Cenozoic ichthyofaunas of the North American Western Interior, and palaeoclimatic and palaeoenvironmental reconstructions

by

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ABSTRACT

The Cenozoic fluvial fish faunas of the North American Western Interior are poorly known in comparison to better preserved lake ichthyofaunas, such as that of the Green River Formation. However, fluvial fishes are typically represented by disarticulated material, which is more commonly preserved than articulated specimens, and floodplain riverine environments correspond to areas of maximal taxonomic diversity in modern freshwater environments. Therefore, disarticulated fluvial material should preserve a greater number of taxa than articulated lacustrine material, allowing a more complete understanding of the formation of the North American modern fish fauna since the Late Cretaceous.

The freshwater fishes of four North American Western Interior assemblages are here described. These assemblages were recovered from the southern Saskatchewan mid-Miocene Wood Mountain and Eo–Oligocene Cypress Hills formations, as well as the middle and early Eocene Bridger and Wasatch formations of Wyoming. The diversity of these assemblages is documented and forms the basis of palaeoclimatic and palaeoenvironmental reconstructions, founded on the specific tolerance ranges of the fish taxa present.

Both Canadian assemblages are highly diverse, typical of lowland, well-oxygenated and varied floodplain environments, and indicate warm-temperate to subtropical climates at time of deposition. The Wyoming assemblages, although also indicative of warm environments, are relatively less diverse.

However, these indicate that the early Paleogene ichthyofauna of North America was similar to that of the Late Cretaceous.

Based on the comparison of the assemblages described in this thesis with one another and with other described assemblages, the evolution of the North American freshwater fish fauna through the Cenozoic is reconstructed, from the Mesozoic to the present. The turnovers that led to the formation of the modern fauna appear to have been relatively uninfluenced by the K-Pg transition, but to have occurred in two phases instead, one in the mid-Paleogene and the other in the late Neogene. These coincide with the increase of seasonality in North America between the middle and late Eocene, and the gradual cooling of climates leading to the Plio-Pleistocene glaciations, respectively.

PREFACE

Most of this thesis has been or will be published as separate journal articles. Additionally, all data chapters have formed the basis of abstracts that have been published or accepted for publication in conference proceedings.

A slightly abridged version of Chapter 2 has been published as Divay, J. D., and A. M. Murray. 2013. A mid-Miocene ichthyofauna from the Wood Mountain Formation, Saskatchewan, Canada. Journal of Vertebrate Paleontology 33:1269–1291. This chapter also formed the basis of a conference abstract as Divay, J. D., and A. M. Murray. 2012. The ichthyofauna, palaeoenvironment and palaeoclimate of the mid-Miocene Wood Mountain Formation, Saskatchewan, Canada. Society of Vertebrate Paleontology 72nd Annual Meeting, Raleigh, North Carolina, Program and Abstracts 2012:87.

Chapter 3 of this thesis has been accepted for publication and is currently in press as Divay, J. D., and A. M. Murray. The late Eocene–early Oligocene ichthyofauna from the Eastend area of the Cypress Hills Formation, Saskatchewan, Canada. Journal of Vertebrate Paleontology. The chapter also formed the basis for a conference abstract, as Divay, J. D., and A. M. Murray. 2013. Ichthyofauna of the Cypress Hills Formation (late Eocene–early Oligocene), Eastend Area, Saskatchewan, Canada. Society of Vertebrate Paleontology 73rd Annual Meeting, Los Angeles, Program and Abstracts 2013:116.

Chapters 4 and 5 formed the basis of a conference abstract that has been accepted for publication as Divay, J. D., and A. M. Murray. 2014. Fluvial ichthyofaunas of the Wasatch and Bridger Formations (early and early-middle Eocene), Sweetwater County, southwestern Wyoming, U. S. A. Society of Vertebrate Paleontology 74th Annual Meeting, Berlin, 2014: p.x. Additionally, Chapter 4 is in preparation for submission as Divay, J. D., and A. M. Murray. The fishes of the Farson Cutoff Fishbed, Bridger Formation (Eocene), greater Green River Basin, Wyoming, U. S. A. Journal of Vertebrate Paleontology. Chapter 5 is in preparation for submission as Divay, J. D., and A. M. Murray. An early Eocene fish fauna from the Bitter Creek area of the Wasatch Formation of southwestern Wyoming, U. S. A. Journal of Vertebrate Paleontology.

In all cases, A. M. Murray's contribution was supervisory and editorial. L. Ditschun and H. Stewart provided assistance with the ammonium chloride coating of fossils prior to photography for Chapter 3, and Chapters 4 and 5, respectively.

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CHAPTER 1—GENERAL INTRODUCTION

The importance of palaeoichthyology to other research disciplines

INTRODUCTION

Although fresh and salt waters represent approximately 1 and 70% of the Earth's surface, respectively, there are 13,000 extant freshwater fishes known, as compared to 16,000 marine species (Lévêque et al., 2008), therefore representing 45 and 55% of the total number of known fish species, respectively (Fig. 1.1). The disproportionate variety of freshwater fishes implies a substantial diversity of adaptations to a range of environmental conditions found in freshwater habitats, due to the greater number of geographical barriers in freshwaters compared to marine environments. Different fishes are found in different areas, depending on environmental conditions and dispersal opportunities. Fishes have been found in any aquatic environment with a pH between 4 and approximately 10, and with salinities below 90‰ (Davenport and Sayer, 1993). Their distribution within this wide range of potentially suitable environments is constrained by the tolerance levels of each individual species (Davenport and Sayer, 1993). Among the most important environmental factors determining which fish species are physiologically capable of occupying an area are temperature, salinity and oxygenation level.

Temperature

Most fishes are poikilothermic ectotherms, and even those capable of partial endothermy have internal temperatures related to external conditions (Davenport and Sayer, 1993). As a result, the physiology of fishes is influenced by environmental temperatures to a great extent, and taxa adapted to specific temperatures will incur increased costs of maintenance and lower muscle performance rates outside of their natural temperature ranges (Davenport and Sayer, 1993). Therefore, most fishes are physiologically constrained to particular temperature ranges, and adapt their lifestyles and activity levels to a particular environment (Davenport and Sayer, 1993). Other species thermoregulate behaviourally, by moving from one environment to another in order to actively select a particular temperature (e.g., Neverman and Wurtsbaugh, 1994). Migratory behaviours may represent extreme cases of behavioural thermoregulation, although other factors such as food availability may also be related to these behaviours (Davenport and Sayer, 1993).

Salinity

The relative productivity of marine and fresh waters, and therefore food availability in these environments, has also been suggested as the main cause leading to the evolution of diadromous fish migrations (Gross et al., 1988). Sudden changes in salinities are fatal to most fishes, as an increase in salinity requires the fish to deal with salt intake and water loss, while a decrease in salinity requires the fish to deal with water intake and loss of salts (Davenport and Sayer, 1993). Euryhaline fishes must therefore be capable of pumping salt ions both in and out of their bodies and of regulating the permeability of their gills in order to survive changes in salinities. Although some fishes, such as the cyprinodontiform *Fundulus parvipinnis* Girard, 1854, the Californian killifish, are capable of occupying a wide diversity of salinities ranging from fresh waters to hypersaline conditions (Feldmeth and Waggoner, 1972), most fish taxa are restricted to a narrow range of salinities corresponding to the usual conditions of their natural habitats. Taxa adapted to extreme and rapid changes in salinity tend to be restricted in their activity levels and tolerance to low oxygen levels because of the reduced permeability of their gills, a trade-off sometimes termed the osmorespiratory compromise (Davenport and Sayer, 1993). In contrast, many diadromous species, such as migratory salmonids, acclimate to different salinities over relatively long periods of time through profound physiological alterations, enabling them to maintain high activity levels during their migration (Davenport and Sayer, 1993).

Oxygenation

Several freshwater fishes have evolved the ability to breathe air, especially in swamps and other areas where dissolved oxygen levels are reduced because of stagnant waters, high temperatures and high organic loading (Davenport and Sayer, 1993). This ability is emphasized in amphibious forms, some of which are capable of aestivating for months, hundreds of meters away from the nearest body of water (e.g., Neill, 1950). Other amphibious fishes may not be able to tolerate such long periods of emersion, but can move over land, and at least one family (the Anabantidae, or climbing perches) is known to climb over emerged obstacles (Davenport and Abdul Matin, 1990). Therefore, certain taxa may be constrained in their distribution to higher water qualities, others have evolved alternative adaptations enabling them to occupy less well oxygenated areas, and yet others have the capacity to move over land in order to reach favourable environments.

Given that different “fishes”—used here in the paraphyletic sense as in Nelson (2006), including all non-tetrapod craniates—have adapted to environmental conditions through widely different strategies, the distribution of specific taxa should correspond to particular environmental conditions depending on their tolerance levels. Certain environmental conditions of an area can therefore be determined from its fish fauna, as the overlap in environmental preferences of the fishes found there should correspond to the conditions of the area. The abiotic and biotic conditions that can be inferred from the presence of fishes are here summarized.

FISHES AS INDICATORS OF ABIOTIC ENVIRONMENTAL CONDITIONS

Temperature

Fishes are metabolically constrained by environmental temperatures, as most forms can only thermoregulate behaviourally (Davenport and Sayer, 1993). Therefore, sedentary species lacking cold-environment adaptations are restricted in the latitudinal extent of their ranges by environmental temperatures. For instance, the ranges of typically warm-water species, such as the bowfin *Amia calva* Linnaeus, 1766, are constrained in their northern-most limits by temperatures (Scott and Crossman, 1973), despite the lack of physical barriers restricting their northward dispersal. Conversely, cold-adapted species are restricted in their latitudinal ranges by the maximal temperatures they can sustain, although the relationship may be more indirect in this case. Many fishes specialised to live in cold environments compensate the slowing effect that low temperatures usually have on the activity levels of ectothermic animals by having higher metabolic rates (Davenport and Sayer, 1993). Higher temperatures would increase these species' activity levels, and therefore their energy requirements, to the point where food availability may constrain them to relatively high latitudes (Davenport and Sayer, 1993). A more direct limitation of cold-adapted fishes to lower temperatures is likely, however, as farmed cold-water species, such as the Arctic charr *Salvelinus alpinus* (Linnaeus, 1758), show signs of stress and poor health above their natural maximal temperatures even in captivity (Quinn et al., 2011). This interpretation is strengthened by the observation that thermal stress resistance varies according to genetic background (Quinn et al., 2011). Therefore, specific fish taxa are indicative of a specific range of temperatures to which they are physiologically adapted. When several taxa co-occur, the overlap of their temperature ranges can be used to estimate the temperature conditions of an area. For example, approximate temperatures can be inferred from a North American locality found to sustain the inconnu *Stenodus leucichthys* (Güldenstädt, 1772), the broad whitefish *Coregonus nasus* (Pallas, 1776), the burbot *Lota lota* (Linnaeus, 1758), and the yellow perch *Perca flavescens* (Mitchill, 1814). *Stenodus leucichthys*, *C. nasus* and *L. lota* are species characteristic of northern latitudes, with ranges reaching the Arctic Ocean (Scott and Crossman, 1973). However, these taxa have different high temperature tolerance levels, as the ranges of both *S. leucichthys* and *C. nasus* do not usually extend far south of the 60th parallel, while *L. lota* can be found as far south as 40°N (Scott and Crossman, 1973). *Perca flavescens* is a relatively warm-water fish, as it is found as far south as the Florida panhandle

(Scott and Crossman, 1973). However, *P. flavescens* is also found slightly north of Great Slave Lake (approximately 61°N), in the Northwest Territories of Canada, at the northern-most limit of their range (Scott and Crossman, 1973). Therefore, a locality with these fish taxa would be inferred to correspond to conditions similar to those found around 60°N, such as those of Great Slave Lake, as the area is cool enough to sustain *S. leucichthys* and *C. nasus*, and warm enough for *P. flavescens*. Great Slave Lake is situated just south of the Arctic treeline, where the summer surface atmospheric isotherm is approximately 12.5°C at most (MacDonald et al., 1998). Therefore, the sampled locality would be likely to have an annual atmospheric temperature maximum slightly above this value.

In addition to limiting ranges, environmental temperatures also constrain growth in a number of fishes. For instance, warm-water species such as the white crappie *Pomoxis annularis* Rafinesque, 1818a grow to their greatest sizes in the warmer parts of their ranges, while adults from relatively cold areas may only reach approximately half these lengths (Scott and Crossman, 1973). Therefore, comparing growth between populations can also be indicative of temperature differences between the ranges of these populations.

Oxygenation

Most freshwater environments are saturated with oxygen (normoxic): flowing water is oxygenated through exchanges with the atmosphere facilitated by turbulence, and standing clear waters may be oxygenated through photosynthetic activity of aquatic vegetation (Davenport and Sayer, 1993). Fish species that are normally found in these water qualities show immediate signs of physiological stress when their environment is hypoxic (Davenport and Sayer, 1993). Other forms have adapted to fluctuations of the oxygen content of their environments through alternative means of maintaining their oxygen uptake. These adaptations include changes in vertical habitat use, as surface waters usually maintain an equal oxygen pressure to that of the atmosphere above it, while lower layers may be hypoxic because of the slow diffusion of oxygen in water (Kramer, 1987), or because of the greater consumption of oxygen by benthic bacteria. This use of surface water layers for their generally higher oxygen content is termed aquatic surface respiration, or ASR (Kramer, 1987). Some fishes are bimodal in their oxygen uptake, in that they are capable of exploiting oxygen dissolved in water as well as atmospheric oxygen through air-breathing (Davenport and Sayer, 1993; Kramer, 1987). These bimodal forms are capable of surviving severely hypoxic or anoxic water conditions, and in some cases, of remaining out of water for several months (e.g., Neill, 1950). When photosynthetic activity causes hyperoxic conditions, however, fish respond by reducing their ventilation rates and remain otherwise unaffected (Davenport and Sayer, 1993).

Therefore, well-oxygenated environments can be exploited by fishes adapted to any oxygen levels, while the absence of forms lacking adaptations to hypoxic conditions characterises lower oxygenation conditions. For example, presence of salmonids can be interpreted as an indication that the environment is normoxic or hyperoxic, as these fishes are among the least tolerant of lower water qualities (Davenport and Sayer, 1993). An area that lacks species restricted to higher oxygenation levels, but possessing taxa such as the ictalurid *Ictalurus punctatus* (Rafinesque, 1818b), the channel catfish, which is known to be capable of ASR (Kramer, 1987), can therefore be interpreted as being hypoxic but not anoxic. Lastly, an environment only populated by bimodal forms, such as *Amia calva* or *Lepisosteus* spp. (gar) that can assimilate atmospheric oxygen in their highly vascularised swimbladder (Scott and Crossman, 1973), can be interpreted as being hypoxic to the point that non-air-breathing forms are unable to exploit it.

Water Clarity

Different fishes may be expected to be found in waters of different murkiness as a consequence of their physiological tolerance levels to variables other than water clarity. For example, a taxon intolerant of low oxygen levels may avoid murky waters with high organic loading, not because of their murkiness, but rather because these may be depleted in oxygen. However, certain taxa have adapted to water clarities, and may be indicative of these conditions.

Visual predators such as *Esox lucius* Linnaeus, 1758 (Northern Pike) will favour clear waters (Scott and Crossman, 1973), and will be indicative of good visibilities. Likewise, nearly all species of *Etheostoma* (darters), as well as several other small percids, such as the logperch *Percina caprodes* (Rafinesque, 1818b), are rarely ever found in murky waters (Scott and Crossman, 1973). This may be at least partly because the benthic invertebrates that they primarily feed on might be scarcer and more difficult for them to detect in turbid environments (Scott and Crossman, 1973).

Conversely, predators relying on senses other than (or in addition to) sight are not indicative of particular clarity conditions. For example, *Amia calva* uses smell as much as sight to detect prey (Scott and Crossman, 1973) and is therefore found in both clear and turbid conditions. Likewise, certain taxa have adapted to poor visibility conditions by developing other senses instead, such as the "tasting" sensory cells abundant on the barbels of ictalurid catfishes (Scott and Crossman, 1973). Although these fishes have adapted to rely less on their eyesight, implying that they would not be restricted to waters with good visibilities, their presence does not indicate murky conditions. In fact, some ictalurid catfishes are typical of clear-water conditions, such as *Noturus flavus* Rafinesque, 1818c (stonecat) and the tadpole madtom *N. gyrinus* (Mitchill, 1817) for instance (Scott and Crossman, 1973).

However, in the case of other highly visual predators, such as *Stizostedion* (the walleyes), the retinal tapetum lucidum enhances light sensitivity to the point that these fishes are negatively phototrophic, and rarely found in clear waters (Scott and Crossman, 1973). Instead, their capacity to effectively see in low light conditions is used in turbulent, turbid or deep waters, where most other fishes lacking their photosensitivity are at a disadvantage (Scott and Crossman, 1973). Therefore, *Stizostedion* spp. are indicators of poor visibilities, in spite of being visual predators themselves.

Salinity

Saline and hypersaline conditions may be encountered in fluvial systems as a result of marine influence or as a result of relatively high rates of evaporation compared to inflow and outflow volumes. The latter case is typical of hydrological systems that are not connected to oceans (endorheic systems), but instead flow to an enclosed basin accumulating dissolved minerals and salts resulting from erosion. In such terminal basins, salt concentrations increase as water evaporates, resulting in variously saline conditions, depending on the inflow volume. Saline conditions resulting from marine influence or from evaporation are likely to fluctuate over time through marine transgressions and regressions, or variations in the inflow and outflow volumes, respectively. As relatively few fishes are adapted to withstand large changes in salinities, areas subjected to oscillations in salinities should have relatively low diversities composed of euryhaline species. Since stenohaline fish taxa are constrained to specific salinity levels, these would only be found alongside the euryhaline forms in areas where salinities correspond to their physiological adaptations. Areas that are extremely hypersaline (above approximately 90‰) should be devoid of all fish species (Davenport and Sayer, 1993). Therefore, different species are present in areas of different salinities and of different salinity variations, and the physiological constraints of fishes allows their use as proxies to identify saline environments, saline phases in usually freshwater environments, or a decrease of salinities in usually hypersaline environments.

