articular pits. The variation in development of ridges and pits between the neural arch pits and on the lateral surface of the centra, and the degree to which the neural arch articular pits approach each other, appears to be size-related. Variation that can be attributed to regional variation along the column includes the length of the parapophyses and the degree to which the neural arch base approaches the anterior end of the centrum.

The centra of morphoseries IIA-2 are generally similar to the anterior precaudal centra of morphoseries IIA-1 in the size and orientation of the parapophysis, the absence of distinct rib articular pits, and the shape of the neural arch articular pits. However, the ventral surface of the centra in morphoseries IIA-2 never has the bulbous, ventral projection present in morphoseries IIA-1, a mid-ventral pit or foramen is never present in morphoseries IIA-2 but generally present in IIA-1, and a mid-dorsal ridge subdividing the mid-dorsal pit is present in morphoseries IIA-2, but absent in IIA-1. Support for the hypothesis that morphoseries IIA-1 and IIA-2 are from different kinds of fishes is provided by their different distribution in the Dinosaur Park Formation. Morphoseries IIA-1 is dominant in the fluvial deposits of Dinosaur Provincial Park below the Lethbridge Coal Zone and less common in localities preserved in the mud-filled estuarine channel deposits within the Lethbridge Coal Zone of the Manyberries area. Morphoseries IIA-2 is abundant in localities preserved in the mud-filled channels within the Lethbridge Coal Zone (Eberth and Brinkman, 1997) and rare in the fluvial beds of Dinosaur Provincial Park. These two morphoseries are likely from two different kinds of fishes with distinct distribution patterns. The similarity between morphoseries IIA-2 and the anterior precaudal centra of morphoseries IIA-1 is interpreted as evidence of a close relationship between the two species represented by these centra.

Morphoseries IIA-3
Figure 5.1–5.13

Material examined.—TMP 89.1.61 (L1105), twelve; TMP 93.93.36 (L1105), four; TMP 93.93.38 (L1105), five; TMP 90.48.21 (L1106), seven; TMP 90.48.20 (L1106), two; TMP 90.67.34 (L1113), two; TMP 93.93.43 (L1101), one; TMP 93.93.39 (L1101), two; TMP 93.93.37 (L1103), one; TMP 93.93.40 (L1103), one; TMP 93.93.41 (L1112), one; TMP 93.93.42 (L1111), one; TMP 93.93.35 (L1101), five; TMP 93.93.34 (L1102), one; TMP 93.92.30 (L1101), one.

Description.—Precaudal centra oval in end view (Fig. 5.4, 5.5, 5.9, 5.10), wider than high; centra shorter than wide; two pairs of deep fossae present dorsally (Fig. 5.2, 5.7); median pair, possibly neural arch articular pits, separated by mid-dorsal ridge; lateral pair smaller, located posterior to parapophyses; three deep fossae of subequal size present ventrally (Fig. 5.3, 5.8); mid-ventral fossa, and pair of fenestra at base of parapophyses.

Mid-precaudal centra (Fig. 5.6–5.10) with posterior cavity slightly deeper than anterior cavity; parapophyses long, laterally directed rods of bone with little development of struts or flanges at base; antero-dorsal edge of parapophyses continuous with a thickened ridge that borders the antero-dorsal edge of the centrum (Fig. 5.7); dorsal-median pair of fossae (? neural arch articular pits) extend full length of centrum, separated from each other and from dorsolateral pair of fossae by stout, rounded ridge, with delicate network of bone forming well defined circular foramen at base; dorsolateral fossae small round pits postero-dorsal to parapophyses (Fig. 5.7); three ventral fossae extend nearly full length of centrum, separated from each other by pair of stout parasagittal ridges; ventral parasagittal ridges occasionally paralleled or buttressed by more slender bars.

Anterior-precaudal centra (Fig. 5.1–5.5, 511–5.13) with saddle-shaped anterior articular surface (Fig. 5.1, 5.5), ventral portion flat, dorsal portion projecting forward; deeply amphicoelous posteriorly (Fig. 5.4); transverse process variably developed, may be an elongate bar of bone with forked lateral end (Fig. 5.13), two small processes (Fig. 5.2), single small process, or absent (Fig. 5.11, 5.12); dorsomedian pair of fossae (Fig. 5.2, 5.11–5.13) small, round, located on anterior projection, separated from each other by narrow bar of bone; dorso-lateral pairs of fossae reduced to small, foramen-like pit behind the transverse process; area between dorsomedial and dorsolateral pair of fossae broad, smooth,