For example, the largest saline lake in North America, the Great Salt Lake of Utah, USA, is the terminal basin of an endorheic system (Jones et al., 2009). This system is the remnant of the much larger Lake Bonneville, which underwent an overall decrease of water volume starting from approximately 11.6 ka (Benson et al., 2011), through several transgressive and regressive cycles (Oviatt et al., 2005), with fluctuations in water salinity (Jones et al., 2009). At approximately 11.9 ka, immediately before the main regressive phase, the lake supported fishes adapted to cold, freshwater, oligotrophic environments, such as cottids, salmonids and catostomids (Madsen et al., 2001). Fish diversities decreased during the transition from freshwater Lake Bonneville to hypersaline Great Salt Lake, with cold and freshwater forms first disappearing from the area (Madsen et al., 2001). As salinities increased to modern levels, fishes became rare (Madsen et al., 2001), until hypersaline conditions resulted in the absence of fishes from Great Salt Lake (Stephens, 1990). In historical times, during which Great Salt Lake has been one of the most hypersaline environments in the world (Jones et al., 2009), the only fish species ever found established in the lake is a cyprinodontiform killifish, *Lucania parva* (Baird and Girard, 1855), which was only found during a period of exceptionally low salinities (Stephens, 1990).

Substrate Type

Unless substrate type influences water chemistries to the point of altering a physiologically restricting variable such as pH (Davenport and Sayer, 1993), associations between fishes and substrate types are ecological rather than physiological in nature. However, these ecological associations between fishes and substrates have wide implications, as substrates may determine such variables as the availability of invertebrate prey (Flecker and Allan, 1984), of shelter, or of appropriate spawning areas. These associations are restrictive enough for different fishes to be found over different substrates; therefore, an area in which only species associated with rocky substrates are found, such as the rock bass *Ambloplites rupestris* (Rafinesque, 1817), can be inferred to have this type of substrate (Scott and Crossman, 1973).

FISHES AS INDICATORS OF BIOTIC ENVIRONMENTAL CONDITIONS

Aquatic Vegetation

Several sedentary fishes are restricted in their distributions by the presence of aquatic vegetation; their presence can therefore be used as an indication of these conditions. Ambush predators such as *Esox* spp. (pikes and pickerels) or *Amia calva* are ecologically linked to abundant vegetation in which they can hunt effectively (Scott and Crossman, 1973). *Esox* spp. and *A. calva* are also limited in their ranges by the presence of aquatic vegetation because of their use of this vegetation for spawning (Scott and Crossman, 1973). A variety of centrarchid sunfishes also spawn in vegetation, and may be indicative of these environments. This is the case for the pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), as well as *Pomoxis nigromaculatus* (Lesueur, 1829) and *P. annularis* (black and white crappies), all of which build nests associated with nearby vegetation (Scott and Crossman, 1973). Several other taxa, including other centrarchids, are limited in their distribution to vegetated areas. This is the case for the bluegill *Lepomis macrochirus* Rafinesque, 1819 and the longear sunfish *L. megalotis* (Rafinesque, 1820), for instance, which do not use vegetation for nest-building, but are strongly associated with vegetated environments (Scott and Crossman, 1973). Therefore, some fishes can be used as indicators of aquatic vegetation.

Riparian Vegetation

Riparian vegetation is influential on presence of fish in freshwater environments, particularly when it provides cover over bodies of water. Most notably, vegetation cover mitigates temperature extremes in aquatic environments (Welcomme, 1979). This is a significant effect, as fishes are physiologically limited to specific temperature ranges of variable breadths (cf. section entitled Temperature, p. 5). Therefore, riparian vegetation may allow the establishment of species where temperature fluctuations would have been too great for their presence otherwise, when overhanging vegetation provides shade for cool-water species, for instance. A diverse riparian vegetation, including trees, shrubs and grasses, would also provide a diverse range of environments in the floodplain, which could in turn be expected to influence the diversity of the ichthyofauna present in the area. This is supported by the observation that arid environments, generally areas with relatively little cover and uniform vegetation, are relatively species-poor in North America (MacAllister et al., 1986).

IMPLICATIONS OF FRESHWATER FISH BIOGEOGRAPHY

As most freshwater fishes are unable to move over land, their dispersal is limited by hydrological connections between watersheds. In most cases, the sharing of a fish species between two adjacent drainage basins will indicate a connection between both watersheds, which allowed the dispersal of the fish from one to the other. Biogeographical patterns of most freshwater fishes can therefore aid in the reconstruction of the history of connections between drainage basins. Furthermore, the specific characteristics of taxa shared between catchments may indicate the environmental conditions at the connection between the drainage areas, especially if the faunal similarity is limited to forms with common physiological or ecological features (cf. sections entitled Fishes as Indicators of Abiotic / Biotic Environmental Conditions, pp. 5–14).

For example, the northern drainages of North America were extensively connected at the end of the last glacial interval by large melt-water lakes (Dyke, 2004), which enabled the postglacial recolonization of these drainages. Currently, several salmonid species are widely distributed in these northern watersheds (Scott and Crossman, 1973), suggesting that conditions in the melt-water lakes were favourable for their survival, with high oxygen content, for example, as salmonids are sensitive to hypoxia (Davenport and Sayer, 1993).

Another illustration of the use of biogeographical patterns to determine conditions for dispersal is the peculiar absence of stenohaline fishes in Cascadia, in the northwest United States (McPhail and Lindsey, 1986). Because Cascadia was entirely glaciated, the current fish fauna of the area is the result of post-glacial dispersals. The restriction of the current fauna to euryhaline fishes strongly suggests that the drainage system has remained isolated from other freshwater systems since the last glaciation, and that the only recolonisation route available for fishes was through marine waters (McPhail and Lindsey, 1986).

The same principles can be applied at larger geographical and temporal scales. For example, *Esox lucius* has a Holarctic distribution and is only capable of surviving in very weakly brackish waters (Scott and Crossman, 1973). Therefore, its current distribution suggests the previous existence of freshwater links between North America and Eurasia that would allow the dispersal of this fish throughout its present range.

IMPORTANCE OF PALAEOICHTHYOLOGICAL DEVELOPMENTS TO MOLECULAR CLOCKS

Rationale and Goals of Molecular Clocks

The goal of molecular clocks is to provide a quantified estimate of how long ago two extant taxa shared their last common ancestor, based on the comparison of neutral variation in particular nucleic or amino acid sequences. The initial establishment of a “molecular evolutionary clock” concept (Zuckerkandl and Pauling, 1965) was based on the observation that homologous amino acid sequences seemed to be more similar between more closely related organisms (Margoliash, 1963). This observation led to the hypothesis that molecular similarity between two organisms is influenced by the amount of time since their last common ancestor rather than by the extent of morphological changes that have occurred since their evolutionary divergence (Margoliash, 1963) or their potential differences in life history traits (Kumar, 2005). The implication was that if the rate of mutation can be determined, a quantified estimate of divergence times between lineages can be calculated from molecular similarities.

The recognition that the type, rather than the number, of amino acid substitutions influences phenotypic changes (Zuckerkandl and Pauling, 1965) suggested that molecular changes may remain constant enough through geologic time to derive absolute time estimates for divergence events (Hedges and Kumar, 2009). However, the rate of heritable mutations is influenced by generational, rather than absolute, time (Laird et al., 1969). Therefore, organisms with different generation times should also have different mutation rates (Kohne 1970). This means that a single rate of mutation is insufficient to derive divergence time estimates across phylogenies. As generation times are different in different organisms, mutation rates will be different in different lineages. Generation times may also change during the evolutionary history of a lineage; therefore, mutational rates may vary through evolutionary time.

“Relaxed” molecular clock models allow for different rates of change in different lineages included in the same tree (Hedges and Kumar, 2009; Kumar, 2005), and treat mutation rates themselves as heritable traits (Kumar, 2005; Thorne et al., 1998). When modelled as heritable traits, mutation rates are constrained to be similar to those of closely related branches through autocorrelation, while probable rate changes through evolutionary time are approximated using a constant (Thorne et al., 1998).

Molecular Clock Calibration

In order to be effective, these “relaxed” clock models must be calibrated to events whose real geological time is known. Fossil evidence provides independent, historical data that can constrain several divergence time estimates within a phylogeny. Typically, fossils hypothesized to represent early members of a lineage are used as minimal time divergence points for the cladogenic event having produced their branch in the phylogenetic hypothesis (Benton et al., 2009). As a result of this calibration, the model should provide more reliable estimates for divergence events for which no fossil evidence is known.

For the autocorrelation of mutation rates throughout the "timetree" (Hedges and Kumar, 2009) to be most effective, fossil calibration points should span the phylogeny as widely as possible. This would ensure that mutation rates take into account the full diversity of generation lengths represented in the phylogeny, so that divergence times estimated for closely related lineages can be calculated using more reliable mutation rates.

As freshwater fishes are disproportionately diverse compared to marine taxa (cf. introductory section, p. 2), molecular clocks for these animals can be used to derive time estimates for a correspondingly high number of divergence events. However, freshwater fishes also have widely variable generation times, from annual cyprinodontiform killifishes (e.g., Nordlie, 2000), which may only live long enough to spawn in seasonal puddles, to *Acipenser* spp. (sturgeons) that may live for over a century and a half (Scott and Crossman, 1973). Therefore, fossil calibration points are crucial to the reliable application of molecular clocks to freshwater fishes.

CONCLUSION—IMPORTANCE OF MICROVERTEBRATE FOSSIL MATERIAL

The study of fossil fishes can be used to infer the environmental conditions discussed above as well as ancient hydrological links between watersheds through palaeobiogeographical patterns. However, fossil studies that focus on articulated specimens are restricted to the calm-water environments where this material is most often preserved. Because different fishes have different environmental tolerances and preferences, calm environments are occupied by subsets of the total taxonomic diversity present in a floodplain (Welcomme, 1979). Restricting palaeoichthyological reconstructions to calm-water species may therefore limit known fossil diversities because of the resulting under-representation of taxa that favour flowing waters (Smith et al., 1988). This final section highlights the importance of incorporating microvertebrate material to palaeoichthyological studies.

Overview of Microvertebrate Preservation Characteristics

The preservation of freshwater microvertebrate material does not require the calm depositional settings that are usually needed for the preservation of articulated specimens. Therefore, microvertebrate fossils are expected to be preserved in a wider variety of environments than articulated specimens. Because of their more common preservation, microvertebrates should also provide a better geographical and temporal resolution to our understanding of freshwater fish faunas than articulated fossils. Moreover, although it cannot be assumed that all species of a given area would be represented in an assemblage, these microvertebrate fossil localities typically achieve maximal known diversities in their geographic areas (Brinkman et al., 2005). Therefore, microvertebrates represent the best source of information on local taxonomic diversities at time of deposition.

The main period of sediment deposition in fluvial environments is the flooding phase (Welcomme, 1979). Such a high-energy environment of deposition would be expected to preserve fish remains as disarticulated specimens in most cases. Furthermore, this type of deposition would result in faunal mixing, in which animals that occupied different environmental patches are preserved together. Therefore, the study of microvertebrate freshwater fish material should provide information on the diversity of environments present in an area.

Limitations and Disadvantages of Microvertebrate Material

Despite the advantages of using microvertebrate material for palaeoenvironmental reconstructions, this material has several limitations and disadvantages as well. Microvertebrate elements are often disarticulated and fragmentary, which may make taxonomic attributions difficult. In addition to fossils that are too fragmentary to preserve any diagnostic features and can therefore not be identified or included in a study, some elements may only preserve features allowing their attribution at higher taxonomic levels. The uncertainty in identification of such elements limits their use for environmental and climatic reconstructions, as well as for the reconstruction of palaeobiogeographic ranges and molecular clock calibration. Some skeletal elements may also be less diagnostic than others within a single taxon, regardless of state of preservation. When highly diagnostic and less diagnostic material is preserved together within an assemblage, their attribution to a single taxon relies on the assumption that the less diagnostic material does not represent a different, closely related, taxon. In order to limit the influence of these uncertainties, diagnostic features must be identified for every skeletal element attributed to a particular taxon, and the taxonomic level to which these can be attributed must be specified.

Microvertebrate material is also typically influenced by processes that may result in both lateral and vertical mixing during deposition. Because the flooding phase is the main depositional period in a floodplain (Welcomme, 1979), and because microvertebrates have a high transport potential due to the small size of the elements that constitute such material, the geographic origin of the taxa that are represented is often impossible to determine with certainty. A certain degree of lateral mixing may be beneficial in that it could allow the reconstruction of several different environments represented in the vicinity of the studied locality (cf. Overview of Microvertebrate Preservation Characteristics, p. 19), but it also results in loss of information on the precise environmental conditions of the study site. Generally, fidelity of a palaeoenvironmental reconstruction increases as the desired resolution decreases, and reconstructions of wide-scale communities are more reliable than detailed faunal patterns (Behrensmeyer et al, 2000). Likewise, vertical mixing can occur because, in most attritional settings, taxonomic turnover rates tend to be less than sedimentation accretion rates, resulting in several segregated communities being mixed within a single sedimentary layer (Behrensmeyer et al., 2000). Reworking produces similar results through other means: elements could be re-worked into a stratum outside of the original life habitat or outside of the original time period. Vertical mixing typically also results in lateral mixing when it occurs shortly after the initial period of deposition because of the lateral migration of river channels on the floodplain (Welcomme, 1979). However, in extreme cases, the mixing may result in the preservation of taxa from completely different environments and time periods, such as when Cretaceous shark and dinosaur teeth were recovered from fluvial Cenozoic localities in Wyoming, Utah, and New Mexico (Eaton et al., 1989). Such processes may also result in taphonomic sorting and bias through the selective destruction of more fragile elements, which could result in the absence of certain body parts or taxa. Therefore, these processes can also result in fossil assemblages that do not accurately represent their source communities. The degree to which elements have been transported and therefore mixed can be assessed by taking into account the sedimentology of the studied localities, but lateral and vertical mixing of faunas is unavoidable in cases where the studied assemblage includes elements recovered from several distinct localities. However, most fish skeletal material is relatively delicate, and can be expected to be destroyed or damaged beyond recognition by such processes, limiting their influence on fish microvertebrate material.

Use of Microvertebrates in Environmental Reconstructions, Palaeobiogeography, and Phylogenetics

Because fishes that may have occupied different environmental patches are represented alongside one another in microvertebrate fossil localities, this material may provide otherwise unobtainable palaeoenvironmental indications, despite the loss of information caused by taphonomic influences. Fishes may be used as indicators of a wide variety of environmental conditions:

temperatures, oxygen levels, water clarity, salinity, substrate types, and presence of aquatic and riparian vegetation can all be interpreted from the fishes recovered in an assemblage. As a more complete fauna can be obtained from microvertebrate material, the overlap in tolerance ranges of the taxa recovered should give more precise environmental indications than interpretations based on a restricted variety of articulated forms. Because of lateral faunal mixing during deposition, indications on the environment of the surrounding area can be derived, contrasting with palaeoenvironmental reconstructions of a specific locality. Using the presence of indicator species in a fish fauna can give indications on the lateral variability of water clarities at the time of deposition; for example, if taxa are found that unambiguously indicate the presence of both turbid and clear conditions. Moreover, the study of microvertebrate material should also increase the level of detail of biogeographical reconstructions, as the greater temporal and spatial resolutions of this material should allow better documentation and timing of faunal exchanges both between and within continents. Finally, the greater temporal resolution of this material is useful to phylogenetic studies by potentially providing more species that can be used to reduce ghost lineages, and allows the incorporation of more calibration points in molecular timetrees.

Major Goals and Selection of Studied Localities

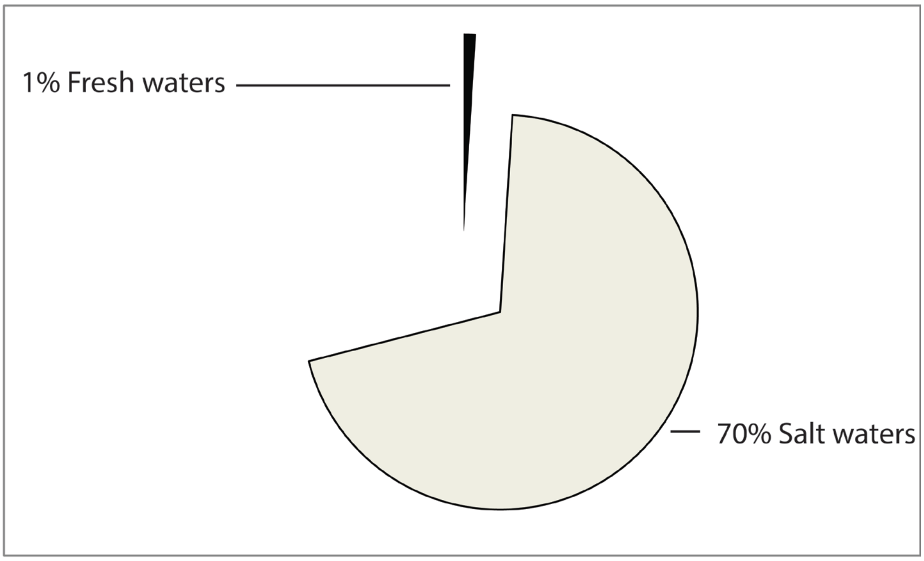
This thesis aims to develop the use of fish microvertebrate material for palaeoclimatic, palaeoenvironmental, and palaeobiogeographical reconstructions as well as for reducing ghost lineages and providing calibration points for molecular clocks. The localities studied were selected so as to span the Cenozoic of the North American Western Interior in order to allow the identification of the faunal turnovers that resulted in the formation of the modern ichthyofauna of this region. In particular, one of the questions addressed was the degree to which the freshwater ichthyofauna of the North American Western Interior had been impacted by the end-Cretaceous mass extinction event. This is particularly relevant because freshwater environments have previously been suggested to offer shelter from the sudden heat pulse that would have been caused by the Chicxulub impact, thereby potentially reducing the influence of the K-Pg extinction event (Robertson et al., 2004). More generally, the degree to which the modern ichthyofauna was the result of sudden or gradual faunal turnovers has been addressed.

The formation of this fauna was reconstructed through the comparison of the fish material recovered from several discrete Cenozoic localities to one another and to the relatively well-known Cretaceous fish faunas of the North American Western Interior (e.g., Brinkman and Neuman, 2002; Brinkman et al., 2013; Brinkman et al., 2014). Because of this methodology, the suggested faunal turnovers only concern the North American continent, and the extinction of taxa discussed in this thesis do not imply the complete extinction of forms whose geographic distributions are not limited to this continent. Furthermore, because extinctions may be localised and caused by a variety of factors such as climate and competition, and because the interpretations suggested in this thesis are based on comparisons of discrete localities representing different environments, the suggested timing for the extinction of some taxa from North American fresh waters may be due to their localised absence from a studied locality, rather than their true extinction from the continent. Future studies are required in order to test this by sampling a wider diversity of environments, latitudes and time periods.

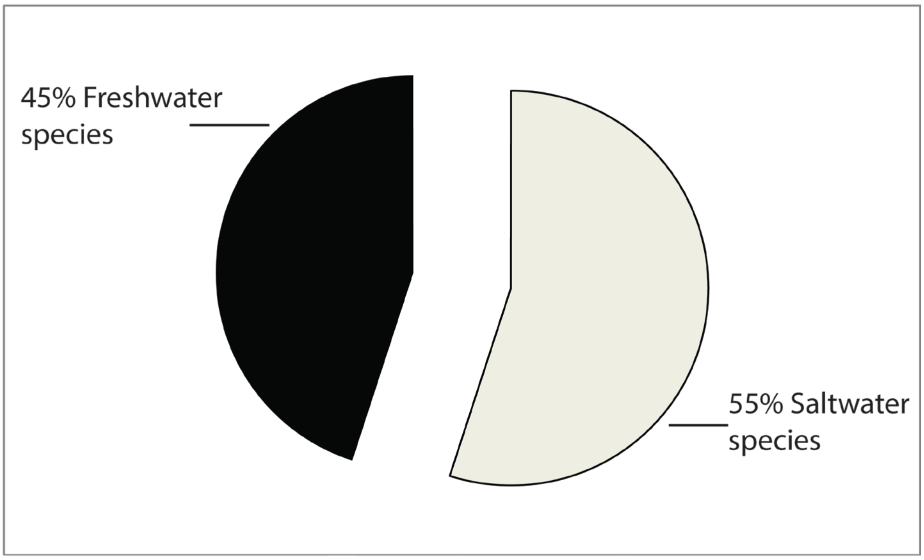
The faunas are presented in reverse chronological order, to allow identifications based on modern comparative material and trace fish lineages through time. The faunas described here were recovered in localities within four different formations: the Saskatchewan Wood Mountain Formation (Miocene), the Saskatchewan Cypress Hills Formation (Eocene–Oligocene), the Wyoming Bridger Formation (early middle Eocene) and the Wyoming Wasatch Formation (early Eocene).

FIGURE 1.1.Comparison of the surface area of the Earth represented by fresh and salt waters with the numbers of extant fish species in both environments. **A**, percentage of the surface of the Earth represented by fresh and salt waters; **B**, percentage of extant fish species found in fresh and salt water environments.

A


1% Fresh waters
70% Salt waters

B


45% Freshwater species
55% Saltwater species

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CHAPTER 2

A mid-Miocene ichthyofauna from the Wood Mountain Formation, Saskatchewan, Canada[*]

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INTRODUCTION

The mid-Miocene Wood Mountain Formation of southern Saskatchewan has been the basis of several publications since the first vertebrate fossil discoveries in the area by Sternberg in 1929 (Storer, 1971). However, the ichthyofauna of the formation has only recently been reported (Murray and Divay, 2011) and not yet formally described. The fishes from the Wood Mountain Formation are here described.

Previous work on this formation has focused on the description of its herpetofauna (Holman, 1970, 1971; Holman and Tokaryk, 1987) and mammalian taxa (Madden and Storer, 1985; Russell, 1976; Storer, 1970, 1971). Most of the amphibians and reptiles are no longer present in the area, being limited to more southern, easterly or westerly ranges (Holman, 1970). This was interpreted by Holman (1970) as indicating that the climate of Saskatchewan in the Miocene was subtropical, with temperatures unlikely to fall below freezing. The later description of the giant tortoise *Geochelone* from four localities in the Wood Mountain Formation (Homan, 1971; Holman and Tokaryk, 1987), including both Yost and Kleinfelder Farm sites, reinforced this interpretation. Furthermore, Holman (1970) proposed a palaeoecological reconstruction of the area based on its herpetofauna, inferring nearby grasslands, mostly based on the presence of *Spea* (spadefoot toad). The presence of a pond turtle and crocodilian were interpreted to indicate permanent water bodies, while the lizard material suggested diverse and abundant vegetation in the area.

The first Miocene mammals were discovered in the Wood Mountain by Sternberg in 1929 (Russell, 1976). Storer (1970) described two genera and seven new species from the Kleinfelder Farm site. Russell (1976) also described a new species from the same site. Forty-nine or fifty other species of mammals are known from the formation as described by Storer (1971).

Storer's (1971) main palaeoclimatic interpretation is that climates were more equable in the Miocene of Saskatchewan than at present, based on the diversity of mammals at various taxonomic levels. This is also suggested from the interpretation made by Holman (1970, 1971) that the east-west North American precipitation zonation was not as marked in the Miocene as it is now. The palaeoecological interpretation based on the mammalian fauna (Storer, 1971) is also consistent with the conclusions reached by Holman (1970, 1971). Woodland taxa (such as *Sciuropterus* sp., a flying squirrel) co-occur with grassland forms (antilocaprids) and understory dwellers (a wide variety of insectivores, rodents and other small mammals). This, together with the absence of large felid, canid and mustelid taxa, and the rarity of largest herbivores (rhinocerotids), led Storer (1971) to hypothesize that grasslands were interrupted by patches of woodland with dense undergrowth.

Geological Setting

The Miocene Wood Mountain Formation of southern Saskatchewan is mostly composed of quartzite and cherts forming unconsolidated fluviatile beds of sands and gravels, locally cemented by calcium carbonate (Kelley and Swanson, 1997). The formation is up to 30 meters thick, and is interpreted as having been deposited by a braided river system flowing north-northeast

(Kelley and Swanson, 1997; Leckie et al., 2004). Leckie et al. (2004) interpreted the depositional environment to have been a system composed of few, broad but shallow channels shifting laterally over time, with flooding episodes widely depositing the sands and cobbles as lag deposits.

Although the age of the formation was initially thought to have been late Miocene (Holman, 1970, 1971; Storer, 1971), Holman and Tokaryk (1987) revised this to middle Miocene. Later, Kelley and Swanson (1997:fig. 2) represented it as falling within the first two thirds of the epoch, and biostratigraphic analysis of the mammalian fauna (Storer, 1971) indicated it was deposited during the 2.6 Ma interval represented by the Barstovian Land Mammal Age (Madden and Storer, 1985). The formation is therefore currently considered to have been deposited between approximately 16.3 and 13.6 Ma in the middle Miocene (Leckie et al., 2004).

Leckie et al. (2004) suggested that the Wood Mountain Formation sediments had been transported over large distances, and Storer recovered three reworked Cretaceous shark teeth and two dinosaur phalanges from the Kleinfelder Farm site (Holman, 1970). However, the fish material in our sample is much more fragile, and is generally very little worn. This is here interpreted as evidence that the fish material was not reworked from different strata, and that most of the elements recovered underwent little transport, probably reflecting a locally derived fauna.

MATERIALS AND METHODS

The majority of the fish material described here was recovered in the same microvertebrate sample obtained from the dry screening of the Kleinfelder Farm site in 1967-8 and 1970 as the herpetological and mammalian faunas previously described (Holman, 1970, 1971; Storer, 1970, 1971; Russell, 1976). Additional material surface-collected from the Wood Mountain Formation site in Yost Farm and a site known as Russell's Miocene Location was also identified and the results of all samples are included in this study. The Yost Farm locality is located immediately to the southwest of Rockglen, Saskatchewan, 3.4 km (originally reported as 2.1 miles) from the Rockglen railway station (W. Langston and L. S. Russell field notes, held in the Canadian Museum of Nature), the Kleinfelder Farm site is located in the same outcrop near Rockglen, legal subdivision (Lsd.) 16, Sec. 31, Tp. 2, R. 30, W. 2nd Meridian (Holman, 1970; Storer, 1970), approximately corresponding to latitude 49.17241, longitude -105.99311. Russell's Miocene Location is a road cut locality on Highway 18, south of Tp. 4, R. 4 (approximately 49.3770 latitude, longitude -106.55056), to the south of Fir Mountain (Fig. 2.1).

Material Examined

The Yost Farm material (named after the owners of the land) is curated in the Canadian Museum of Nature (CMN). Material from the Kleinfelder Farm and Fir Mountain sites is in the Royal Ontario Museum (ROM). Comparative material (Appendix 2.1) is from CMN, ROM, University of Michigan Museum of Zoology, Ann Arbor, Michigan, U.S.A. (UMMZ), University of Kansas Natural History Museum, Lawrence, Kansas, U.S.A. (KU), and

University of Alberta Museum of Zoology, Edmonton, Alberta, Canada (UAMZ).

Methods

Isolated bones were identified based on comparisons with modern taxa. Fossils were coated in ammonium chloride prior to photographing. Photographs of the specimens were taken using a Nikon DXM 1200C digital camera mounted on a Zeiss Discovery.V8 stereo microscope.

Descriptive Characteristics

Spines—Identification of isolated spines was achieved through comparisons with modern taxa, focusing on the morphology of spine bases. Characteristics enabling the identification of spines include the angle formed between the base and the main shaft in anterior view, whether an angle is formed between the base and the main shaft in lateral view (i.e., whether the spine appears straight or concave in lateral view), the presence/shape/location of the basal foramen, the presence/shape/position of locking processes, the presence/position of anterior facets, the extent of the posterior furrow relative to articular condyles (and basal foramen), the torsion of the anterior ridge, and the shape of the basal condyles along with whether these flare out from the base or not. Paired fin spines are distinctive because of their asymmetry, the bases of these projecting out laterally, while median fin spines are almost symmetrical, the bases only being at slight angles from the main axis of the spine on alternate sides along the length of the fin, allowing for its retraction.

Centra—The descriptive characteristics of centra can be broadly classified into five categories: the overall shape of the centra, the presence / shape / location of articular pits, the morphology of the neurapophyses and transverse processes and / or haemapophyses (when these are preserved, usually in holospondylous vertebrae), the presence / location / shape of longitudinal parasagittal processes, and the bone texture on the surfaces of the centrum as well as the potential presence / location / shape of any accessory pits.

Overall Shape—Height / length / width proportions seem to be most useful in determining the position along the spinal column of a centrum of a pre-identified fish taxon (the length of the centra typically increasing caudally), but some general proportions are also broadly diagnostic. “Height” refers to the distance between dorsal and ventral surfaces, “length” refers to the distance between anterior and posterior surfaces (cranio-caudal distance), and “width” refers to the distance between left and right lateral surfaces.

The shapes of the main articular surfaces of the centra (both anterior and posterior) are also typically useful for identification purposes. These may be practically circular, or oval (with the longer axis oriented either horizontally or vertically), and of smooth or angular shapes. Centra may be pierced by a foramen, allowing the notochord to extend throughout the spinal column (through the centra), but the centre of their articular surfaces may only be depressed, lacking the foramen and thus segmenting the notochord. This depression is often central to the articular surface, although in some forms, it is diagnostically located dorsally or ventrally.

Articular Pits, Neural Arches, Parapophyses and Haemapophyses—Autogenous neurapophyses, parapophyses and haemapophyses ossify separately from the centrum, in which case these processes articulate with the centrum via distinct articular pits. The bases of autogenous processes are occasionally preserved articulated within their pits, but are usually still recognisable as separate ossifications from their centra. These pits are termed neural arch, parapophyseal or haemal arch articular pits, respectively. The neural arches and parapophyses are fused to centra in most derived teleosts, a state known as the holospondylous condition.

The transition from abdominal to caudal regions of the vertebral column occurs at the first centrum bearing a haemal arch, usually formed by the parapophyses migrating ventrally through the vertebral series. Anterior caudal centra of some taxa, such as *Esox* (Esocidae), bear apophyses on their lateral surfaces. Several of the anterior-most centra that possess haemal arches may also possess separate parapophyses in some taxa, such as *Pomoxis* (Centrarchidae). Pleural ribs usually articulate with the parapophyses; however, in some forms, rib articulation pits may be visible directly on the centra (e.g., anterior abdominal centra of the Centrarchidae or of the Percidae). Rib articular pits are distinguishable from accessory pits by being of consistent size among different centra, and by never being subdivided by any ridges or bony struts.

The parapophyses of holospondylous vertebrae are often heavily ossified and resilient (at least at their base) in the anterior third to half of the spinal column, projecting laterally. In these cases, the parapophyses form distinct transverse processes, the morphology of which is taxonomically diagnostic.

Longitudinal Parasagittal Processes and Zygapophyses—Bony ridges may be present on the dorsal and ventral sides of centra, often paired and projecting from the surface of the centra. When their long axes are parallel to the vertebral column, these are termed parasagittal processes. These processes sometimes bear anterior and posterior projections articulating with the adjacent centra, acting as zygapophyses. Zygapophyses may be anterior or posterior, dorsal or ventral.

Bone Texture and additional features—Additional pits serving no obvious articular function are often present and diagnostic; these are termed accessory pits. Median dorsal and ventral pits seem to be most useful for identifications, as these tend to be most consistent throughout the vertebral column. Bony struts are often present on the surfaces of centra, and may be diagnostic in their orientation and robustness. As for pits, median or paired dorsal and ventral struts are common, and are especially useful for identifications when they are consistent along the vertebral column. Finer-scale bone texture can also be diagnostic. The bone may lack discernible texture, being massive and practically featureless, or with some limited surface plications. In other cases, the surfaces of the centrum may be composed of a multitude of bony fibres; occasionally possessing many interconnected struts arranged intricately, giving a spongy appearance.

Centra are especially useful elements in the recognition of the taxa present in the source population of a microvertebrate fossil site because each centrum combines several of these taxonomically diagnostic features. Figure 2.2 illustrates the main features of generalized centra, and provides examples of the application of the terminology used above to individual centra.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII Cope, 1887

Order LEPISOSTEIFORMES Hay, 1929

Family LEPISOSTEIDAE Cuvier, 1825

LEPISOSTEUS Lacépède, 1803

(Fig. 2.3A)

Material—Three scales (ROM 65147–65149).

Description—These scales are small (less than 5 mm in longest dimension), rhomboid, covered in unornamented ganoin on their external surfaces, and lack serrations. The anterodorsal process and dorsal peg (sensu Grande, 2010) are inconspicuous.

Remarks—The rhomboid shape and ganoin covering of these scales indicate an affinity to the Lepisosteidae. Within this family, the scales of *Atractosteus* are characterized by surface ornamentations and serrations on the posterior margin of their unoverlapped field (Grande, 2010). The Wood Mountain lepisosteid is attributed to *Lepisosteus* because its scales lack these characteristics. The small relative sizes of the anterodorsal process and dorsal peg suggest that these are caudal scales.

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

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

Family AMIIDAE Bonaparte, 1832

(Fig. 2.3B–D)

Material—One fragmentary tooth plate (ROM 63444), Fig. 2.3B; nine abdominal centra (CMN 54920, 54921, ROM 64812, 64813, 65270–65274), Fig. 2.3C; five caudal centra (ROM 64814, 65261, 65275–65277), Fig. 2.3D.

Description—The tooth plate fragment (Fig. 2.3B) is small, with relatively large, unstriated and hollow teeth, which are conical in overall shape and blunt at their tips. Tooth cross sections are round or slightly oval. The bone of the tooth plate is massive and flat, lacking a fibrous bony texture but is instead lamellar.

The centra are much wider than high or long, and have a distinctive oval shape in end view and rectangular shape in lateral view. The articular surfaces are relatively shallow with a central notochordal foramen. Dorsally, large yet relatively shallow rectangular neural arch pits extend the full length of the centrum from anterior to posterior articular surfaces. The parapophyses are fused to and project from the lateral surface of the centrum, and bear terminal oval articular pits for the ribs. In the abdominal centra (Fig. 2.3C), narrow rectangular pits are present ventrally, located closer to the midline than are the neural arch pits; these ventral pits are the aortal facets for the articulation of a cartilaginous haemal process in *Amia calva* (Goodrich, 1958; Grande and Bemis, 1998). The ventral surface of the caudal centra bears articular pits for the haemal arch instead (Fig. 2.3D). The surface sculpturing of these centra is relatively uniform and shallow, dominated by a network of thin bony struts directed antero-posteriorly.

Remarks—Although the teeth are not highly diagnostic, they are similar to those found in *Amia*. The thin bony plate is not robust enough to be part of a dentary, maxilla, premaxilla or pharyngeal bone, but is morphologically similar to a coronoid plate. This element could represent the same amiine taxon as the isolated centra in the sample; however, it bears no features diagnostic of the subfamily, and it is therefore left as Amiidae indeterminate.

Based on the general shape, structure and surface sculpturing, the centra can also be attributed to the Amiidae. The fusion of parapophyses to the centra additionally allows attribution to subfamily Amiinae, but isolated centra provide no further diagnostic characters that would allow their identification to the generic level (Grande and Bemis, 1998).

Division TELEOSTEI Müller, 1846

Subdivision Indeterminate

Indeterminate Teleost Abdominal centrum

(Fig. 2.3E)

Material—One abdominal centrum (ROM 64815).

Description—This centrum is longer than wide, and about as high as it is long. The articular surfaces are oval, with a slightly ventrally located notochordal foramen, and are surrounded by a narrow margin of smooth bone. The neural arch pits are located dorso-laterally, while the parapophyseal articular pits are ventral of the midline of the lateral surfaces. There are no additional pits on the centrum, and all of its surfaces have a distinctive, shallow surface texture composed of small bony ridges projecting slightly outwards, forming whorls. Rectangular neural arch pits and parapophyseal articular pits extend the entire length of the centrum, from the anterior to the posterior articular surfaces. Each pit is divided in two by a transverse bony ridge. All of these ridges are slightly closer to the anterior end of the centrum than they are to its posterior end. The right lateral parapophyseal articular pit is less well preserved than the rest of the centrum, its edges are irregular and it does not possess the bony dividing ridge.

Remarks—The division of (most) pits by transverse bony ridges is unique in the fossil sample and has not been found in any of the comparative material. This centrum may be pathological, as its parapophyseal articular pits are asymmetrical and irregular; it could be the result of the fusion of two centra (D. Brinkman, pers. comm., 2012). The surface texture of the bone is somewhat similar to that of esocids.

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

Order ?HIODONTIFORMES McAllister, 1968

(Fig. 2.3F)

Material—One anterior abdominal centrum (ROM 64848).