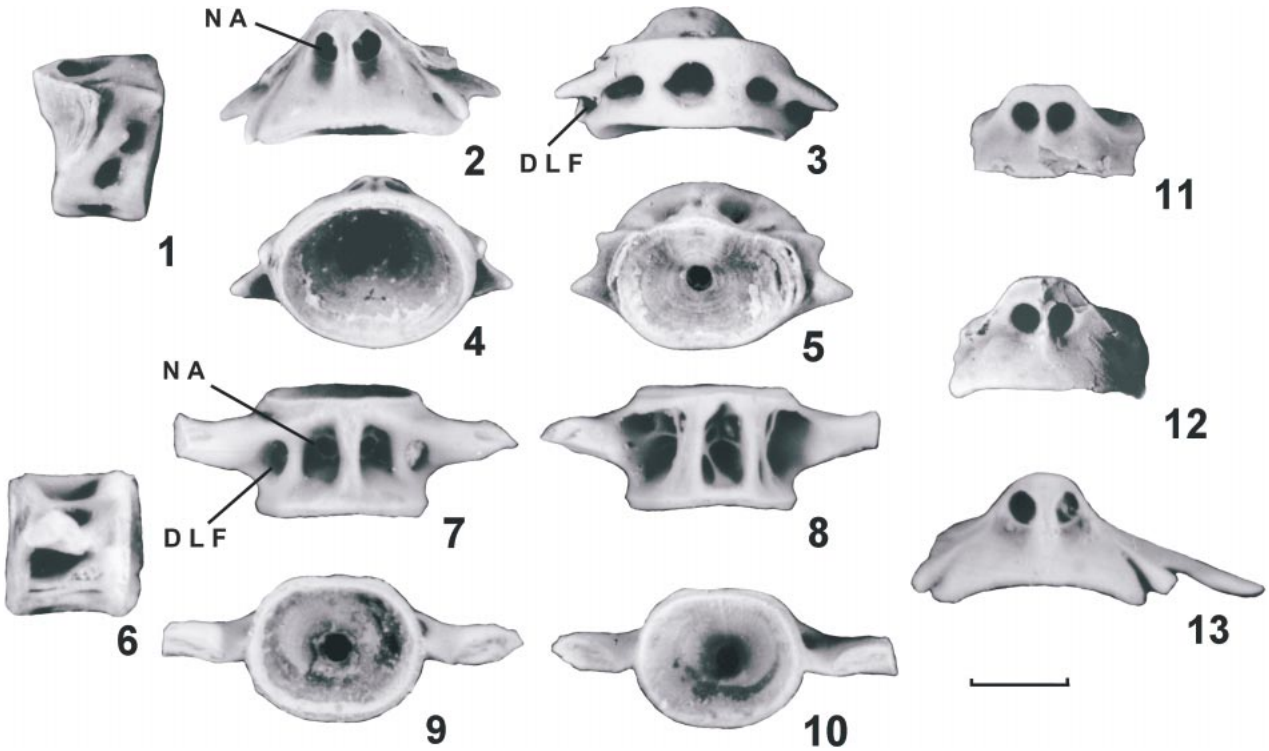

FIGURE 5—Teleost centrum morphoseries IIA-3. *1–5*, specimen 97.19.14, anterior-precaudal centrum in: *1*, lateral; *2*, dorsal; *3*, ventral; *4*, posterior; and *5*, anterior views. *6–13*, specimen TMP 93.93.41, anterior precaudal centrum in: *6*, lateral; *7*, dorsal; *8*, ventral; *9*, posterior; and *10*, anterior views. *11*, specimen 93.124.41 in dorsal view. *12*, specimen 93.93.38 in dorsal view. *13*, specimen 89.1.61 in dorsal view. Abbreviations: N A, neural arch articular pit; D L F, dorso-lateral fossa. Scale bar equals one mm.

and slightly inflated; mid-ventral fossa slightly larger than lateroventral fossae (Fig. 5.3).

Discussion.—The presence of a strongly developed saddle-shaped joint on the anterior-precaudal centra of morphoseries IIA-3 is a unique feature that is unmatched in any other morphoseries from the Dinosaur Park Formation and was not observed in any extant teleost known to us. The delicate network of bone with a circular opening at the base of the presumed neural arch articular pits is also a feature unique to morphoseries IIA-3. Thus although the presence of the group IIA characteristics of fused parapophyses and an autogenous neural arch conforms with the basic osteoglossomorph pattern, the unusual features present in morphoseries IIA-3 suggest that this morphoseries is from a fish that is distinct at a high taxonomic level.

Group IIB

Description.—Precaudal centra with shallow neural arch articular pits, lacking parasagittal processes extending dorsally from the posterior end of the centrum.

Discussion.—In hiodontids among modern osteoglossomorphs, and two morphoseries of supergroup II centra from the Dinosaur Park Formation, the neural arch articular pits are shallow, largely filled in by cancelous bone. Although the taxonomic utility of this feature is uncertain, it is a consistently reliable feature that can be used to define a distinct group of supergroup II centra.

Morphoseries IIB-1
Figure 6.6–6.18

Material examined.—TMP 86.22.69 (BB 54), one; TMP 86.60.32 (BB 54), two; TMP 86.43.83 (BB 54), one; TMP 86.20.56 (BB 54), one; TMP 86, 193.9 (BB 104), two; TMP 86.194.12 (BB 104), one; TMP 86.198.42 (BB 104), one; TMP 86.195.9 (BB 104), two; TMP 86.196.29 (BB 104), one; TMP 86.242.68 (BB 104), two; TMP 86.11.70 (BB 86), one; TMP 86.10.61 (BB 86), one; TMP 87.30.35 (BB 106), one; TMP 86.220.17 (BB 106), one; TMP 86.215.21 (BB 51), one; TMP 86.7.65 (BB 98), one; TMP 86.53.81 (BB 102), one; TMP 87.158.29 (BB 78), six; TMP 89.1.63 (L1105), one; TMP 93.93.95 (L1105), two; TMP 93.93.94 (L1102), one; TMP 90.43.63 (L1107), two.

Description.—Precaudal centra amphicoelous, small (1.2 to 1.5 mm high), circular or higher than wide in end view (Fig. 6.14, 6.18); length greater than or subequal to width; neural arch articular pits (Fig. 6.6, 6.11, 6.15) oval, shallow, extending nearly full length of centrum; fossa between neural arch articular pits variably developed, when present (Fig. 6.15), not subdivided by mid-dorsal ridge; rib articular pit deep (Fig. 6.12, 6.16), circular, located at base of parapophysis, meets neural arch articular pit; ventral (Fig. 6.8, 6.13, 6.17) and lateral (Fig. 6.7, 6.12, 6.16) surface of centrum formed by closely woven network of bone resulting in many small circular to oval foramina, occasionally oriented in rows, or more generally, evenly distributed across the surface.

Anterior to mid-precaudal centra (Fig. 6.11–6.14) with transverse processes laterally directed; neural arch pits separated by solid ridge (Fig. 6.11) or ridge with small fossa at one end; ventral surface of centrum between transverse processes convex.

Posterior precaudal centra (Fig. 6.15–6.18) with transverse processes directed ventro-laterally; neural arch articular surfaces separated by ridge with pits at both ends or single deep pit (Fig. 6.15); ventral surface of centrum between transverse processes flat or concave.

Atlas centrum (Fig. 6.6–6.10) with tripartite anterior articular surface (Fig. 6.9); anterior end of centrum platycoelous, posterior