Description—This centrum is shorter and slightly narrower than high, and oval in articular view. The notochordal foramen is located slightly dorsally on the articular surfaces. The dorsal surface of the centrum has a pair of shallow neural arch pits restricted to the anterior half of the centrum. These pits are separated by a triangular bony ridge widening posteriorly. There is a medial triangular pit on the posterior half of the dorsal surface, widening posteriorly. The edges of these three pits project slightly from the dorsal surface of this centrum. A rib articular pit is approximately central to the lateral surface of the centrum. Left and right pits are asymmetrical, probably either as a result of preservation or of pathology. The left rib articular pit is approximately rectangular, while the pit is markedly wider anteriorly on the right lateral surface. Both sides are similar in that a slightly projecting bulge of smooth bone separates the pits from the anterior articular surface, while the separation from the posterior surface of the centrum is narrower. A deep, wide and rectangular pit occupies the whole of the ventral surface of this centrum. On the posterior edge of this pit, a low bony ridge extends inwards toward the core of the centrum. Bone texturing is shallow and inconspicuous on all surfaces of this element. This texturing consists of shallow pitting showing no clear arrangement, except on the ventral side of the right lateral surface, where the pits form rows parallel to the ventral edge of the parapophyseal articular pit.

Remarks—The neural arch pits being shallow and restricted to the anterior half of the dorsal surface suggest that this centrum is from a hiodontiform fish, however, several characteristics are inconsistent with those seen in the only living hiodontiform family currently found in North America (the Hiodontidae). In hiodontids, abdominal centra have a distinctive subtriangular shape in articular view. More posterior centra are oval in end view, but those have long, fused parapophyses, unlike the fossil. Additionally, none of the hiodontid comparative material has a single median ventral pit, as seen in this element.

Order HIODONTIFORMES McAllister, 1968

Family HIODONTIDAE Valenciennes in Cuvier and Valenciennes, 1846

HIODON Lesueur, 1818a

(Figs. 2.3G, 2.4A, B)

Material—One first centrum (ROM 65153), Fig. 2.3G; four anterior abdominal centra (ROM 64849–64851, 65207), Fig. 2.4A; two posterior abdominal centra (ROM 64852, 65208) Fig. 2.4B.

Description—The anterior surface of the first centrum (Fig. 2.3G) has a pair of laterally flaring, anterodorsal articular facets for articulation with the exoccipitals, and a pair of median, anteroventral articular facets for articulation with the basioccipital. A large notochordal foramen is central to this anterior surface. The posterior articular surface is oval, being slightly wider than high, with a centrally located notochordal foramen. The dorsal surface has a pair of round neural arch pits, separated by a narrow ridge. An oval accessory pit is on the lateral surface, extending anteriorly to the contact point between anterodorsal and anteroventral articular facets, and posteriorly to the rim of the posterior articular surface. The ventral surface of this centrum has a pair of oval pits separated by a thin median ridge. The anterior abdominal centra (Fig. 2.4A) are higher than wide or long, and have a distinctive triangular shape in end view, being wider and flatter ventrally than they are dorsally. The more posterior abdominal centra (Fig. 2.4B) are distinctive in being oval in end view and wider than high. The notochordal foramen is central to the articular surface. A pair of shallow, oval-shaped neural arch pits is present on the dorsal surface. These are restricted to the anterior part of the centrum, and are separated by a narrow bony ridge that is either of constant width, or is slightly hourglass-shaped. The parapophyses are broken in all fossil elements, but their bases are fused to the ventral part of the lateral surfaces, and a shallow rib articular pit is immediately posterior to the parapophyseal bases. The lateral surface has either no accessory pitting, or a long and narrow pit extending from the anterior to the posterior articular surfaces in the dorso-lateral area. In anterior centra, a narrow, slit-like median ventral pit extends between anterior and posterior articular surfaces. The ventral surfaces are otherwise distinctively flat in all centra, extending laterally to the bases of the parapophyses. The bone texturing of the lateral surfaces is inconspicuous, dominated by shallow pitting forming no clear pattern, while these superficial pits are slightly bigger on the posterior part of the dorsal surfaces.

Remarks—The distinctive first centrum can be attributed to *Hiodon* based on its two pairs of anterior articular facets. It differs from the comparative material of *Hiodon alosoides* (Fig. 2.3H) in the larger relative size of its anterior notochordal foramen and lateral accessory pit, and in the presence of a pair of ventral pits. These differences could be ontogenetic, as the fossil was probably derived from a juvenile individual, considering the small size of the centrum. All other characteristics of the centra described above closely correspond to *H. alosoides* (Fig. 2.4C), which still currently occurs in Saskatchewan (Scott and Crossman, 1973). The only other extant hiodontid is the congeneric *H. tergisus*, which is also currently found in North America (Scott and Crossman, 1973).

Subdivision OSTARIOCLUPEOMORPHA Arratia, 1997 (= OTOCEPHALA Johnson and Patterson, 1996)

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

Order CYPRINIFORMES Bleeker, 1859

Family CATOSTOMIDAE Gill, 1862a or CYPRINIDAE Bonaparte, 1832

(Figs. 2.4D, 2.5A)

Material—One very fragmentary (ROM 64853), and six complete first Weberian centra (ROM 64854–64857, 65154, 65280), Fig. 2.4D; two partial (anterior portion) second Weberian centra (CMN 54922, ROM 65143), Fig. 2.5A.

Description—The first Weberian centra (Fig. 2.4D) are characteristic in being much higher and wider than long, essentially disc-shaped. Their anterior articular surfaces are either flat or irregularly bulging along their outer margins, while their posterior articular surfaces are concave. The shape of their articular surfaces is angular, forming a narrow, terminally flattened ventral keel. The centra expand to their widest point on the dorso-lateral margin and narrow to form a dorsal keel neither as expansive nor as flattened as on the ventral surface. The dorsal surface has a median ridge bearing a narrow central longitudinal depression of variable depth. This median dorsal ridge is bordered by two deep, characteristically circular pits for articulation with the scaphium. The dorsal half of the lateral surfaces is flat and essentially featureless. In all of these centra, the area adjacent to the posterior articular surface projects outward where the centrum is widest, bearing a worn or broken process base, presumably of the transverse processes. The ventral half of the lateral surfaces has a wide but shallow depression. The ventral keel is flat and essentially featureless.

All processes are broken in both second Weberian centra, but weathering is minimal, especially in CMN 54922 (Fig. 2.5A). The anterior articular surface is angular and keeled ventrally, broadly rounded dorsally, with a central notochordal foramen. The posterior articular surface is much smaller than the anterior one, angled dorsally and oval in shape, being higher than wide. A pair of ventro-lateral ridges connects the posterior articular surface to the ventral keel of the centrum. In CMN 54922, the bases of the neural arch are preserved in articulation with the centrum, but are broken distally. The neural arch bases are not preserved in the second specimen (ROM 65143), which has deep neural arch pits on its dorsal surface instead. The surface between these neural arch bases or articular pits is spongy but shows no evidence for superficial pitting, except for a small depression in the posterior area in CMN 54922 that may be due to weathering. At the widest point of the anterior articular surface, transverse processes protrude laterally. At approximately the mid-length of the centrum, these processes are deflected ventrally and connect to ridges flaring out from the ventral keel to form a triangular projection pointed posteriorly. The surfaces of these triangular projections have a median antero-posterior ridge and show superficial pitting. The lateral surface of the centrum is flat and lacks pitting in an area adjacent to the anterior articular surface, extending from the ventral keel to the lateral processes. All other surfaces show spongy textures with extensive superficial pitting.

Remarks—These characteristic first Weberian centra (Fig. 2.4D) closely correspond to the first centrum of catostomids (Fig. 2.4E) and cyprinine cypinids (Fig. 2.4F), which forms the link between the basioccipital and the more modified centra of the Weberian apparatus (2^{nd} and 3^{rd} centra) in these fishes. The unevenness of the fossil centra in lateral view, the angular articular surfaces and the ventral keel closely correspond to the anterior articular surface of the fragmentary second Weberian centra (Fig. 2.5A). It therefore seems likely that the first and second Weberian centra were from the same Miocene taxon.

The taxonomic affinity of this Wood Mountain Formation fish remains obscure, because both modern catostomids and cyprinines show comparable morphologies in this area of their vertebral column. However, the only cyprinid subfamily present in North America is the Leuciscinae, and they occur in Oligocene and Miocene deposits (Cavender, 1998). Catostomids are also found in North America from the Paleogene onwards, and are thought to have diversified in the Oligocene (Cavender, 1998). Most modern leuciscines are much smaller than the fossil, and none of the comparative material examined has a conspicuously smaller posterior articular surface as seen in the fossil. None of the catostomid material examined matches the size and spongy texture of the bone (Fig. 2.5B). Cyprinines resemble the fossil element in size and robustness, but lack the ventral keel (Fig. 2.5C). Thus, the fossils described here might either indicate a previously unrecognised presence in North America of cyprinine cyprinids, or the presence of an indeterminate catostomid. In either case, they can be distinguished from Taxon 2 below because of their large size, but whether or not they are distinct from Taxon 1 below cannot be determined.

Family CATOSTOMIDAE Gill, 1862a or CYPRINIDAE Bonaparte, 1832

(Fig. 2.5D–F)

Material—Twenty anterior abdominal centra, of variable state of preservation representing two different taxa. Taxon 1 is larger, and is represented by 16 centra (ROM 64858–64871, ROM 65210, 65263), Fig. 2.5D, E. Taxon 2 is a much smaller animal represented by four anterior abdominal centra (ROM 64872–64874, ROM 65281), Fig. 2.5F.

Description Taxon 1—Height, width and length of these centra (Fig. 2.5D, E) are subequal. The notochordal foramen is located slightly dorsally on the articular surfaces. A single, longitudinal, slit-like median dorsal pit extends the full length of the centrum from anterior to posterior edges. This dorsal pit is undivided and deep, reaching the centre of the centrum. In all elements, the broken bases of the neural arch extend the full length of the centra on either side of the dorsal pit. The lateral surfaces of the centra have very extensive and deep rectangular parapophyseal articular pits; some specimens (e.g., ROM 64858, Fig. 2.5E) preserve the bases of the parapophyses articulated in this pit. A single accessory pit is present, dorsal to the parapophyseal articular pit. This accessory pit is deep, narrower than the parapophyseal pit, and extends the full length of the centrum. It is bisected approximately at mid-length by a bony ridge that links the dorsal edge of the parapophyseal articular pit to the neural arch bases. This bony ridge is approximately vertical, sometimes slightly angled anteriorly. The ventral surface of each centrum has a single median pit, sharing all characteristics of the dorsal pit. These centra mostly lack bone texturing, although the ridges separating accessory and parapophyseal articular pits are sometimes slightly porous.

Description Taxon 2—These centra (Fig. 2.5F) are oval-shaped in end view, rather than being angular. The notochordal foramen is central. All other characteristics are identical to the abdominal centra of Taxon 1 described above, except that the other cypriniform centra reach distinctly larger sizes.

Remarks—All of the characteristics seen in these centra are found in vertebrae belonging to both the Catostomidae (Fig. 2.5G) and the Cyprininae (Fig. 2.6A), with no features enabling their differentiation. The fossils are clearly different from the characteristic centra of leuciscine cyprinids, but their taxonomic attribution cannot be narrowed any further. Whether or not any of these centra represent the same taxon as the first and second Weberian centra described above cannot be determined, but the size of centra belonging to Taxon 1 is consistent with that of the other material.

Two characteristics differentiate the four centra of Taxon 2 from those of the cypriniform Taxon 1: they are oval in articular view, rather than being wider and flatter ventrally, and the parapophyseal articular pits are smaller (relative to the total centrum size) than in the other cypriniform material. Therefore, these four centra are interpreted to indicate the presence of a second, smaller, unidentified cypriniform fish in the Wood Mountain Formation.

Family CYPRINIDAE Bonaparte, 1832

Subfamily LEUCISCINAE Günther, 1868

(Fig. 2.6B)

Material—Three abdominal centra (CMN 54923, ROM 64875, 64876).

Description—These centra are slightly wider than high and rectangular in end view. The articular surfaces are deeply concave, with a central notochordal foramen, and are surrounded by a slightly projecting margin of smooth bone. The length of the centrum is slightly greater dorsally than ventrally, giving a somewhat wedge-shaped appearance in lateral view. The width is greater at the articular surfaces than at mid-length of the centrum, giving an hourglass shape which is most conspicuous in dorsal view. On the dorsal surface, the bases of the neural arch extend the full length of the centrum, delimiting a flat, smooth surface that has a central, rounded, shallow pit. A deep parapophyseal articular pit is located at the anterior edge of the lateral surface of the centrum. This pit is triangular, being wider anteriorly than posteriorly. Surfaces ventral to the parapophyseal articular pits are dominated by a network of bony struts predominantly oriented longitudinally but with numerous interconnections, giving a spongy appearance to ventral and ventro-lateral surfaces.

Remarks—These centra compare favourably with a variety of members of the subfamily Leuciscinae, especially *Luxilus cornutus* (Fig. 2.6C) and *Ptychocheilus oregonensis* (Fig. 2.6D), but the large size of the fossils is most comparable to that of *Ptychocheilus*. However, none of the comparative material examined shows a comparable network of bony struts on the ventral surface. The comparative material has a single ventral pit or smooth bone on the ventral surface of their centra. Because the fossil specimens are weathered, it is possible that the ventral ridges represent internal structures that would have been covered by smooth bone in intact centra. The internal morphologies of centra belonging to *P. oregonensis* and *L. cornutus* were examined by CT scans, but neither had internal ventral ridges that could correspond to those of the fossils. Therefore, the fossil specimens cannot be attributed to a specific genus, and probably indicate the presence of a large unidentified leuciscine taxon.

Order SILURIFORMES Hay, 1929 (sensu Fink and Fink, 1996)

Family ICTALURIDAE Bleeker, 1863

(Fig. 2.6E, F)

Material—One fragmentary parasphenoid (ROM 65144), Fig. 2.6E; one fragmentary basioccipital (ROM 65282), Fig. 2.6F.

Description—The parasphenoid (Fig. 2.6E) is incomplete posteriorly and weathered, but is very robust. The anterior process is horizontal and flat. Its ventral surface is featureless while the dorsal surface has a median ridge and several paired longitudinal ridges fanning out laterally from the region of the alar process. This region is thicker than the anterior part of the element, and has two pairs of fossae on its lateral surfaces. The parasphenoid is more concave posteriorly, where it has a pair of low longitudinal median ridges on its dorsal surface.

The basioccipital (Fig. 2.6F) is robust but weathered and incomplete anteriorly. Its near-vertical posterior articular surface is pentagonal, with a dorsally located notochordal foramen and a slight ventral notch. The dorsal side of this element has a robust median longitudinal ridge separating a pair of oval pits that are wider than long and adjacent to the posterior articular surface. A second pair of oval pits is anterior to these. These more anterior pits are longer than wide, and separated from the posterior pits by narrow ridges. The more anterior part of the element is uneven and weathered. The ventral surface of the element has a single deep median pit adjacent to the posterior articular surface, but is otherwise featureless. Adjacent to the posterior articular surface, the lateral surface of the basioccipital has a very shallow fossa that is obscured by weathering. The bony texture of the element is inconspicuous, although it may have been obscured by weathering as well.

Remarks—The parasphenoid closely resembles that of a large ictalurid. It differs from *Noturus* in lacking the laterally extensive alar processes characteristic of that genus. The morphology of both *Ameiurus* and *Ictalurus* is more consistent with that of the fossil, however, none of the preserved characteristics of the fossil allow its unambiguous attribution to either one of these two genera. It is therefore left as Ictaluridae indeterminate.

The basioccipital can be attributed to the Ictaluridae on the basis of its robustness, and of its pentagonal posterior articular surface with a dorsal notochordal foramen and a ventral notch. The deep median pit on the ventral surface of the fossil is absent in *Noturus*, but present in both *Ameiurus* and *Ictalurus*. The fossil therefore probably represents one of these two last genera, but remains Ictaluridae indeterminate.

Family ICTALURIDAE Bleeker, 1863

AMEIURUS Rafinesque, 1820a

(Fig. 2.7A, C, E)

Material—Three pectoral fin spines (ROM 65145, 65155, 65283), Fig. 2.7A; one first centrum (ROM 64877), Fig. 2.7C; one anterior abdominal centrum (ROM 64878), Fig. 2.7E.

Description—The pectoral fin spines (Fig. 2.7A) have a long and narrow basal recess on their posterior surface, as well as a widely flared dorsal articulating process. The shaft is oval in cross section, and surfaces that are not weathered show sinuous surface plications along its length. The anterior edge of the spine shaft has very fine serrations, while the serrations of the posterior edge are very prominent.

The first centrum (Fig. 2.7C) is slightly higher than wide, and much wider than long. The articular surfaces are rectangular. The notochordal foramen is markedly located dorsally on the articular surfaces. The ventral margin of the articular surfaces is prominently notched, and growth rings on the articular surfaces reflect this ventral notch. The dorsal surface of the centrum has a single, median bony ridge bordered by a pair of deep circular pits for articulation with the scaphium. There are no lateral pits. The ventral surface has a single large but shallow median depression with the same surface texture as the other surfaces of the centrum. The ventral depression is bordered by a pair of parasagittal processes. Two articular pits are located on the lateral side of these processes. The pits extend between the anterior and posterior articular surfaces, curving laterally in their posterior-most section, forming a J-shape (clearly seen in the left pit). The margins of the ventral pits project outwards from the surface of the centrum. The centrum has a bony texture formed by a complex network of bony struts extending longitudinally and transversally. This gives a sponge-like appearance to most surfaces of the centrum.

The anterior abdominal centrum (Fig. 2.7E) is slightly wider than high, and is higher than long. The articular surfaces are triangular, being wider dorsally than ventrally. The notochordal foramen is central to the articular surfaces. The dorsal surface has a single median pit bordered by the neural arch bases extending the full length of the centrum. Additional pitting is present lateral to these, obstructed by a laterally oriented bony strut on the left side only. The neural arch bases are linked to the transverse processes anteriorly and posteriorly by projecting processes parallel to the articular surfaces. The transverse processes are strongly ossified and project from the dorso-lateral surfaces of the centrum. Lateral surfaces of the centrum have no accessory pitting. The ventral surface has a long, narrow median pit, bordered by a pair of thin bony struts, themselves bordered by a pair of likewise long, narrow pits. The bone texture is spongy, consisting of a complex arrangement of shallow pits with no preferential arrangement.