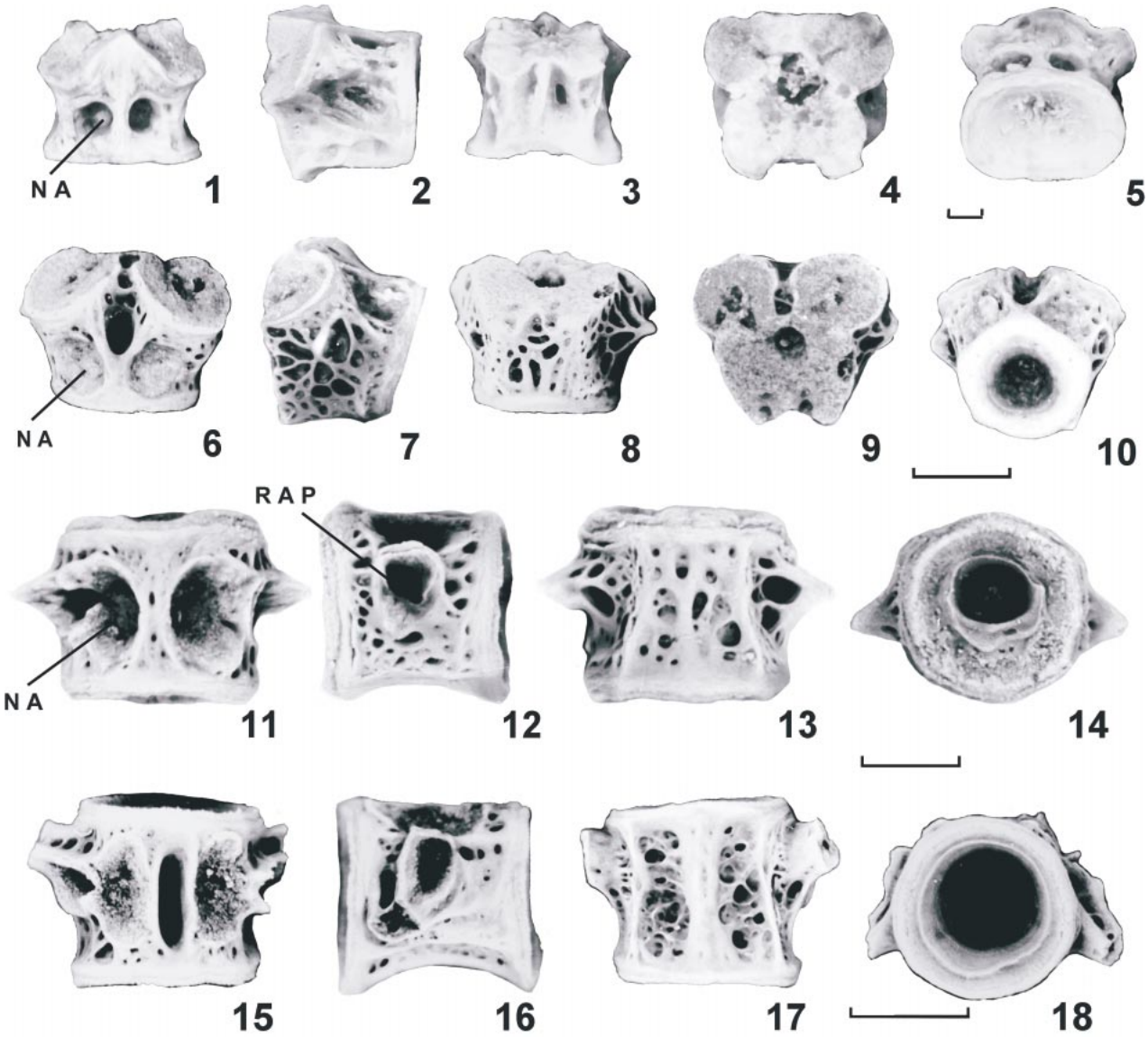

FIGURE 6—Hiodontid precaudal centra. *1–5,* atlas centrum of *Hiodon alosoides*, specimen TMP 90.7.197, in: *1,* dorsal; *2,* lateral; *3,* ventral; *4,* anterior, *5,* posterior views. *6–18,* centra of teleost centrum morphoseries IIB-1. *6–10,* specimen TMP 87.158.29, atlas centrum in: *6,* dorsal; *7,* lateral; *8,* ventral; *9,* anterior, *10,* posterior views. *11–14,* specimen TMP 86.171.36, anterior precaudal centrum, in: *11,* dorsal; *12,* lateral; *13,* ventral, and *14* anterior views. *15–18,* specimen TMP 95.180.37, posterior precaudal centrum in: *15,* dorsal; *16,* lateral; *17,* ventral, and *18* anterior views. Abbreviations: N A, neural arch articular pit; R A P, rib articular pit. Scale bar equals one mm.

end amphicoelous (Fig. 6.10); ventral surface with parasagittal ridges anteriorly, subdued posteriorly (Fig. 6.8), so centrum round in posterior view (Fig. 6.10).

Discussion.—The centra here referred to morphoseries IIB-1 are easily recognizable by the presence of shallow, oval pits for the neural arch and the loose woven network of bone covering the ventral and lateral surfaces of the centrum. They are of consistently small size, typically 1.2 to 1.5 mm high.

Morphoseries IIB-1 can be identified as from a member of the Hiodontidae, on the basis of the structure of the atlas centrum, which is distinctive for the family (Taverne, 1977). Hiodontids are one of the rare primitive teleosts where a vertebra does not fuse to the basioccipital during embryonic development. The basioccipital does not have the shape of a half vertebra posteriorly, so typical of most primitive teleosts. The exoccipitals are large and, with the basioccipital, form the occipital condyle for articulation with the first vertebra. The anterior articular surface of the first veterbra is rough and quadrilobate, not circular as in most primitive teleosts (Ridewood, 1904; Taverne, 1977; Rosen, 1985). The atlas centrum of morphoseries IIB-1 matches that of *Hiodon* (Fig. 6.1–6.5) in: 1) the triparite anterior articular surface (Fig. 6.4, 6.9); 2) the presence of a platycoelous anterior articular surface (Fig. 6.4, 6.9); 3) the presence of neural arch articular pits that are shallow and located on the posterior half of the centrum (Fig. 6.1, 6.6); and 4) the presence of a pair of ventral parasagittal ridges that are expressed on the anterior end of the centrum but become subdued posteriorly (Fig. 6.3, 6.8). A tripartite anterior surface on the atlas is also seen in advanced neoteleostians. However, the neoteleostean condition differs from the condition in *Hiodon* and the atlas of morphoseries IIB-1 centra in having an amphicoelous anterior articular surface.

The centra of morphoseries IIB-1 are similar to the posterior

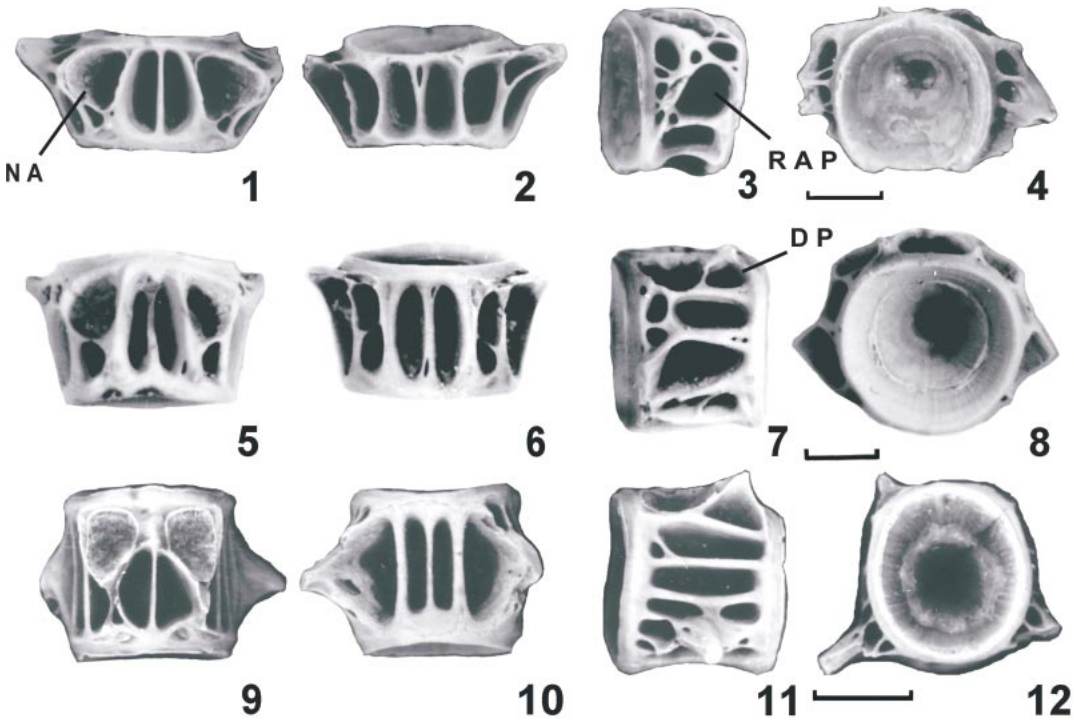

FIGURE 7—Teleost centrum morphoseries IIB-2. *1–4*, specimen TMP 93.93.32, anterior precaudal centrum in: *1*, dorsal; *2*, ventral, *3*, lateral, and *4*, anterior views. *5–8*, specimen TMP 93.93.28, mid-precaudal centrum in *5*, dorsal; *6*, ventral; *7*, lateral; and *8*, posterior views. *9–12*, specimen TMP 2000.22.1 posterior precaudal centrum in: *9*, dorsal; *10*, ventral; *11*, lateral, and *12* anterior views. Abbreviations: D P, dorsal process; N A, neural arch articular pit; R A P, rib articular pit. Scale bars equal one mm.

precaudal centra of *Hiodon* in the presence of shallow neural arch pits that are oval in shape, and rib articular pits that are similar in size and position relative to the transverse process. *Hiodon tergisus*, the mooneye, has centra similar to those of morphoseries IIB-1 in having a loose network of bone on the ventral surface of the centrum. In *Hiodon alosoides*, the goldeye, a single mid-ventral pit is present on all but the first two or three centra. The precaudal centra of *Hiodon* differ from the centra of morphoseries IIB-1 in that the neural arch articular pits are shorter, the rib articular pit does not reach the neural arch articular pit and a distinct fossa is present between the rib articular pit and the neural arch articular pit. Also, in the extant *Hiodon* and the fossil hiodontid *Eohiodon* this fossa is subdivided by a prominent mid-lateral ridge (Wilson, 1977). Thus, morphoseries IIB-1 is distinct from any of the later members of the Hiodontidae.

Morphoseries IIB-2
Figure 7.1–7.12

Material examined.—TMP 89.1.66 (L1105), seven; TMP 93.93.24 (L1105), one; TMP 93.93.25(L1105), three; TMP 93.93.30 (L1109), fifteen; TMP 93.93.28 (L1109), fifteen; TMP 93.93.32 (L1109), fourteen; TMP 2000.22.1 (L1109), four; TMP 93.93.33 (L1110), one; TMP 93.93.29 (L1111), one; TMP 93.93.31 (L1112), thirteen; TMP 93.93.27 (L1112), four; TMP 93.91.28 (L1101), one.

Description.—Precaudal centra amphicoelous; neural arch articular pits shallow; a pair of deep fossae present dorsally, separated by a sharp mid-dorsal ridge (Fig. 7.1, 7.5, 7.9); mid-ventral ridge present (Fig. 7.2, 7.6, 7.10).

Anterior precaudal centra (Fig. 7.1–7.4) circular in end view (Fig. 7.4) but slightly wider than high; centrum shorter than wide; parapophyses laterally directed, long; neural arch articular pit triangular, shallow, extending nearly full length of centrum, lateral corner of neural arch articular pit extending onto parapophysis (Fig. 7.1); pair of deep fossae separated by sharp mid-dorsal ridge, separating neural arch articular pits; rib articular pit deep, circular, located posterior to parapophysis, not reaching neural arch pit (Fig. 7.2); two pairs of deep fossae present ventrally, separated from one another by a mid-ventral ridge and a pair of parasagittal ridges; medial pair of fossae smaller than lateral pair of fossae (Fig. 7.3).

Intermediate centra (Fig. 7.5–7.8) circular in end view (Fig. 7.8) with neural arch articular pits about half length of centrum, separated by mid-dorsal fossae (Fig. 7.5); dorsally-extending parasagittal processses present on either side of mid-dorsal fossa posterior to neural arch articular pits (Fig. 7.6); parapophyses reduced to short flange on antero-ventral edge of centrum (Fig. 7.8); rib articular pits distinct (Fig. 7.7).

Posterior precaudal centra (Fig. 7.9–7.12) higher than wide (Fig. 7.12); neural arch articular pits circular, less than half length of centrum, contacting each other at midline anterior to pair of mid-dorsal fossae (Fig. 7.9); short, dorsally-extending parasagittal processses present on either side of the mid-dorsal fossa posterior to the neural arch articular pits (Fig. 7.11); parapophyses elonate, ventrally directed (Fig. 7.12); rib articular pits not distinct; space between parapophyses and neural arch articular pits divided into two deep fossae by mid-lateral ridge (Fig. 7.11); usually two deep fossae present ventrally between parapophyses, separated from each other by mid-ventral ridge (Fig. 7.10), although the latter sometimes reduced or lost leaving a single mid-ventral fossa.

Discussion.—The centra described here as anterior precaudal and posterior precaudal centra are combined in a single morphoseries because of the shared features in the pattern of neural arch articular pits, and the similar pattern of fossae and ridges dorsally and ventrally, and because they are bridged by centra

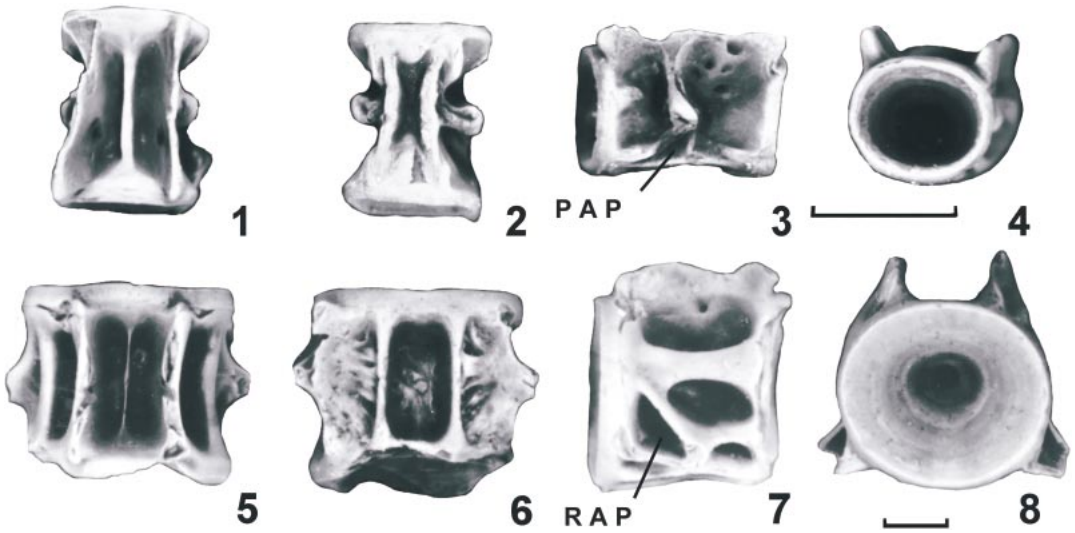

FIGURE *8*—Teleost centra of group IIIA. *1–4*: morphoseries IIIA-1. Specimen TMP 97.19.5 in: *1,* dorsal; *2,* ventral; *3,* lateral; and *4,* anterior views. *5–8*: morphoseries IIIA-2. Specimen TMP 93.93.93 in: *5,* dorsal; *6,* ventral; *7,* lateral; and *8,* anterior views. Abbreviations: P A P, parapophyseal articular pit; R A P, rib articular pit. Scale bar equals one mm.

with a transitional morphology. As well, they have a similar distribution among the localities sampled. The taller centra with reduced parapophyses are identified as posterior precaudal centra because they approach the caudal centrum morphology in their proportions. However, they may prove to be more anterior in the column.