Remarks—The pectoral spines are attributed to the Ictaluridae based on their posterior basal recess and flared dorsal articulating process. The pectoral spines of *Ictalurus* are round in cross section, have a relatively wider basal recess than the fossil, and lack serrations on the anterior edge of the spine shaft. Pectoral spines of *Noturus* have a shorter basal recess, and a shaft that is oval in cross section with an unserrated posterior edge and a strongly serrated anterior edge. The fossils are most similar to *Ameiurus* (Fig. 2.7B) in having a long and narrow basal recess, and a spine shaft with fine serrations on the anterior edge and prominent serrations on the posterior edge. The fossils are therefore attributed to this genus.

The first centrum is recognisable as coming from an ictalurid based on the characteristic shape of its ventral pits and their bordering parasagittal processes, as well as its ventrally notched articular surfaces. The first centrum of *Ictalurus* is shorter and lacks the surface texture of the fossil, while that of *Noturus* has relatively deep lateral pitting and a characteristically pronounced 'upside-down heart' shape in end view, instead of having rectangular articular surfaces. The fossil centrum closely resembles *Ameiurus* (Fig. 2.7D) in all of these characteristics; it is therefore attributed to this genus.

The anterior abdominal centrum is attributed to the Ictaluridae because of its robustness and the characteristic pattern of its neural arch bases. The fossil differs from *Ictalurus* in its spongy bone texture, and *Noturus* lacks the recognisable ventral pitting of the fossil centrum. *Ameiurus*, especially smaller species of the genus such as *A. natalis* (Fig. 2.7F), is most similar to the fossil, sharing both its bone texture and ventral pitting. The specimen is therefore attributed to this genus.

ICTALURUS Rafinesque, 1820a

(Fig. 2.8A)

Material—One mostly complete anterior abdominal centrum (ROM 64879).

Description—This centrum is shorter than high or wide, with angular articular surfaces approximating a pentagon. Flattened and narrow on the ventral side, the centrum widens dorsally, reaching its widest point on the dorso-lateral margin. The notochordal foramen is located slightly dorsally, at the same level as the maximal width of the articular surfaces. Projecting margins of smooth bone surround the articular surfaces. The dorsal surface is essentially flat and featureless, apart from a median longitudinal slit-like pit. This area is laterally delimited by the neural arch bases extending the full length of the centrum. The anterior and posterior ends of the neural arch bases are connected to processes extending laterally, adjacent to the articular surfaces of the centrum. The lateral extremities of these processes are connected by a robust bony strut extending longitudinally on the dorso-lateral margin of the centrum. Lateral surfaces are essentially devoid of bone texture. The ventral side has a single deep and longitudinally extensive pit, bordered by a pair of robust ridges.

Remarks—This centrum is recognisable as an ictalurid element based on its robustness and on the shape of its dorsal neural arch bases. It can be attributed to *Ictalurus* (Fig. 2.8B) based on its markedly angular, pentagonal shape in end view and on the robust paired longitudinal ridges of its ventral surface. The anterior abdominal centra of *Ameiurus* have a series of ventral pits, while those of *Noturus* lack ventral pitting altogether. The ventral pit of the fossil lacks the network of very thin bone seen in *Ictalurus*, however weathering would be expected to break these delicate features relatively quickly.

cf. *NOTURUS* Rafinesque, 1818a

(Fig. 2.8C, E)

Material—Two dorsal fin spine fragments (CMN 41935, ROM 65212), Fig. 2.8C; four partial pectoral fin spines, lacking proximal and distal ends (ROM 30620, 65213, 65214, 65264), Fig. 2.8E.

Description—The robust symmetrical dorsal fin spines (Fig. 2.8C) have a triangular base, with a centrally placed circular basal foramen. The spine shafts have an anterior median ridge, a posterior medial furrow and lateral striations.

The pectoral spine fragments (Fig. 2.8E) are elongate and oval in cross-section. Serrations extend along one edge only, the other side is smooth. The surfaces of the fragments have sinuous, longitudinal plications occasionally joining one another.

Remarks—Based on the symmetry, triangular base, circular basal foramen and general robustness, the dorsal spine fragments can be identified as ictalurid dorsal fin spines. Dorsal fin spines of *Ictalurus* lack an anterior median ridge, while those of *Ameiurus* have much more widely flared basal lateral condyles than those of the fossils. In the morphology and proportion of their base, possession of an anterior median ridge, a posterior medial furrow and lateral striations, the elements match a *Noturus* dorsal fin spine (Fig. 2.8D).

The pectoral spine fragments are not identical to the comparative material examined; however, the surface plications, oval cross-section (contra *Ictalurus*), serrations absent from one side (contra *Ameiurus*) and hooked medially on the other, correspond most closely to *Noturus* (Fig. 2.8F). The pectoral fin spines of *Noturus* differ from the fossils in that their surface plications tend to originate at the proximal end of the bases of the serrations, extending toward the spine base from there without joining one another. For these reasons, the material is here attributed to cf. *Noturus*.

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

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

Order ESOCIFORMES Berg, 1940

Family ESOCIDAE Cuvier, 1817

ESOX Linnaeus, 1758

ESOX (*ESOX*) Linnaeus, 1758

(Figs. 2.8G, H, J, 2.9A, C)

Material—Twenty-one isolated teeth (CMN 54924, ROM 65156–65160, 65215–65227, 65265, 65284), Fig. 2.8G; one fragmentary basioccipital (ROM 65146), Fig. 2.8H; three first centra (ROM 64880–64882), Fig. 2.8J; 19 abdominal centra (CMN 54925, ROM 64883–64898, 65285, 65286), Fig. 2.9A; one fragmentary centrum of uncertain position (ROM 64899); ten caudal centra (CMN 54926, ROM 64900–64908), Fig. 2.9C.

Description— The teeth (Fig. 2.8G) are unstriated, with an oval cross-section. Unserrated carinae extend for their full length, between the base and the tip.

The basioccipital (Fig. 2.8H) is robust, weathered dorsally, and incomplete anteriorly. It is thickest along the midline, markedly tapering towards its lateral edges. The near-vertical posterior articular surface is wider than high, with a slight ventral keel and a ventrally located notochordal foramen. The dorsal surface has a wide median longitudinal ridge separating a pair of deep, rectangular pits. The ventral surface has a pair of small but deep, circular pits. The broken anterior part of the basioccipital shows that the sheet of bone forming the bases of the dorsal pits is underlain by a second bony sheet forming the ventral surface of the element. Both sheets of bone are separated by a predominantly horizontal space. The less weathered surfaces of the element have a texture dominated by bony struts mostly oriented longitudinally. On the ventral surface of the element, this arrangement is most conspicuous along the midline of the basioccipital, while the bony struts fan out laterally on either side of the midline.

The abdominal centra are shorter than high, especially the anterior-most centra which are almost disk-shaped, and are round in end view, although dorsal and ventral sides are sometimes slightly flattened. Caudal centra are higher than wide, with centra becoming longer more posteriorly in the series. The articular surfaces are surrounded by a slightly projecting margin of smooth bone. The notochordal foramen is located centrally. The neural arch pits and parapophyseal articular pits are deep and extend the full length of the centra in abdominal centra, except in the first centrum (ROM 64880–64882, Fig. 2.8J), which lacks parapophyseal pits. The neural arch pits are separated by a narrow stretch of characteristically textured bone. This area sometimes also has a shallow, slit-like longitudinal pit. The neural arch pits in the abdominal centra (Fig. 2.9A) are sub-rectangular in shape, with a slight ridge along the inside of the pits, extending towards the core of the centrum. This ridge is occasionally large enough to give the pit a somewhat hourglass shape. The parapophyseal articular pits are located laterally, shifting ventrally along the vertebral series. They are of same size or larger than neural arch pits but otherwise of similar shape, often with a slightly more pronounced ridge running towards the core of the centrum on the ventral side of the pit. In caudal centra (Fig. 2.9C), the neural and haemal arches fuse to the centrum. Some caudal centra possess lateral apophyses, projecting from the surface of the centrum as bulges adjacent to the anterior articular surface. The bone texture is clearly dominated by longitudinally arranged bony fibres, despite limited interconnections between them. In caudal centra the longitudinal fibres are arranged into bundles forming a multitude of long and narrow pits between them.

Remarks— The teeth bear no discrete characteristic features enabling their unequivocal identification; however, their general morphology and size are consistent with the dentition of modern esocids. The only other fish identified from the Wood Mountain Formation possessing a comparable dentition is *Stizostedion*, and its caniniform teeth lack carinae. Therefore, these teeth probably represent esocid material, and are here assigned to the only esocid taxon represented by more diagnostic material.

All characteristics of the basioccipital closely correspond to *Esox*. However, the basioccipital of *E. niger* (chain pickerel) does not taper laterally as the fossil element does, and instead has wide lateral facets. The basioccipital of *E. niger* is also laterally constricted, which gives its dorsal pits an hourglass shape, whereas they are rectangular in the fossil. The comparative material of *Esox lucius* (Northern Pike, Fig. 2.8I) shares the same characteristics as the fossil.

The shape of the pitting seen in the centra, including the ridges running towards the core of the centrum in both neural arch pits and parapophyseal pits, as well as the bone surface texture, closely correspond to comparative material of *Esox*. The centra of *E. niger* have transversally oriented parapophyseal articular pits, however, while those of *E. lucius* (Fig. 2.9B) and *E. masquinongy* (muskellunge) are oriented longitudinally, as in the fossil material. The caudal centra of *Esox niger* also have a distinctive morphology, being thinner at mid-length than at anterior and posterior ends. The Wood Mountain esocid caudals resemble those of *Esox lucius* (Fig. 2.9D) and *E. masquinongy* instead. The first centrum of *Esox lucius* (Fig. 2.8K) also strongly resembles the fossil material, aside from the absence of a median ventral pit in the Wood Mountain first centra.

The fossils can therefore be referred to a taxon of closer affinities with pikes (*Esox lucius* and *E. masquinongy*) than with pickerels (e.g., *E. niger*), supporting an attribution to subgenus *Esox*, following the esocid classification proposed by Grande et al. (2004). Although the neural and haemal arches of esocids are autogenous, they commonly become fused to the centrum in the caudal region of the vertebral series of modern specimens, as seen in some of the fossil elements described here. The anterior caudal centra of modern esocids also possess the lateral apophyses observed in some of the fossil elements.

Superorder ACANTHOMORPHA Rosen, 1973 (sensu Johnson and Patterson, 1993)

PERCOMORPHA Rosen, 1973

Order PERCIFORMES Bleeker, 1859

Family ?MORONIDAE Jordan, 1923

(Fig. 2.9E)

Material—Thirteen abdominal centra (ROM 64943–64953, 65193, 65194).

Description—These centra are approximately as long as they are high, with a width equal to their height or smaller; as a result, their articular surfaces range from being circular to oval in shape. The articular surfaces are surrounded by a slightly projecting margin of smooth bone and have a centrally placed notochordal foramen. The dorsal surface of each centrum is composed of loosely arranged bony fibres extending between the more robustly ossified areas adjacent to the anterior and posterior articular surfaces of the centrum. This area is flanked by the projecting bases of the broken neural arch. These neural arch bases are robust and fused to the centrum in their anterior and posterior sections, forming a bridge of bone above the centrum at mid length in several specimens. The anterior edge of the broad, wing-like parapophyses originates at mid-height of the centrum close to the anterior articular surface, while the posterior edge inserts on the ventro-lateral margin, at mid-length of the centrum. The lateral surface bears no pitting or any characteristic feature, aside from being most robust at mid-height of the centrum. The ventral surface bears a pair of bony ridges from which the posterior edge of the parapophyses project, and a median pit between these ridges. The median ventral pit is of variable shape and length, small and circular in some specimens, but rectangular and extending the full length of the centrum in others. The bone texture is relatively inconspicuous: the mostly poorly defined bony fibres are most visible on dorsal and ventral surfaces, and are arranged longitudinally, except on the parapophysis and around its base, where the fibres are parallel to the long axis of the transverse process.

Remarks—These centra are different from all of the comparative material examined, but are most similar to those of Moronidae (Fig. 2.9F), based on the characteristically fibrous dorsal surface, the more robust attachment of the neural arches in their anterior and posterior sections, the broad wing-like parapophyses and the placement of their points of attachment to the centrum, and the ventral paired ridges flanking a median ventral pit. However, moronid centra are relatively longer than the fossil centra, their lateral bone texture is more elaborate, and their ventral features are only similar for a limited number of centra along the vertebral series. Therefore the attribution of the fossil specimens to the Moronidae is tentative. Fossil moronids are found in several European sites from the Eocene onwards (e.g., Bannikov, 1993; Přikryl, 2008), but are rare in North America, having only been found in a single Piacenzian (3 Ma) locality, the Sand Draw local fauna, in Brown County, Nebraska, according to Böhme and Ilg (2003).

Family ?CENTRARCHIDAE Gill, 1862b

(Fig. 2.9G)

Material—Two first centra (ROM 64954, 65269).

Description—These fossils are recognisable as first centra based on their tripartite anterior surface for articulation with the basioccipital and exoccipitals. The centra are longer dorsally than ventrally (wedge-shaped in lateral view). The articular surface for the basioccipital is tear-drop shaped, while the posterior articular surface is oval. The notochordal foramen is located dorsally. The paired facets for articulation with the exoccipitals are weathered, but appear to have been broadly joined medially. The posterior third of the dorsal surface has a pair of rounded neural arch pits separated by a ridge. The facets for articulation with the exoccipitals project from the lateral surface of the centrum and are joined posteriorly to heavily ossified, laterally placed, postzygapophyses. The bone texture is fibrous to spongy, but is mostly obscured by weathering. The ventral surfaces of the centra are also superficially weathered and seem to lack any characteristic features other than texturing.

Remarks—The weathering of these specimens make their precise identification comparatively difficult. However, the articular facets for the exoccipitals being joined medially would suggest an affinity with the Centrarchidae, as they are separate in the first centra of other perciforms examined. The specimens lack the circular mid-ventral pit characteristic of *Pomoxis*; this is either because of the poor preservation of the centra, or indicates the presence of another, morphologically similar, centrachid in the Wood Mountain Formation.

Family CENTRARCHIDAE Gill, 1862b

cf. *POMOXIS* Rafinesque, 1818b

(Figs. 2.10A, B, E, G, I, 2.11A)

Material—One almost complete right premaxilla (ROM 63446, Fig. 2.10A); one partial left premaxilla (ROM 63445, Fig. 2.10B); three first centra (ROM 64955, 64956, 65296), Fig. 2.10E; 33 anterior-most abdominal centra (CMN 54945, ROM 64957–64981, 65195–65199, 65297–65299), Fig. 2.10G; 29 anterior abdominal centra (CMN 54946, 54947, ROM 64983–65004, 65200–65203, 65300), 14 posterior abdominal centra (CMN 54948, ROM 65005–65014, 65204, 65301, 65302), Fig. 2.10I; one pathologically altered abdominal centrum (ROM 64982), Fig. 2.11A.

Description—The better preserved right premaxilla (ROM 63446, Fig. 2.10A) is incomplete posteriorly, and it is slightly weathered, but is otherwise robust and well preserved. The ascending and articular processes are angled widely apart from one another, and the ascending process is striated longitudinally along its internal surface. The maxillary process is large, of similar height to the articular process. A shallow canal sub-parallel to the tooth row is located on the lateral surface of the alveolar process, extending caudally from the same level as the anterior-most margin of the maxillary process. Tooth bases are small relative to the size of the premaxilla, arranged in poorly defined rows over a tooth-bearing area of constant width present along the full length of the preserved portion of the alveolar process.

The partial left premaxilla (ROM 63445, Fig. 2.10B) is very fragmentary, preserving only the anterior part of the alveolar process and the articular process. However, it is similar to ROM 63446 (Fig. 2.10A) in that the broken base of the ascending process is angled away from the articular process, the shape of the articular process is similar in both specimens, and ROM 63445 (Fig. 2.10B) also has small tooth bases covering a tooth-bearing surface of constant width. Based on these similarities, the two specimens are attributed to the same taxon.

The first centra (Fig. 2.10E) share almost all characteristics of the ?Centrarchidae first centrum described above. A transverse ridge projects from the dorsal surface of the centrum, immediately posterior to the articular facets for the exoccipitals, unlike in ROM 64954 (Fig. 2.9G) but this may be worn away in the latter. Unlike in ROM 64954, the ventral surface of the centrum has a small median circular ventral pit.

The anterior-most centra of the abdominal series (Fig. 2.10G) are shorter than high, their width being similar to their height. Their shape in end view is distinctively triangular, being wider dorsally than ventrally. In more posterior positions along the vertebral series, the articular surfaces gradually become oval in shape, being wider than high, which is most pronounced in the 14 posterior abdominal centra noted in the materials (Fig. 2.10I). The notochordal foramen is central to the articular surfaces. The medial portion of the dorsal surface is composed of bony fibres predominantly arranged longitudinally, becoming more loosely arranged in the most posterior centra. The bases of the neural arch fuse to the centrum dorsally, on either side of the median dorsal surface. Anteriorly, the neural arch bases project laterally towards the transverse process of the centrum. The transverse process is strongly ossified and fused to the centrum; it is shorter in anterior-most centra, becoming longer in more posterior regions of the vertebral series. The transverse process bears a dorsal keel, which forms the connection to the neural arch bases of the centrum and delimits the anterior edge of the rib articular pit on the lateral surface of the centrum. The ventral side of the rib articular pit bifurcates posteriorly, forming a poorly defined ridge joined to the edge of the posterior articular surface of the centrum, and a sharper, vertical ridge connected to the neural arch bases. The ventral surface bears a pair of longitudinal ridges, marking the lateral edges of a median ventral pit, rectangular in shape, extending the full length of the centrum from anterior to posterior articular surfaces. The ventral surface of these centra is often asymmetrical; one of the paired ridges is commonly thicker than the other, resulting in the ventral pit being laterally located. The ventro-lateral surface of anterior-most centra is composed of tightly arranged longitudinal bony fibres. These fibres become looser in more posterior centra. Bony texture is also looser in smaller centra than in larger ones, where fibres are sometimes fused at mid length, but tend to separate close to the anterior and posterior articular surfaces of the centrum. The pathologically altered specimen (ROM 64982, Fig. 2.11A) is recognisable as the same taxon based on the shape of its posterior articular surface and characteristic neural arch base shape. Its anterior, lateral and ventral surfaces are too altered to be used for identification purposes; it may therefore represent a different, but closely related, taxon.