The centra of morphoseries IIB-2 share with hiodontids the presence of shallow neural arch articular pits and deep rib articular pits posterior to the paraphyses. However, in proportions and presence of long, laterally directed parapophyses, the anterior precaudal centra of morphoseries IIB-2 are generally similar to the mid-dorsal centra of morphoseries IIA-1. In addition to the difference in the depth of the neural arch articular pits, the anterior precaudal centra of morphoseries IIB-2 differ from morphoseries IIA-1 in the consistent presence of mid-dorsal and mid-ventral ridges, which are never present in morphoseries IIA-1. As well, the posterior precaudal centra of morphoseries IIB-2 are unlike any of the centra in morphoseries IIA-1 in the presence of parasagittal processes from the posterior end of the centrum, and in that the neural arch articular pits are restricted to the anterior end of the centrum and meet each other at the mid-line.

While the presence of fused parapophyses and an autogenous neural arch is similar to the condition in osteoglossomorphs, some features of morphoseries IIB-2 are more similar to the precaudal centra of ostariophysans and suggest that these centra are from a member of that group. These include the presence of parasagittal processes on the posterior ends of the centrum, and the presence of neural arch bases restricted to the anterior end of the centrum on at least part of the column. Morphoseries IIB-2 is similar to the centra of the gonorhynchid *Notogoneus montanensis* from the Two Medicine Formation of Montana (Grande and Grande, 1999) in the presence of long parapophyses on the anterior precaudal centra and posterior precaudal centra with a series of distinct fenestrae and ridges along the side of the centrum. The neural arches appear to be fused to the centrum in that specimen, although since the specimen is articulated, they may be separate but preserved in place. Among extant gonorhynchids, *Aethalionopsis* has autogenous nerual arches (Proyato-Ariza, 1996). Thus, although the identity of the fish from which morphoseries IIB-2 was derived remains uncertain, both osteoglossomorph and ostariophysan relationships are possible.

Teleost centrum supergroup III

Description.—Precaudal centra with fused neural arch, neural arch base elongate, pierced by one or more foramina.

Discussion.—Fusion of the neural arch and the centrum is a feature present in many derived teleosts, including the percopsiforms, aulopiforms, and acanthomorphs, as well as advanced members of some other clades, including certain clupeomorphs, osmeroids, umbrids, ostariophysans and anguilliforms. The precaudal centra from the Dinosaur Park Formation of supergroup III can be subdivided into groups representing two grades according to the presence or absence of derived acanthomorph features.

Group IIIA

Description.—Mid-dorsal ridge present between neural arch bases.

Discussion.—Precaudal centra with a mid-dorsal ridge between the bases of the neural arch (Fig. 8.1, 8.5), is a feature present in two morphoseries of supergroup III. No evidence for the acanthomorph features of an axis with a tripartite articular surface or for zygapophysial articulations is present in either of these two morphoseries. Also, the parapophyses are located low on the ventro-lateral edges of the centrum, in contrast to the condition in at least the anterior precaudal centra of acanthomorphs, where the ribs articulate high on the centrum or on the neural arch.

Morphoseries IIIA-1
Figure 8.1–8.4

Material examined.—TMP 95.182.41 (BB 86), one; TMP 95.145.8 (BB 51), two; TMP 95.181.41 (BB 104), eight; TMP 95.143.20 (BB 135), one; TMP 95.151.30 (BB 137), one; TMP 2000.22.11 (L1101), five; TMP 2000.22.9 (L1102), one; TMP 97.19.7 (L1108), two; TMP 95.157.52 (L1108), five; TMP 2000.22.10 (L1108), eight; TMP 97.19.5 (L1115), one.

Description.—Precaudal centra oval in end view, wider than high (Fig. 8.4), longer than wide; neural arch base elongate, extending full length of centrum (Fig. 8.1); mid-dorsal ridge between neural arch bases narrow; parapophyses autogenous, parapophysis articular pits located midway along side of centrum near ventro-lateral edge (Fig. 8.3); rounded ridge extending vertically from dorsal margin of parapophyseal pit to neural arch

(Fig. 8.3); sides of centrum anterior and posterior to this ridge without distinct ridges or pits, thus cone-shaped in lateral view; ridge along antero-ventral edge of centrum extending from anterior edge of centrum to parapophyseal articular pit; mid-ventral pit present, bordered by low rounded ridges (Fig. 8.2), ridges ending in low, ventrally directed processes posteriorly; comparable processes formed by posterior tip of neural arch present on posterodorsal end of centrum.

Serial variation present in size of parapophyseal articular pit and length of the vertically oriented ridge extending dorsally from parapophyseal pit to base of neural arch; on anterior precaudal centra, parapophyseal pits covering much of lateral surface of centrum and reaching nearly to neural arch so vertical ridge extending from neural arch to parapophysis articular pit short; more posteriorly, parapophysis articular pit restricted to ventral edge of centrum, vertical ridge elongate (Fig. 8.3). In posteriormost centra, vertical ridge extending to ventral edge of centrum; flange extending from ridge to antero-ventral edge of centrum.

Discussion.—Morphoseries IIIA-1 can be identified as from a teleost of intermediate grade on the basis of the group III features of a fused neural arch with a foramen passing through the base of the neural arch. However, the affinities of the teleost from which this morphoseries is derived is unknown.

Morphoseries IIIA-2
Figure 8.5–8.8

Material examined.—TMP 90.67.38 (L1113), twenty-eight; TMP 93.93.84 (L1102), nine; TMP 93.92.17 (L1102), four; TMP 93.93.91 (L1109), twenty-two; TMP 93.93.92 (L1109), six; TMP 93.93.88 (L1109), twelve; TMP 93.93.80 (L1109), twenty-five; TMP 93.93.82 (L1110), twelve; TMP 93.93.78 (L1111), three; TMP 93.93.81 (L1111), three; TMP 93.93.77 (L1111), fourteen, TMP 93.93.76 (L1112), nine; TMP 93.93.83 (L1112), thirty-one; TMP 93.93.79 (L1112), twenty-three; TMP 93.93.90 (L1101), ten; TMP 93.93.86 (L1101), seven; TMP 93.93.89 (L1105), twenty-seven; TMP 89.1.54 (L1105), eleven; TMP 93.93.87 (L1103), five; TMP 93.93.93 (L1104), four; TMP 93.91.27 (L1101), thirty-seven.