Remarks—The more complete premaxilla (ROM 63446, Fig. 2.10A) is similar to those of both *Micropterus* (Fig. 2.10C) and *Pomoxis* (Fig. 2.10D) in the relative sizes of maxillary and articular processes, and the wide angle formed by the articular and ascending processes. It resembles *Micropterus* in the presence of striations along the internal surface of the ascending process, and in its overall size and robustness, but the width of the tooth bearing area is greater anteriorly than posteriorly in *Micropterus*, and the distance between ascending and maxillary processes is relatively greater in *Micropterus*. The fossil additionally shares with *Pomoxis* the shallow canal on the lateral surface of the alveolar process and the constant width of the tooth bearing area. The fossil premaxillae are therefore referred to cf. *Pomoxis* despite the lack of striations on the internal surface of the ascending process in extant *Pomoxis*. These probably represent a large species related to the extant *P. annularis* and *P. nigromaculatus*.

The first centra (Fig. 2.10E) can be attributed to the Centrarchidae because of the wide junction of the paired articular surfaces for the exoccipitals. The postzygapophyses projecting laterally, rather than dorso-laterally, and the presence of a single median ventral pit in the first centrum are features only seen in *Pomoxis* (Fig. 2.10F), suggesting an affiliation to this genus.

The morphology of the dorso-lateral surface of abdominal centra (Fig. 2.10G, I), including the transverse processes, rib articular pits and fused neural arches, is characteristic of centrarchid fishes. In the extant comparative material examined (*Lepomis*, *Micropterus* and *Pomoxis*), the articular surfaces of the first few centra are taller and more angular than the rest of the abdominal vertebral series, which are essentially oval in end view, being wider than tall. Although centrarchid centra usually have a single median dorsal pit, the anterior-most centra of *Micropterus* and *Pomoxis* (Fig. 2.10H) resemble the fossil material in having a flat dorsal surface composed of tightly packed longitudinal bony fibres instead. The median dorsal pit is present in all of the centra that bear transverse processes in *Micropterus*, while in *Pomoxis* the first few centra bearing transverse processes have the characteristically fibrous bony texture. The ventral pit in the posterior abdominal centra differentiates most of the fossil elements from *Micropterus*, which possesses a shallow longitudinal trench on the ventral surface instead. Additionally, unlike in *Micropterus* and *Lepomis*, the ventral surfaces of the fossils are clearly fibrous in texture, as in *Pomoxis* (Fig. 2.10J). The fossil elements are therefore attributed to cf. *Pomoxis*.

Family ?PERCIDAE Bleeker, 1859

(Fig. 2.11B, C)

Material—Four first centra (ROM 65015–65017, 65260), Fig. 2.11B; 13 anterior abdominal centra (ROM 65018–65029, 65205), Fig. 2.11C.

Description—The first centra (Fig. 2.11B) are similar to the cf. *Pomoxis* first centra (Fig. 2.10E) described above in their wedge shape in lateral view, as well as in the presence of a tripartite anterior articulation, the dorsally located notochordal foramen on a tear-drop shaped articular surfaces, the pair of rounded neural arch pits, and the robust, laterally placed postzygapophyses. However, the facets for articulation with the exoccipitals are not joined medially, and the surface texture of these centra is characteristically made up of bony fibres separated by series of shallow pits. The ventral surface of the centra also has a pair of shallow triangular pits.

Similarly, the 13 anterior abdominal centra (Fig. 2.11C) resemble those attributed to cf. *Pomoxis* above (Fig. 2.10G) in their triangular shape in end view, their centrally placed notochordal foramen, and their fused neural arches that project anteriorly as dorsal prezygapophyses in the anterior-most centra. These centra also have dorsal postzygapophyses that are placed laterally. However, unlike the centra attributed to cf. *Pomoxis*, these abdominal centra have the same surface texture as the first centrum, and several of these centra possess shallow triangular pits on their ventral surfaces.

Remarks—Although the first centra of centrarchids and percids are very similar morphologically, the fossils are attributed to ?Percidae based on the medial separation of their dorso-lateral articular surfaces. This morphology is different from all centrarchid comparative material examined, but resembles the percids *Stizostedion* and *Perca* instead. The facets for articulation with the exoccipitals are in medial contact in one specimen (ROM 65260). However, because this centrum has the characteristic bone texture and triangular ventral pits seen in the other centra described here, it is also attributed to ?Percidae. The apparent contact between the dorso-lateral articular surfaces of this specimen may be the result of weathering, or may be due to individual variation.

The abdominal centra can be identified as belonging to the same taxon as the first centrum based on their surface texture and the paired shallow triangular pits on their ventral surfaces. Therefore, these centra are here attributed to ?Percidae, but are distinct from *Stizostedion* and *Perca*, so are not assigned to any genus.

Family PERCIDAE Bleeker, 1859

STIZOSTEDION Rafinesque, 1820a (syn. *SANDER* Oken, 1817)

(Fig. 2.11D, F)

Material—One mostly complete right premaxilla (CMN 54209), Fig. 2.11D; four anterior abdominal centra (ROM 53651–53653, ROM 65030), Fig. 2.11F.

Description—The slightly weathered premaxilla (Fig. 2.11D) is missing its ascending process and the distal part of its alveolar process. The articular process is broad and angled posteriorly. The alveolar process has a single tooth row. The majority of the alveolar process bears relatively small teeth, but the two anterior-most teeth are of intermediate size and are worn. These are followed by a large caniniform tooth and a large socket indicating a probable second large caniniform tooth.

The centra (Fig. 2.11F) are higher and wider than long, with oval or slightly teardrop-shaped articular surfaces bearing a notochordal foramen located slightly dorsally. These articular surfaces are surrounded by slightly projecting margins of smooth bone. The dorsal surface is characteristically flat, smooth and essentially featureless. Ventral and lateral surfaces form a wide arc extending ventrally from robust zygapophyses that are fused to the centrum. The dorsal prezygapophyses are immediately anterior to the rib articular pits, hook-shaped and fused with the neural arch. The bases of the neural arch are fused to the centrum, extending longitudinally from the prezygapophyses to the posterior articular surface, and extend laterally along the edge of the rib articular pits. The posterior dorsal postzygapophyses are widely flared and fuse to the centrum dorso-laterally. The ventral and lateral surfaces are covered by a network of bony struts predominantly oriented longitudinally. These struts represent the edges of a series of sheet-like structures extending radially from the notochordal canal area, connecting anterior and posterior articular surfaces (as determined from examination of a partially broken centrum, ROM 53653).

Remarks—The premaxilla was attributed to *Stizostedion* on the basis of the presence of caniniform teeth (Murray and Divay, 2011), which are unique to this genus in the Percidae, and is most similar to the condition in *Stizostedion vitreum* (Fig. 2.11E). The only difference between the fossil and the modern material is that the fossil has a single tooth row along the entire length of its alveolar process, whereas *S. vitreum* has an inner row of smaller teeth and an outer row of larger ones posterior to the caniniform teeth. The centra are morphologically identical to the anterior abdominal centra of *Stizostedion vitreum* (Fig. 2.11G). These elements represent the earliest evidence of the Percidae in North America (Murray and Divay, 2011). The presence of percids in the Wood Mountain Formation is biogeographically relevant, because the formation is older than some of the dates suggested for the dispersal of the family to the North American continent, and supports Cavender's (1998) suggestion of the family having a Holarctic distribution in pre-glaciation Cenozoic times.

DISCUSSION

The ichthyofauna of the Wood Mountain Formation represents a diverse assemblage with more than sixteen taxa. Miocene fish assemblages have previously been recovered, notably from deposits west of the Continental

Divide, such as the Deer Butte Formation of Oregon (Kimmel, 1975) and the Poison Creek Formation of Idaho (Smith and Cossel, 2002). However, the Wood Mountain Formation represents the northern-most Miocene fish fauna known to date, and is among the most taxonomically diverse Miocene assemblages described. The fauna corresponds to the last known occurrence of an amiid and lepisosteid west of the Great Lakes in Canada. Both taxa had previously been abundant in the area since the Mesozoic, but neither had been found in sediments younger than Oligocene in age (Grande and Bemis, 1998; Grande, 2010). The tentative moronid of the formation may be the first North American representative of the taxon, extending the known range of the family by approximately 10 Ma on this continent. The percid material described here (and by Murray and Divay, 2011) also predates the previously reported first occurrence of the family in North America (Murray et al., 2009) by approximately 10 Ma.

Many of the taxa identified here represent relatively large and probable piscivorous fishes, such as *Lepisosteus*, the amiine, the hiodontid, *Esox* (*Esox*), the centrarchid and *Stizostedion*. As the modern relatives of these taxa feed on various smaller fishes, chiefly small cypriniforms (Scott and Crossman, 1973), the assemblage studied here is probably a subset from a richer source community that would have included more taxa of smaller adult size that either were not preserved or, more likely, were not collected.

The *Lepisosteus* material is notably rare and small in the Wood Mountain collection. This is unlikely to be the result of sampling bias, as *Lepisosteus* have robust centra and large lateral scales. It is possible that they were limited to a region upstream of the depositional area; only small elements would be expected to stay in suspension long enough to reach the depositional environment, which could explain why *Lepisosteus* is only represented by the smaller caudal scales in the Wood Mountain Formation. Alternatively, or additionally, the scarcity could have been due to ecological causes—lepisosteids and amiids are ecologically similar and probable competitors, being large, piscivorous fishes, tolerant of anoxic conditions, but not restricted to waters with low oxygen concentrations (Scott and Crossman, 1973). As there is much more amiid than lepisosteid material in the collection, the rarity of lepisosteids being caused by amiids filling the available niche cannot be ruled out.

Palaeoclimatic Reconstruction

Although some modern relatives of the fishes in the Wood Mountain deposits are common in boreal waters, such as hiodontids, esocids and *Stizostedion*, their current ranges extend south to the southernmost areas of the Mississippi drainage, indicating that these fishes are not restricted to cold waters (Scott and Crossman, 1973). The Hiodontidae are the only family reliably identified in the Wood Mountain Formation whose southernmost range rarely extends to the Gulf coast, being mostly limited to the northern areas of the state of Mississippi (Scott and Crossman, 1973). However, it has been reported from the freshwaters of Louisiana (Douglas, 1974), and may therefore not be temperature-limited to areas north of this. *Noturus* and *Esox* (*Esox*) spp. are absent from areas farther south than northern Mississippi or southern Tennessee (Scott and Crossman, 1973), possibly because of their temperature tolerance range.

The assemblage also contains many forms whose modern relatives are no longer found in Saskatchewan waters, having shifted their ranges to the south and east since the Miocene (e.g., *Amia*, *Pomoxis*). Higher Miocene temperatures are suggested by the abundance of warm water taxa within the sample (notably centrachids and cypriniforms), as well as by the large size of the Wood Mountain *Pomoxis,* a genus that becomes stunted in cooler waters (Scott and Crossman, 1973). The presence of these fishes, and the larger sizes of at least some, are here interpreted to indicate that the Wood Mountain area was much warmer than at present.

This interpretation is corroborated by the absence of cold-water taxa in the Wood Mountain collection, especially salmoniform fishes, many of which are currently found in the Hudson Bay drainage and Saskatchewan (Scott and Crossman, 1973). These fishes are relatively large and their skeletons are as robust as those of the taxa recovered in the Wood Mountain sample. Therefore, their absence from the locality is likely a true absence from the source community, rather than a taphonomic or collecting bias. East of the Rocky Mountains, the modern distribution of the Salmonidae is restricted to latitudes north of 40°N (Scott and Crossman, 1973), therefore, their absence from the Wood Mountain Formation supports the interpretation that the palaeoclimate was similar to modern temperatures typical of northern Mississippi or southern Tennessee.

The fishes of the Wood Mountain Formation indicate average monthly temperatures in the Miocene ranging between 28.2–5.1°C, compared to the current range of 18.8– -11.4°C, based on modern temperature data. A comparison with the nearby weather station in Opheim, northern-most

Montana (station ID: GHCND: USC00246236, located about 37 km southwest of the Wood Mountain Formation, Fig. 2.1B), indicates that the locality currently has normal maximal temperatures ranging between 27.6–10°C, with an average of 18.8°C. Minimal temperatures range -5.4– -14.4°C, with an average of -11.4°C (N.O.A.A., 2012). In contrast, normal temperatures of northern Mississippi or southern Tennessee (based on the Memphis international airport weather station in Tennessee; station ID GHCND: USW00013893, located about 5 km north of the Mississippi-Tennessee border, Fig. 2.1A) range between 33.2–23.2°C, with an average of 28.2°C, during the warmest month of the year. Normal temperatures for the coldest month of the year range between 9.9–0.3°C, with an average of 5.1°C. The composition of the fish fauna being similar to that now found in southern Tennessee therefore corroborates herpetofaunal indications of much warmer, sub-tropical, climates in southern Saskatchewan during the Miocene (Holman, 1970, 1971; Holman and Tokaryk, 1987). In particular, the normal lowest winter temperature indicated by the fish fauna (0.3°C) closely matches Holman's (1971) suggestion that Miocene winter temperatures would not drop below freezing, as indicated by the presence of the giant tortoise *Geochelone*.

Palaeoenvironmental Reconstruction

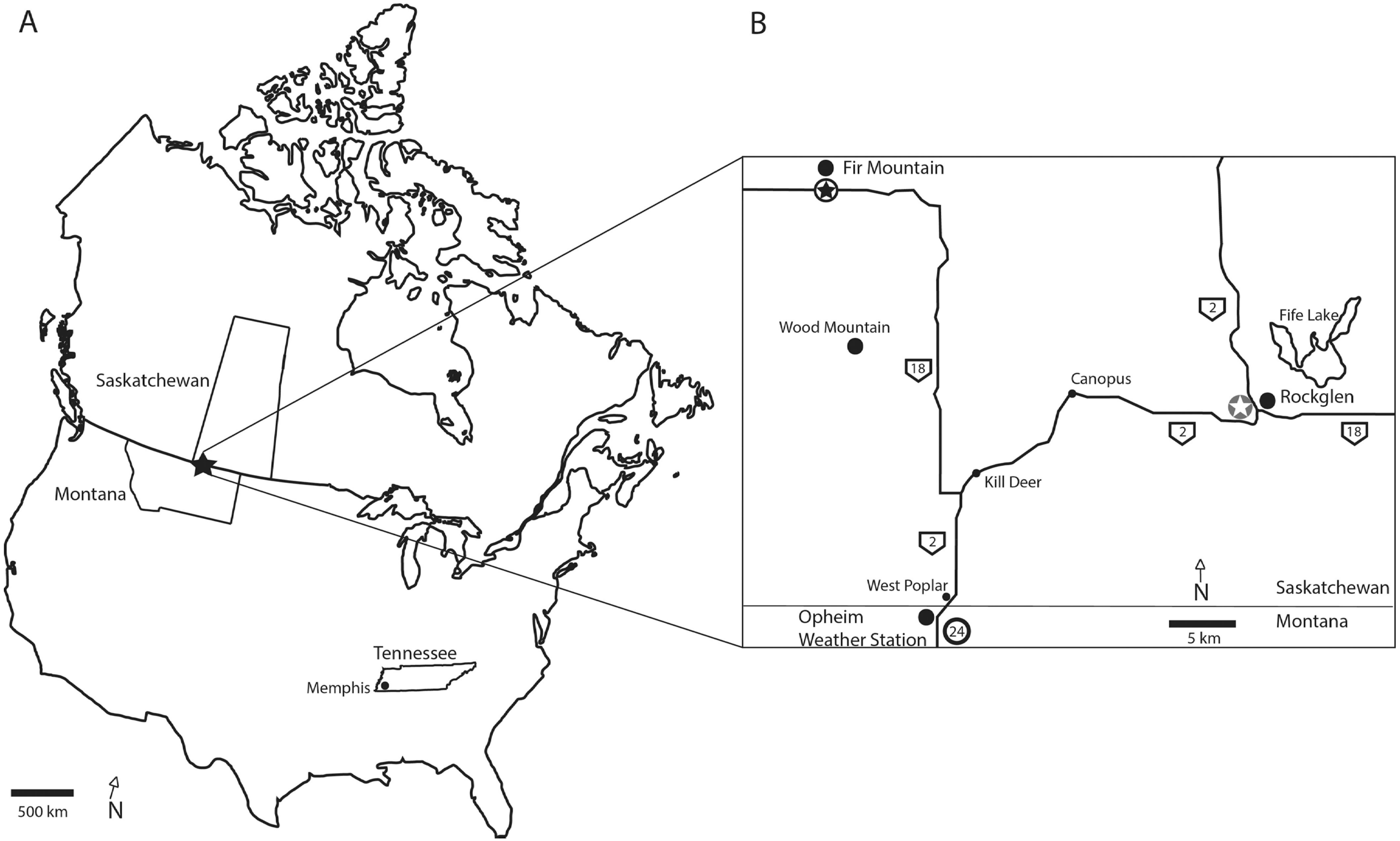
The Wood Mountain Formation ichthyofauna indicates a well-oxygenated, lowland fluvial environment at the time of deposition. Some fishes of the Wood Mountain Formation are sometimes found in anoxic (*Lepisosteus*, amiid) and brackish (moronids, *Stizostedion* and other taxa) conditions; however, the fauna as a whole does not indicate that these conditions were prevalent. Centrarchids, cyprinids and ictalurids have been previously found to be abundant in North American lowland freshwater deposits from the Miocene onwards (Cavender, 1998). The extant representatives of the Centrarchidae are typically found in warm, shallow lakes and ponds, as well as slow-moving rivers (Scott and Crossman, 1973). *Pomoxis*, in particular, is usually found in clear to slightly turbid low-flow areas with rocky, sandy, or muddy substrates and abundant aquatic vegetation (Scott and Crossman, 1973). This type of environment is also indicated by the abundant Wood Mountain *Esox* (*Esox*) sp. material, as pikes typically inhabit the sluggish, heavily vegetated areas of relatively clear streams, where they can detect, ambush and capture their prey (Scott and Crossman, 1973). Other fishes from the formation indicative of relatively low-energy environments include *Hiodon*, as well as the amiid (Scott and Crossman, 1973). This latter is also another indication that abundant aquatic vegetation was present in the area.

However, the ichthyofauna of the Wood Mountain Formation is also indicative of nearby deeper and/or more turbid environments. In particular, *Stizostedion* are sensitive to bright daylight, and are usually found in areas where depth, turbidity or cover are sufficient to provide shelter from the sun, favouring shallow turbid environments (Scott and Crossman, 1973). Additionally, at least one extant species of *Hiodon* (*H. alosoides*) is typically found in silted environments (Scott and Crossman, 1973).

The diversity of the ictalurid fishes is also indicative of a variety of conditions at the time of deposition. *Ameiurus* are mostly found in shallow, low-flow areas with moderate to heavy vegetation, and are found over a variety of substrates, from pebbles to mud, depending on species (Scott and Crossman, 1973). Contrastingly, *Ictalurus* favour deeper, clearer waters over sand, gravel or rubble (Scott and Crossman, 1973). *Noturus* are also most abundant in clear conditions, and several species favour higher currents, being usually found in gravelly riffles (Scott and Crossman, 1973). The presence of all three genera in the deposits indicates that a wide diversity of substrates was present somewhere in the catchment basin.

Overall, this ichthyofauna indicates that the Wood Mountain Formation was deposited in an area of considerable environmental diversity. The relative abundance of the esocid and centrarchid material suggests that the local environment was relatively shallow and clear, with little current and abundant aquatic vegetation. However, the presence of *Ictalurus* indicates that deeper channel-type environments would have been nearby. *Stizostedion* and *Hiodon* may also indicate that murky environments were available in the vicinity. Clear, shallow, relatively high-energy riffles were also probably found in the area, based on the presence of *Noturus*. These indications corroborate and complement the previous palaeoecological reconstructions founded on the tetrapod fauna of Wood Mountain Formation. Both Holman (1970) and Storer (1971) interpret the area to have been a diverse environment of well-mixed woodland, grassland and pond bank habitats. The ichthyofauna additionally indicates that the freshwater environments of the Wood Mountain were diverse as well. The lateral diversity of habitats currently found in major floodplains (Welcomme, 1979) is comparable to the palaeoecological indications of this fauna, suggesting that the Wood Mountain Formation was deposited in such a varied floodplain environment.

FIGURE 2.1. Locality map for the Wood Mountain Formation (marked with a star). **A**, map of Canada and the contiguous United States showing the relative positions of the Wood Mountain Formation, Saskatchewan, Montana, Tennessee and Memphis, TN; **B**, enlarged locality map, showing the relative positions of Russell's Miocene Location, Fir Mountain, SK, Canada (black circled star), the Wood Mountain Formation outcrop containing both Kleinfelder Farm and Yost Farm locations (white circled star), Rockglen, SK, Canada, and Opheim weather station, MT, U.S.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Memphis
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Fir Mountain
Wood Mountain
18
2
Canopus
Kill Deer
West Poplar
Opheim
Weather Station
24
Fife Lake
Rockglen
Saskatchewan
Montana
N
5 km

FIGURE 2.2. Generalized centra showing taxonomically informative features. **A**, anterior abdominal holospondylous centrum; **B**, more posterior abdominal centrum, where the neural arch and parapophyses are autogenous (and omitted); **C**, holospondylous anterior caudal centrum. **Abbreviations**: **a**, apophysis; **aas**, anterior articular surface; **ap**, accessory pitting; **asm**, articular surface margin; **daz**, dorsal anterior zygapophysis (= prezygapophysis); **dpz**, dorsal posterior zygapophysis (= postzygapophysis); **H**, height; **ha**, haemal arch; **hs**, haemal spine; **L**, length; **lpp**, longitudinal parasagittal process; **na**, neural arch; **nap**, neural arch pit; **nf**, notochordal foramen; **ns**, neural spine; **p**, parapophysis; **pap**, parapophyseal articular pit; **rap**, rib articular pit; **vaz**, ventral anterior zygapophysis (= prezygapophysis); **vpz**, ventral posterior zygapophysis (= postzygapophysis); **W**, width. Note: although taxonomically informative, surface bony texture is omitted for clarity.

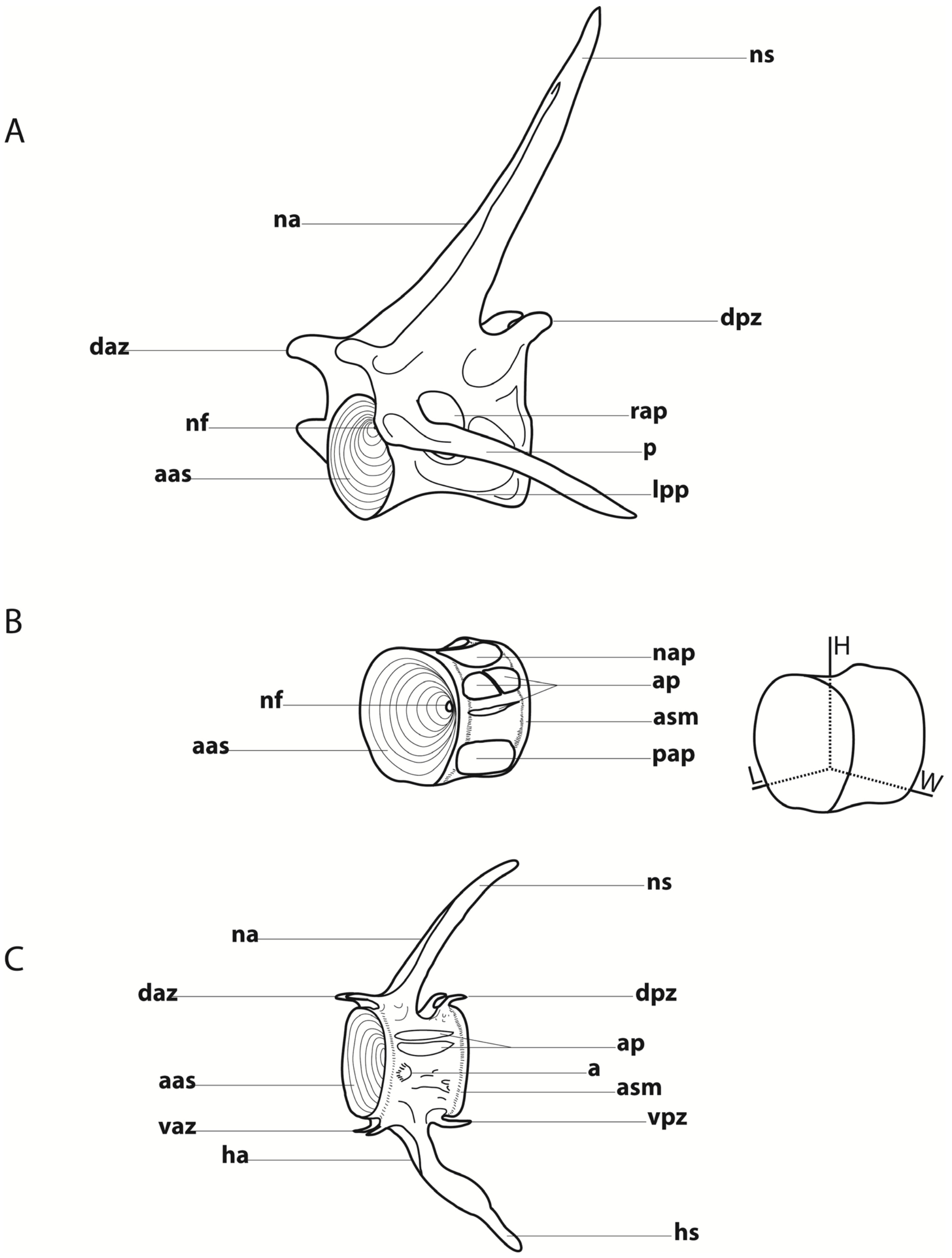
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FIGURE 2.3. Wood Mountain Formation (**A**–**G**) and comparative (**H**) material. **A**, *Lepisosteus* scale (ROM 65147) in lateral and medial views; **B**, indeterminate amiid, probable coronoid tooth plate fragment (ROM 63444); **C**, Amiinae abdominal centrum (CMN 54921); **D**, Amiinae caudal centrum (ROM 64814); **E**, indeterminate teleost abdominal centrum (ROM 64815); **F**,?hiodontiform abdominal centrum (ROM 64848); **G**, *Hiodon* first centrum (ROM 65153); **H**, *Hiodon alosoides* (UAMZ F8556) first centrum. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

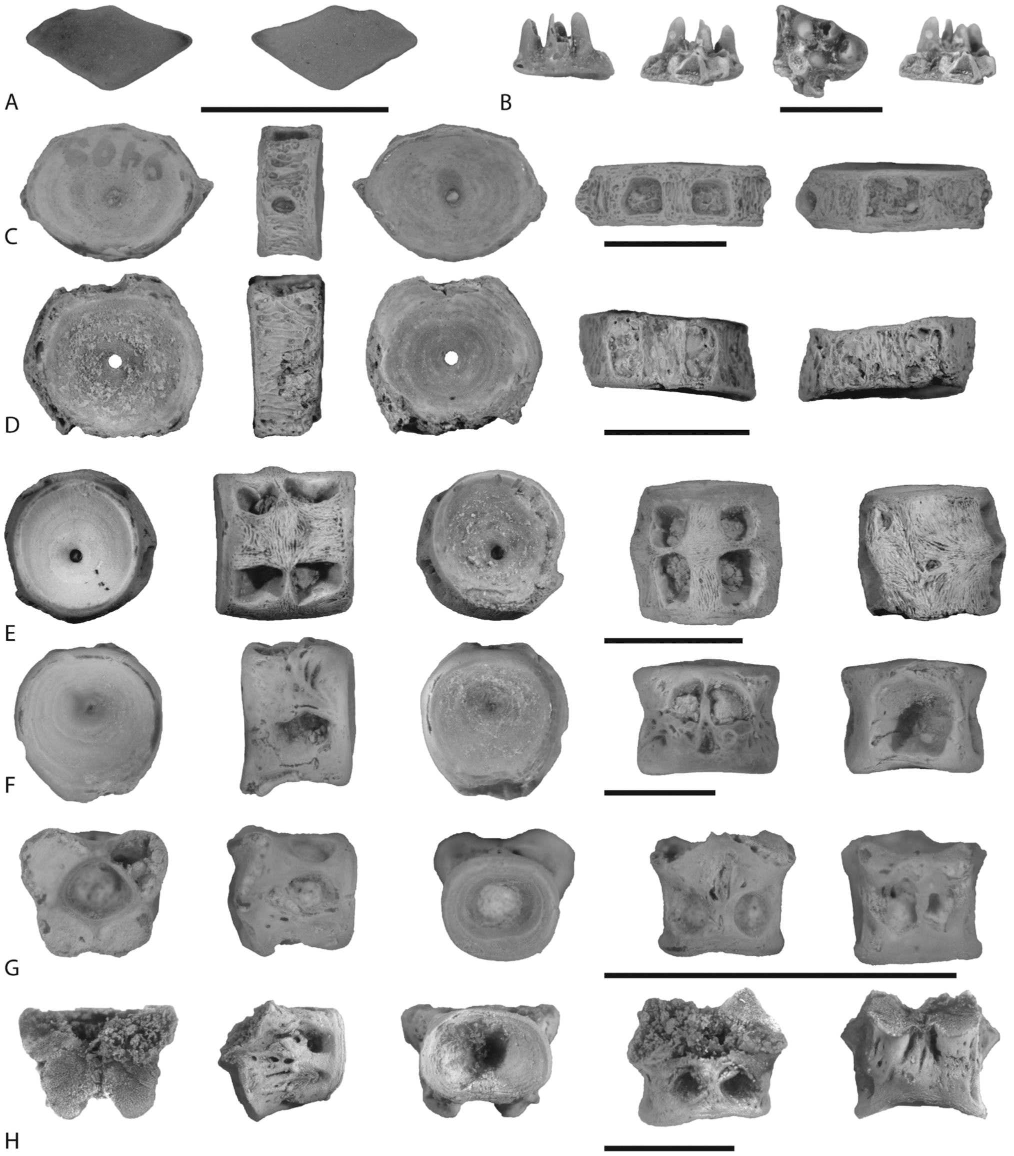
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FIGURE 2.4. Wood Mountain (**A**, **B**, **D**) and comparative (**C**, **E**, **F**) material. **A**, *Hiodon* anterior abdominal centrum (ROM 64849); **B**, *Hiodon* posterior abdominal centrum (ROM 64852); **C**, *Hiodon alosoides* (UAMZ F8556) abdominal centrum; **D**, first centrum of an indeterminate taxon of either Catostomidae or Cyprininae (ROM 64854); **E**, first centrum of *Catostomus catostomus* (UAMZ F8582); **F**, first centrum of *Cyprinus carpio* (UAMZ F8557). Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated with ammonium chloride prior to photographing. All scale bars equal 5 mm.

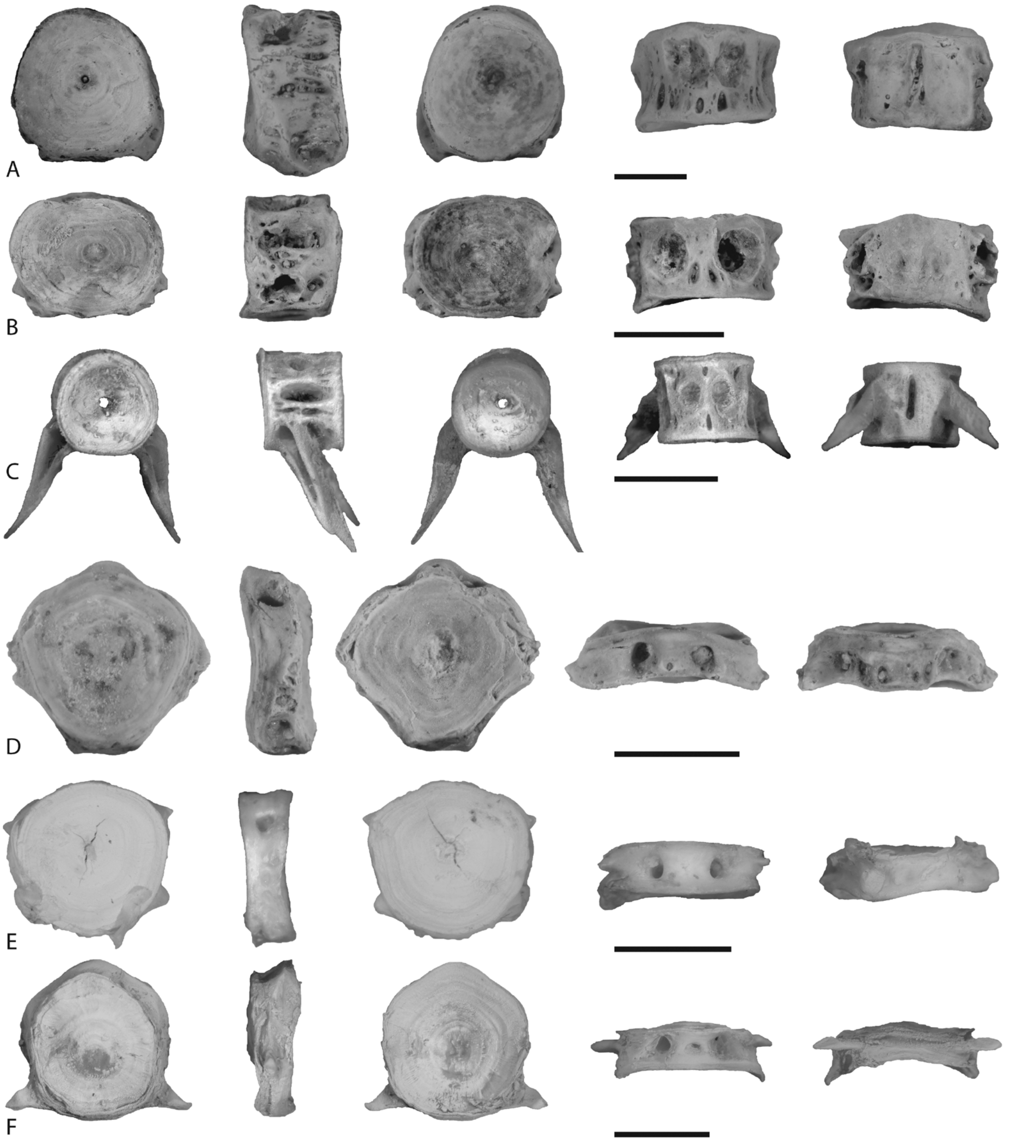
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FIGURE 2.5. Wood Mountain Cypriniformes (**A**, **D**–**F**) and comparative (**B**, **C**, **G**) material. **A**, second Weberian centrum (CMN 54922) attributed to the same catostomid or cyprinine taxon as the first centra illustrated in Fig. 2.4D; **B**, second Weberian centrum of *Catostomus catostomus* (UAMZ F8558); **C**, second Weberian centrum of *Cyprinus carpio* (UAMZ F8557); **D**, abdominal centrum of the indeterminate cypriniform Taxon 1, belonging to Catostomidae or Cyprininae (ROM 64859); **E**, abdominal centrum (ROM 64858) of cypriniform Taxon 1, preserving the bases of the parapophyses in articulation with the parapophyseal articular pits; **F**, abdominal centrum of the indeterminate cypriniform Taxon 2 (ROM 64872); **G**, abdominal centrum of *Carpiodes carpio* (KU 12732), shown without articulated parapophyseal bases, as for cypriniform Taxon 1 in Fig. 2.5D. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