Description.—Precaudal centra with parapophyses fused to centrum; mid-precaudal centra subtriangular in end view (Fig. 8.8), with neural arch bases located close together and parapophyses widely separated and located ventrolaterally on centrum; neural arch bases extending full length of centrum (Fig. 8.5, 8.7); parasagittal processes absent; parapophyses short, extending ventro-laterally, located at anterior end of centrum; rib articular pit a short, sub-circular opening about half length of centrum (Fig. 8.7); parapophysis forms anterior and ventral margin of rib articular pit; lateral surface with stout rounded ridge running between ends of centrum midway between neural arch base and parapophysis (Fig. 8.7); mid-ventral pit present ventrally; mid-ventral pit deep, bordered by two sharp parasagittal ridges (Fig. 8.6), shallow fossa present between parasagittal ridges and transverse processes, crossed by series of buttresses converging on base of transverse process.

Discussion.—The centra of morphoseries IIIA-2 are similar to the centra of morphoseries IIIA-1 in the presence of a mid-dorsal ridge between the neural arch bases, but differ in that parapophyses are fused to the centrum in IIIA-2 but autogenous in IIIA-1. No processes extend from the posterior end of the centrum either dorsally or ventrally in morphoseries IIIA-2 but they are present in morphoseries IIIA-1, and a longitudinally oriented ridge is present along the side of the centrum in morphoseries IIIA-2 but absent in IIIA-1. Morphoseries IIIA-2 differs from acanthopterygian centra in that zygosphene-zygantrum articulations are absent. No evidence for the presence of an atlas with a tripartite anterior articular surface was found.

The centra of morphoseries IIIA-2 resemble centra from the Hell Creek Formation attributed to *Palaeolabrus montanensis* by Estes (l969). Both have a subtriangular shape, neural arch bases and parapophyses fused to the centrum, and rib articular pits located at the ventro-lateral corner of the centrum. Also, both are of relatively large size. Morphoseries IIIA-2 is represented by large centra, up to one centimeter in diameter. However, tooth-bearing elements like those identified as *Palaeolabrus* by Estes (1969) are absent in the Dinosaur Park Formation.

Group IIIB

Description.—Precaudal centra with zygopophyseal articulations, mid-dorsal ridge between neural arch bases absent; parapophyses absent on anterior dorsal centra; ribs articulating in shallow pit on lateral surface of centrum; the rib articular pit located on neural arch or high on centrum. Atlas centrum with tripartite anterior articular surface and with autogenous neural arch; parapophysis and parapophyseal articular pit absent.

Discussion.—The presence of zygopophyseal articulations between the centra, formation of vertebral facets for the exoccipitals on the atlas, and ribs articulating in shallow pits on the lateral surface of the centrum are features present in acanthomorphs, with the first of these features being considered a derived feature of the group by Rosen (1985). Thus the centra included in group IIIB can be identified as those of acanthomorphs.

Morphoseries IIIB-1
Figure 9.1–9.5, 9.11–9.20

Material examined.—TMP 86.195.8 (BB104), one; TMP 86.196.28 (BB104), one; TMP 86.197.23 (BB104), one; TMP 86.242.59 (BB104), three; TMP 86.242.63 (BB104), three; TMP 87.19.38 (BB104), three; TMP 86.32.61 (BB 102), one; TMP 86.53.14 (BB 102), three; TMP 86.8.84 (BB 102), four; TMP 86.58.28 (BB 102), one; TMP 86.184.34 (BB108), two; TMP 86.19.56 (BB 54), two; TMP 86.21.65 (BB 54), one; TMP 86.20.50 (BB 54), two; TMP 86.22.57 (BB 54), one; TMP 86.45.63 (BB 54), four; TMP 86.44.19 (BB 54), four; TMP 86.41.71 (BB 54), one; TMP 86.19,63 (BB 54), two; TMP 87.4.26 (BB 54), twelve; TMP 87.4.27 (BB 54), seven; TMP 86.44.18 (BB 54), three; TMP 86.19.66 (BB 54), two; TMP 86.41.51 (BB 54), one; TMP 86.60.28 (BB 54), seven; TMP 86.45.66 (BB 54), ten; TMP 86.21.59 (BB 54), three; TMP 86.10.66 (BB 86), one; TMP 86.23.77 (BB 86), one; TMP 87.37.60 (BB 86), one; TMP 86.37.62 (BB 86), three; TMP 86.43.50 (BB 86), one; TMP 86.43.51 (BB 86), one. TMP 86.5.27 (BB 31), one; TMP 86.5.38 (BB 31), one; TMP 87.30.36 (BB106), one; TMP 86.239.23 (BB 106), one; TMP 86.214.16 (BB 51), one; TMP 86.215.23 (BB 51), one; TMP 86.218.35 (BB 51), one; TMP 86.219.39 (BB 51), one; TMP 87.22.12 (BB 117), two; TMP 88.212.37 (BB 120), four; TMP 88.211.54 (BB120), four; TMP 87.158.31 (BB 78), two; TMP 86.238.23 (BB94), one; TMP 93.93.61 (L1102), six; TMP 93.93.64 (L1110), three; TMP 93.93.71 (L1111), thirty-two; TMP 93.93.70 (L1111), four; TMP 93.93.63 (L1112), one; TMP 93.93.68 (L1101), seventeen; TMP 93.93.72 (L1101), three; TMP 93.93.67 (L1101), ten; TMP 93.91.21 (L1101), thirty-four; TMP 93.93.73 (L1101), five; TMP 93.93.62 (L1103), two; TMP 93.93.65 (L1103), four; TMP 89.1.57 (L1105), twenty-two; TMP 93.93.59 (L1105), one; TMP 93.93.60 (L1105), sixteen; TMP 93.93.74 (L1105), twenty-four; TMP 93.93.74 (L1105), five; TMP 93.93.69 (L1108), two; TMP 90.48.10 (L1106), nine.

Description.—Atlas centrum (Fig. 9.1–9.5) wedge-shaped in lateral view, with dorsal edge widest (Fig. 9.3); size of anterior surfaces variable, facets for exoccipital may be equal in size to basioccipital articular surface and contact one another or may be smaller and separate from one another (Fig. 9.4); mid-ventral pit usually present, bordered by bundles of antero-posteriorly directed fibers.

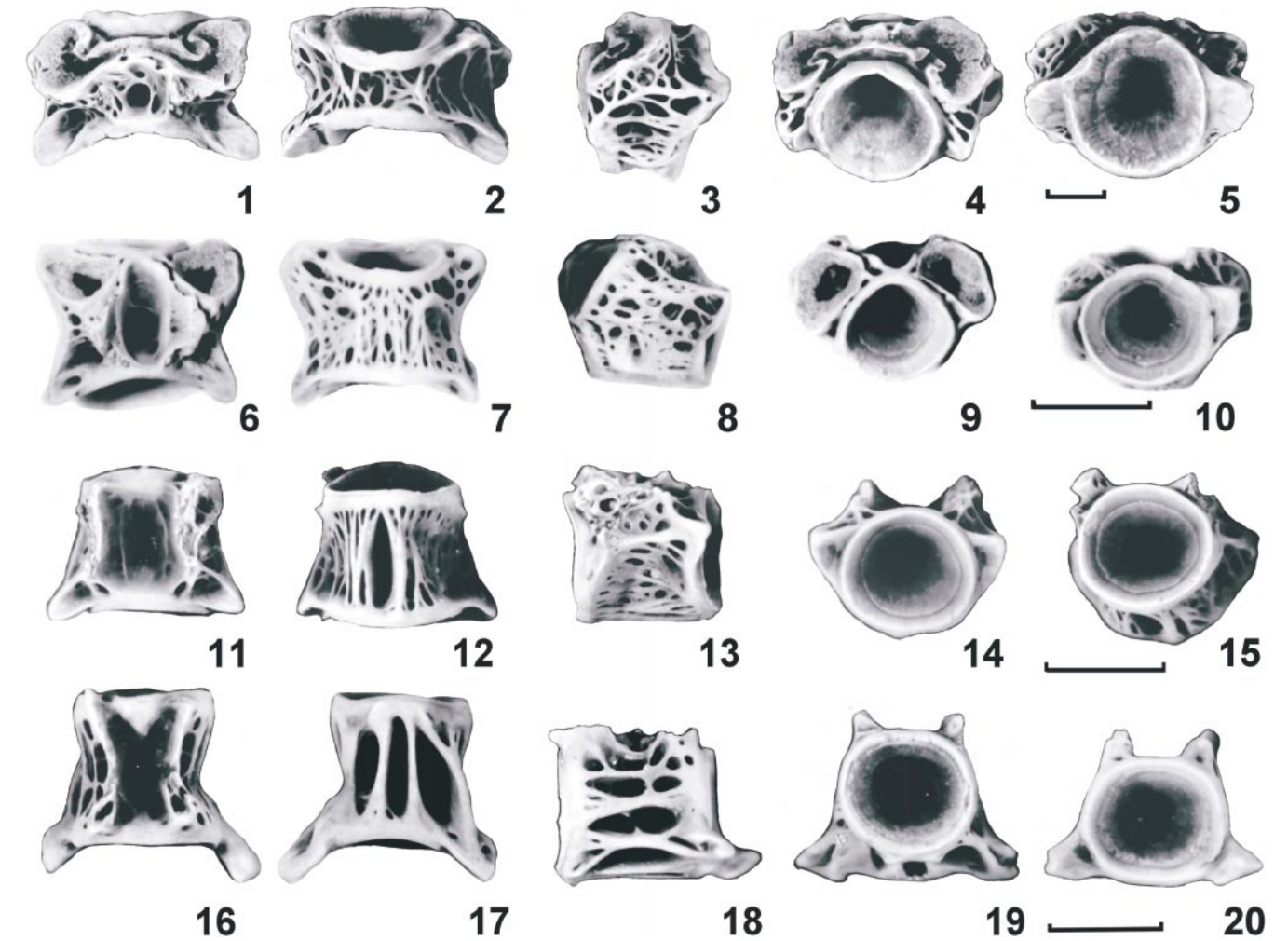

FIGURE 9—Teleost centra of group IIIB. *1–5*, specimen TMP 95.177.68, atlas of teleost centrum morphoseries IIIB-1 in: *1*, dorsal; *2*, ventral; *3*, lateral; *4*, anterior, and *5*, posterior views. *6–10*, specimen TMP 2000.22.2, atlas of teleost centrum morphoseries IIIB-2 in: *6*, dorsal, *7*, ventral; *8*, lateral; *9*, anterior, and *10*, posterior views. *11–15*, specimen TMP 93.93.68, anterior precaudal centrum of teleost centrum morphoseries IIIB-1 in: *11*, dorsal; *12*, ventral; *13*, lateral; *14*, anterior; and *15*, posterior views. *16–20*, specimen TMP 93.116. *12*, posterior precaudal centrum from teleost centrum morphoseries IIIB-1 in: *16*, dorsal; *17*, ventral; *18*, lateral; *19*, anterior, *20*, posterior views. Scale bar equals one mm.

Anterior-precaudal centra (Fig. 9.11–9.15) with postzygapophyseal processes on dorso-lateral edge of posterior end of centrum and corresponding articular surface on anterior edge of centrum (Fig. 9.13); mid-ventral pit present, bordered by two bundles of antero-posteriorly directed bony fibers (Fig. 9.12); parapophyses or parapophyseal articular pits absent.

Mid-precaudal and posterior-precaudal centra (Fig. 9.16–9.20) with zygopophyses hypertrophied to form parapophysial process, located at or below middle of centrum; deep fossa present between parapophysis and mid-ventral fossa (Fig. 9.17).

Discussion.—The centra of morphoseries IIIB-1 can be identified as those of an acanthomorph on the basis of the presence of a specialized atlas with a tripartite anterior articular surface, the absence of parapophyses on the anterior precaudal centra with the ribs articulating in shallow pits on the side of the centra, and zygopophyseal articulations between the anterior precaudal centra.

Morphoseries IIIB-2
Figure 9.6–9.10.

Material examined.—TMP2000.22.4 (L1101), seven; TMP 2000.22.3 (L1102), three; TMP 90.33.70 (L1104), two; TMP 2000.22.8 (L1108), thirteen centra; TMP 2000.22.2 (L1111), one; TMP 2000.22.7 (L1114), four; TMP 2000.22.6 (L1115), one.

Description.—Atlas centrum (Fig. 9.6–9.10) elongate, without mid-ventral pit (Fig. 9.7); sub-rectangular in lateral view (Fig. 9.8). Anterior precaudal centra (not figured) without mid-ventral pit.

Discussion.—A distinct acanthomorph atlas which is relatively more elongate than in teleost centrum morphoseries IIIB-1 and is without mid-ventral pit is recognized as a second distinct kind of acanthomorph centrum. The anterior precaudal centra that are included with the atlas in this morphoseries are united on the basis of a reduced or missing mid-ventral pit. No posterior precaudal centra can be clearly associated with the anterior-precaudal centra. It is likely that the centra of this region of morphoseries 1 and morphoseries 2 cannot be distinguished from one another.

DISCUSSION

Pre-Cretaceous freshwater fish assemblages in North America are dominated by non-teleosts, while those of the Paleocene are made up primarily of teleost species belonging to modern families (Grande and Grande, 1999). Thus, understanding Late

Cretaceous freshwater teleost assemblages is critical to understanding patterns of teleost evolution. The teleost genera that are currently recognized in the Dinosaur Park Formation are the elopomorphs *Paratarpon*, *Paralbula*, and *Coriops*, the osteoglossomorph *Cretophareodus*, and the esocoids *Oldmanesox* and *Estesesox*. In addition, dorsal fin spines indicate the presence of an acanthomorph.

The fifteen different morphoseries described here demonstrate that a much greater level of diversity was present. Most of these morphoseries can be placed into established taxonomic groups at least at a high level. The three morphoseries comprising group IA can be confidently attributed to the Elopomorpha. Within this group, morphoseries IA-1 includes the centra of *Paratarpon*, and morphoseries IA-2 can be tentatively identified as *Paralbula*. Morphoseries IA-3 cannot be reasonably attributed to any elopomorph previously known from these beds. Group 1B can be identified as salmoniform. With two salmoniforms previously recognized in these beds the level of diversity of salmoniforms indicated by the precaudal centra is equivalent to the level of diversity indicated by jaw elements. Morphoseries IC-1 is identified as a member of the Clupeomorpha on the basis of similarity with extant clupeomorphs. Clupeomorphs have not previously been recognized in the Late Cretaceous non-marine beds of North America, although they are present in Tertiary beds and in marine deposits of late Cretaceous age. The characters that define supergroup II are typical of osteoglossomorphs among modern teleosts, although the level of confidence with which the morphoseries can be placed within the Osteoglossomorpha varies. Morphoseries IIB-1 can be identified as from a member of the Hiodontidae on the basis of shared derived features of the atlas centrum. This is the first Cretaceous record of this clade in North America. Morphoseries IIA-1 can be identified as an osteoglossomorph on the basis of the similarity of the parapophyses with those of *Phareodus*, and morphoseries IIA-2 is identified as an osteoglossomorph on the basis of similarities shared with the anterior precaudal centra of morphoseries IIA-1. The centra of morphoseries IIA-3 generally agree with the centra of osteoglossomorphs, but the atlas centrum is unlike this element in other members of the group. The centra of morphoseries IIB-2 have a mixture of osteoglossomoph and ostariophysan features. Ostariophysans have not been reported in the Dinosaur Park Formation, but are known in the Two Medicine Formation (Grande and Grande, 1999), which is, in part, stratigraphically equivalent to the Dinosaur Park Formation. Supergroup III includes centra of derived teleosts. Acanthomorphs, represented by morphoseries IIIB-1 and morphoseries IIIB-2, can be identified on the basis of the atlas centrum and the presence of zygapophyses between the precaudal centra, among other features. Group IIIA includes teleosts of intermediate grade. The affinities of the two morphoseries in this group are unknown.

The presence of hiodontids and clupeomorphs in the Dinosaur Park Formation increases the similarity of the teleost assemblage of the mid-Campanian and that of the Paleocene. Significant differences remain in the diversity of ostariophysans in the assemblage. Ictalurids and percopsids, both of which are present in the Paleocene of western North America (Wilson, 1980; Lundberg, 1975), remain unknown in the late Cretaceous.

To some extent the presence of a high level of diversity of teleosts in the Dinosaur Park Formation may be a result of the presence of two assemblages differing in the relative abundance of taxa present. One assemblage is from the fluvial beds of the Dinosaur Park Formation below the Lethbridge Coal Zone, and the second is from mud-filled channels preserved within the Lethbridge Coal Zone (Table 1). The first assemblage is dominated by morphoseries IIA-1 (an osteoglossomorph, possibly *Cretophareodus*), with successively less abundant elements in the assemblage being centra of IIIB-1 (an acanthomorph), IB-1 (a salmoniform), IB-2 (a salmoniform), IIB-1 (a hiodontid), IIA-2 (an osteoglossomorph), and IIIA-2 (a teleost of intermediate grade). Isolated centra of morphoseries IA-1 (*Paratarpon*) were collected as part of surface collections but were not recovered in screenwashed samples. The remaining morphoseries were not encountered in this setting in the Dinosaur Provincial Park area, although morphoseries IA-2 and IA-3 (both elopomorphs), and IIIB-2 are rare members of the teleost assemblage preserved in fluvial beds in the Manyberries area.

The second assemblage is preserved in mud-filled paleochannels in the Lethbridge Coal Zone of the Manyberries area of southern Alberta. The dominant morphoseries in the assemblage are IIIA-2 (a teleost of intermediate grade), IIIB-1 (an acanthomorph), and IIA-2 (an osteoglossomorph). Morphoseries IIA-1, the osteoglossomorph that is the most abundant teleost in the assemblage preserved in the fluvial beds, occurs in this setting, but in much reduced abundance compared to fluvial-dominated localities. Morphoseries IC-I (a clupeomorph), IIA-3 (teleost of uncertain relationships), and IIB-2 (possible ostariophysan) were found only in this paleoenvironmental setting.

The presence of two distinct assemblages may be a reflection of regional biogeographic patterns or of a difference in the habitat preference of individual kinds of teleosts. A biogeographic explanation is possible because the localities in the Lethbridge Coal Zone occur in an area about 200 km South of the Dinosaur Provincial Park localities. A difference in habitat preference of different kinds of teleost is a possible explanation because these assemblages are found in different environments of deposition. To test the hypothesis that the differences are primarily a result of differences in habitats, two groups of localities from different environments of deposition in the same geographic area were compared. In the Manyberries area of southern Alberta, localities represent both environments of deposition. The three localities preserved in fluvial beds contain a teleost assemblage that is similar in the pattern of relative abundance of the common taxa to the geographically removed, but environmentally similar beds in Dinosaur Provincial Park (Table 1). Thus the presence of two groups of fishes with different, largely non-overlapping, habitat preferences is accepted as the most likely explanation for two teleost assemblages in the Dinosaur Park Formation. However, four morphoseries are present in both environments of deposition in the Manyberries area, but absent in Dinosaur Park, so a biogeographic component may also be present. These alternate hypotheses will be further tested by the study of material from equivalent beds from Montana and localities further south.

The paleoecological complexity of teleost assemblages in the Dinosaur Park Formation suggests that a full understanding of the paleoecology of teleosts in this formation will only be possible with an understanding of assemblages preserved in a variety of environments of deposition. This is likely also the case in other areas and stratigraphic intervals. At present, our understanding of the taxonomic composition of teleost assemblages preserved in lacustrine paleoenvironments is much greater than our understanding of the assemblages present in fluvial beds. Study of the material preserved in fluvial deposits will contribute to a more complete understanding of the paleoecology and evolutionary history of the group, even though the material preserved in these deposits generally consists of disarticulated, isolated elements.

As well as contributing to our understanding of paleoenvironmental patterns within the Dinosaur Park Formation, the

diversity of teleosts contributes to our understanding of biogeographic patterns in the Cretaceous. Of particular interest is the presence of a hiodontid in the assemblage. This is the first Cretaceous record of this group in North America, although the related lycopterids and hiodontids are present in Lower Cretaceous beds in Asia. Since the group appears to have been restricted to freshwater environments throughout its history, its presence in both Asia and North America indicates that interchange between these areas via a fully non-marine route was possible by the mid-Campanian at least. With increased information on the teleost precaudal centra from other late Cretaceous assemblages in North America it may be possible to use teleost fish assemblages to define biogeographic patterns within North America during the late Cretaceous.

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