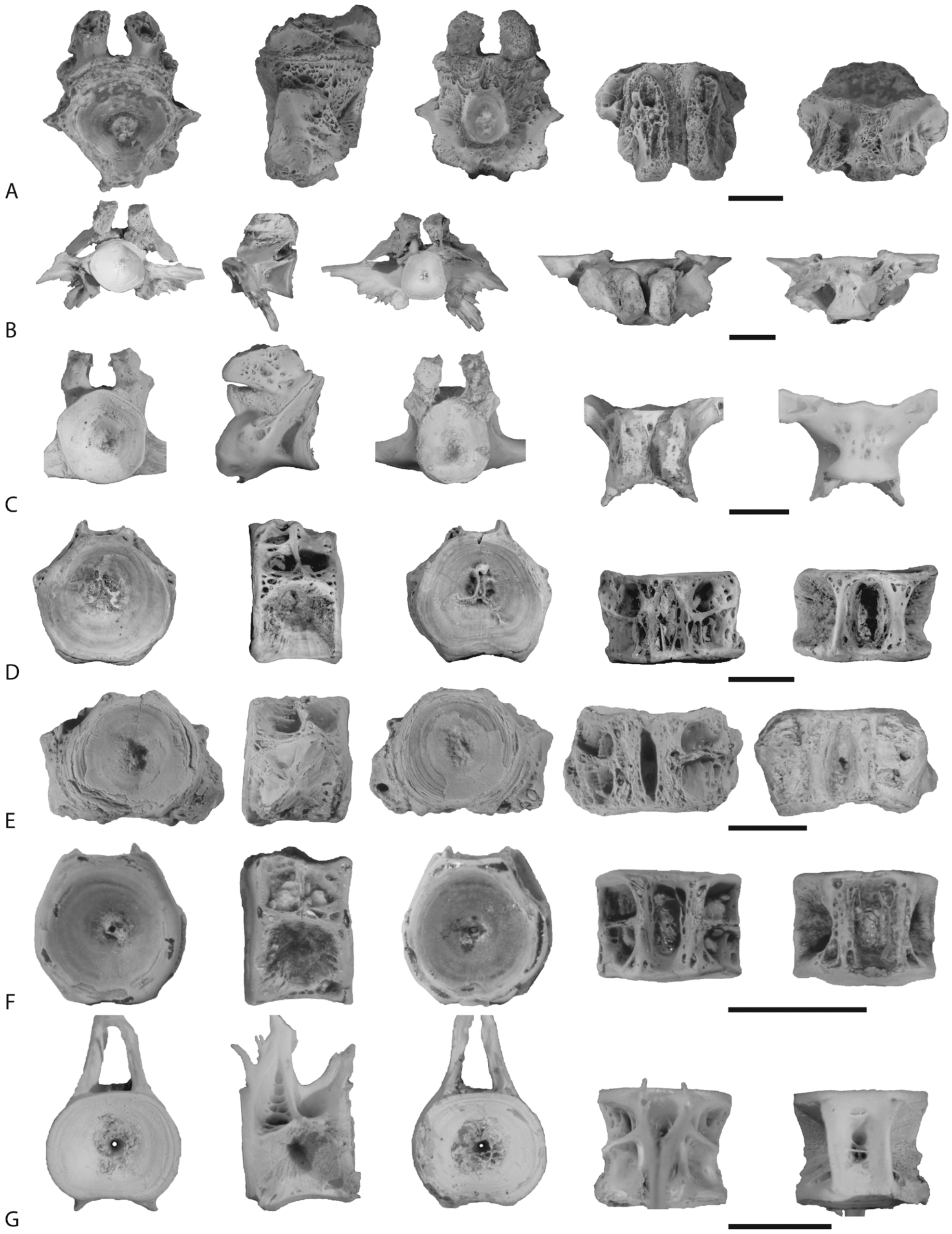
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FIGURE 2.6. Wood Mountain (**B**, **E**, **F**) and comparative (**A**, **C**, **D**) ostariophysan material. **A**, abdominal centrum of *Cyprinus carpio* (UAMZ F8557), shown with the bases of the parapophyses in articulation with the parapophyseal articular pits, as for the Wood Mountain cypriniform Taxon 1 in Fig. 2.5E; **B**, Leuciscinae abdominal centrum (CMN 54923); **C**, abdominal centrum of *Luxilus cornutus* (ROM R6425); **D**, abdominal centrum of *Ptychocheilus oregonensis* (ROM R6513); **E**, fragmentary parasphenoid of an indeterminate ictalurid (ROM 65144) in dorsal, lateral and ventral views; **F**, basioccipital of an indeterminate ictalurid (ROM 65282). The basioccipital and centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

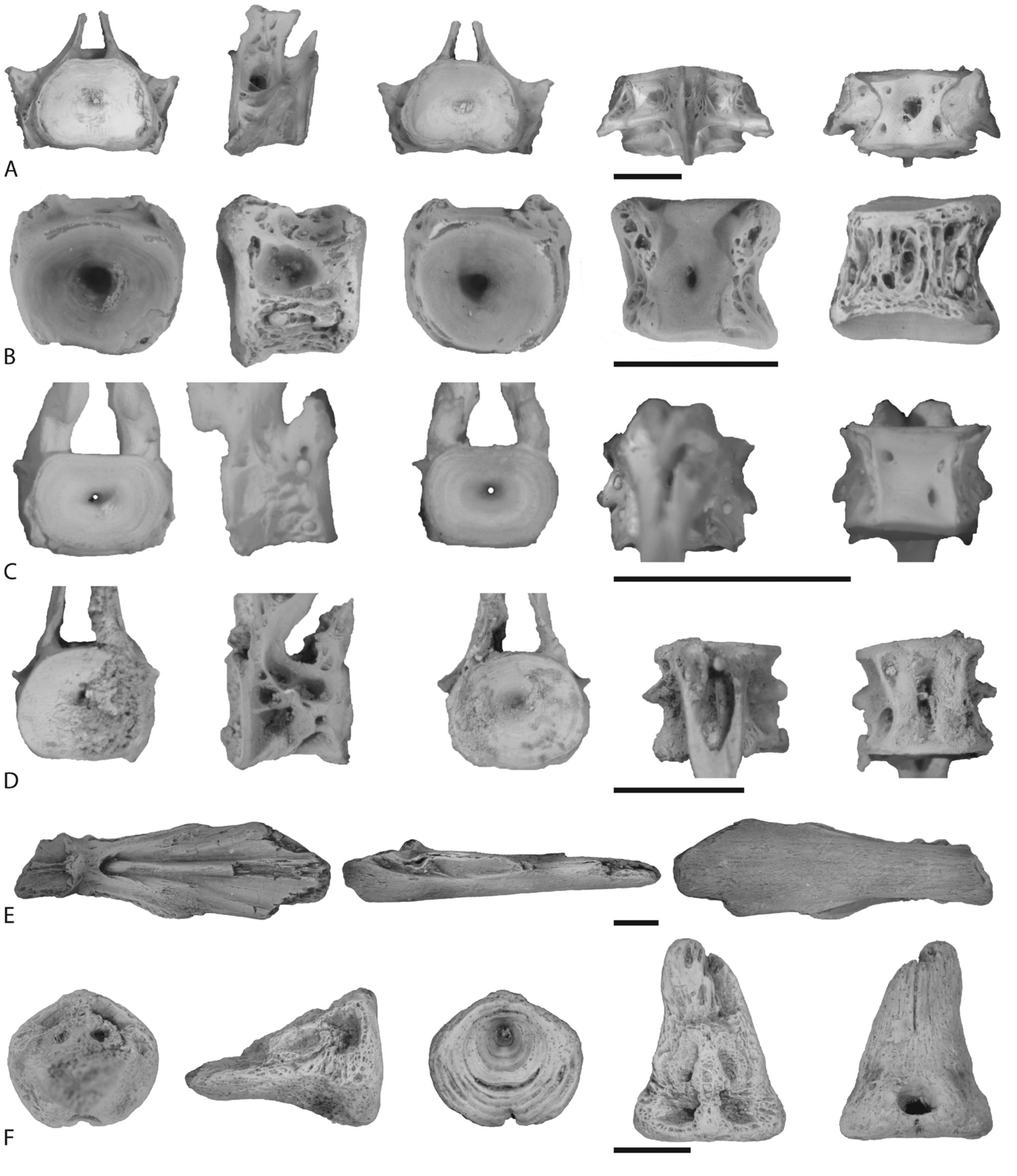
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FIGURE 2.7. Wood Mountain (**A**, **C**, **E**) and comparative (**B**, **D**, **F**) *Ameiurus* material. **A**, pectoral fin spine fragment (ROM 65283) in anterior, lateral and posterior views; **B**, pectoral fin spine of *A. natalis* (ROM 7245) in anterior, lateral and posterior views; **C**, first centrum of *Ameiurus* (ROM 64877); **D**, first centrum of *A. natalis* (ROM 7245); **E**, *Ameiurus* anterior abdominal centrum (ROM 64878); **F**, anterior abdominal centrum of *A. natalis* (ROM 7245). Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.


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FIGURE 2.8. Wood Mountain (**A**, **C**, **E**, **G**, **H**, **J**) and comparative (**B**, **D**, **F**, **I**, **K**) material. **A**, *Ictalurus* anterior abdominal centrum (ROM 64879); **B**, anterior abdominal centrum of *Ictalurus punctatus* (UAMZ F8553); **C**, cf. *Noturus* proximal fragment of a dorsal fin spine (CMN 41935); **D**, dorsal fin spine of *Noturus flavus* (CMN 77-182); **E**, cf. *Noturus* fragmentary pectoral fin spine (ROM 30620); **F**, pectoral fin spine of *Noturus flavus* (CMN 77-182); **G**, isolated tooth (CMN 54924) of ?Esocidae showing anterior, posterior, lateral and proximal surfaces; **H**–**K**, *Esox* (*Esox*) material: **H**, *Esox* (*Esox*) sp. basioccipital (ROM 65146); **I**, basioccipital of *Esox* (*Esox*) *lucius* (UAMZ F8551); **J**, *Esox* (*Esox*) sp. first centrum (ROM 64880); **K**, *Esox* (*Esox*) *lucius* (UAMZ F8551) first centrum. Dorsal fin spines are presented, from left to right, in anterior, lateral and posterior views; pectoral spines are presented in lateral and anterior views. Centra and basioccipitals are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

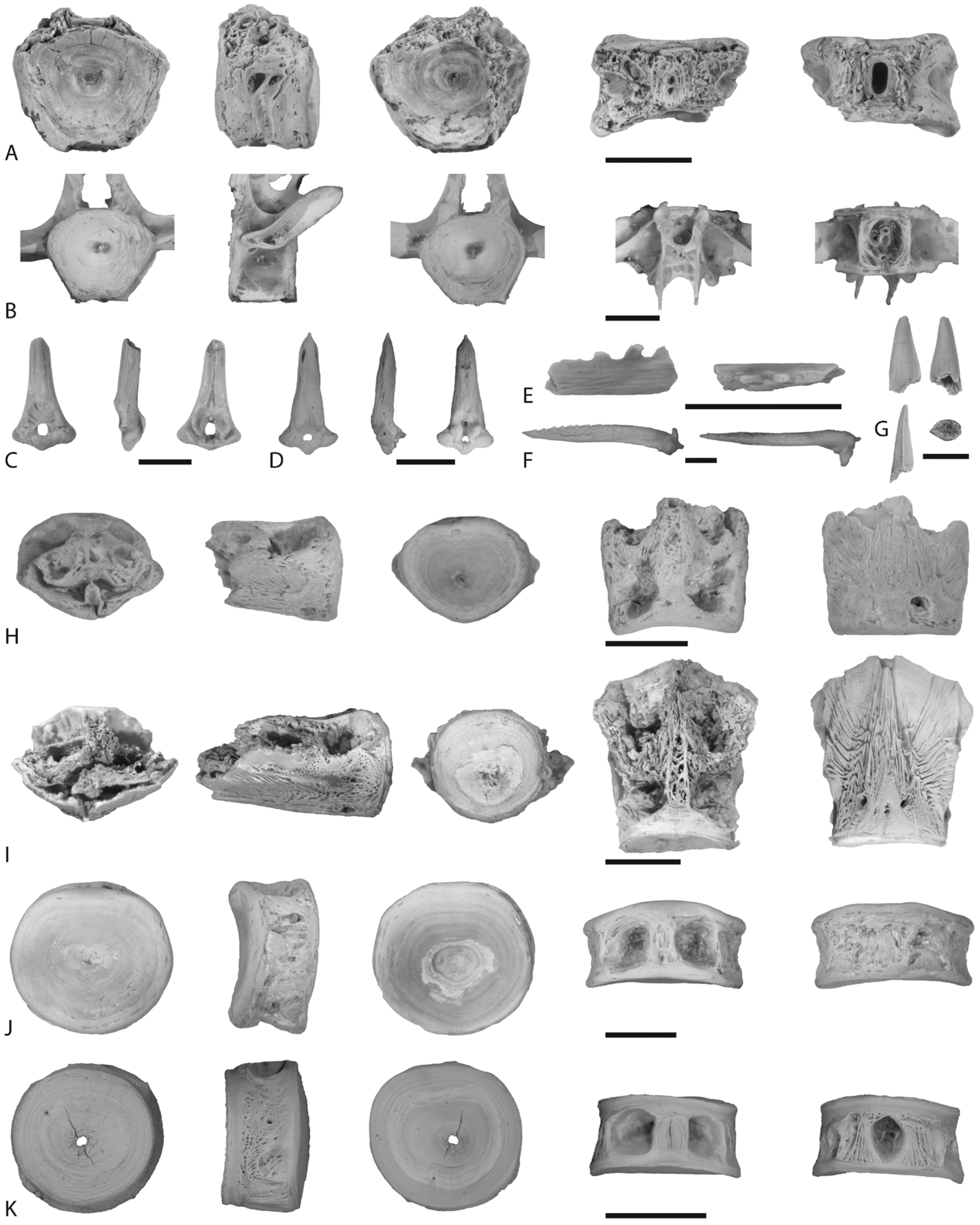
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FIGURE 2.9. Wood Mountain (**A**, **C**, **E**, **G**) and comparative (**B**, **D**, **F**) material. **A**–**D**, *Esox* (*Esox*) material: **A**, *Esox* (*Esox*) sp. abdominal centrum (ROM 64883); **B**, *Esox* (*Esox*) *lucius* (UAMZ F8551) abdominal centrum; **C**, *Esox* (*Esox*) caudal centrum (CMN 54926); **D**, *Esox* (*Esox*) *lucius* (UAMZ F8551) caudal centrum; **E**, abdominal centrum of ?Moronidae (ROM 64943); **F**, abdominal centrum of *Morone saxatilis* (UAMZ F8554); **G**, first centrum of ?Centrarchidae (ROM 64954). Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

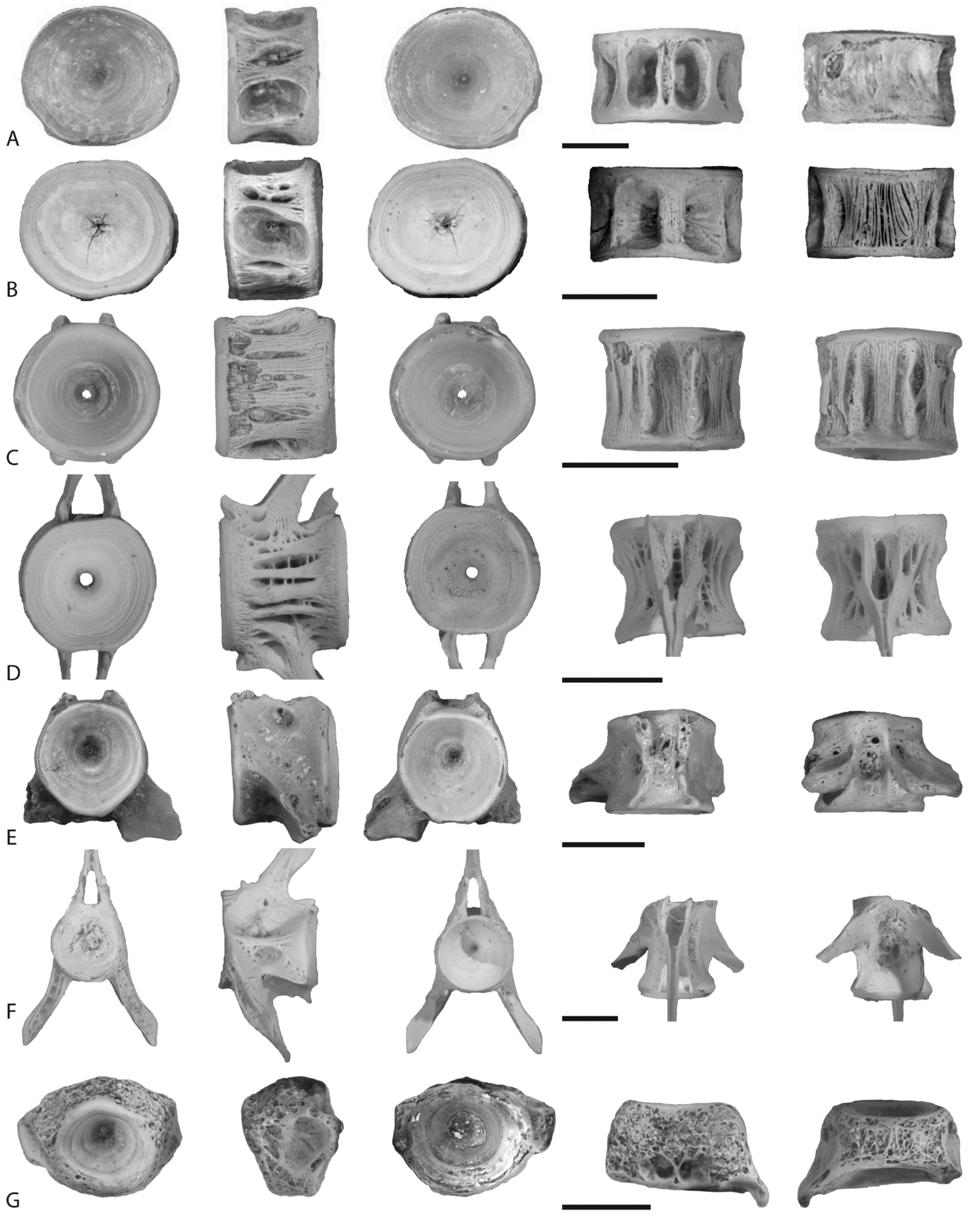
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FIGURE 2.10. Wood Mountain cf. *Pomoxis* (**A**, **B**, **E**, **G**, **I**) and comparative (**C**, **D**, **F**, **H**, **J**) material. **A**, cf. *Pomoxis* right premaxilla (ROM 63446) in lateral, anterior, medial and ventromedial views; **B**, cf. *Pomoxis* fragmentary left premaxilla (ROM 63445) in medial, anterior, lateral and ventromedial views; **C**, *Micropterus dolomieui* (CMN 73-258) right premaxilla; **D**, *Pomoxis nigromaculatus* (CMN 76-075) right premaxilla; **E**, cf. *Pomoxis* first centrum (ROM 64955); **F**, *Pomoxis nigromaculatus* (CMN 76-075) first centrum; **G**, cf. *Pomoxis* anterior-most abdominal centrum (ROM 64957); **H**, *Pomoxis nigromaculatus* (CMN 76-075) anterior abdominal centrum; **I**, cf. *Pomoxis* posterior abdominal centrum (CMN 54948); **J**, *Pomoxis nigromaculatus* (CMN 76-075) posterior abdominal centrum. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

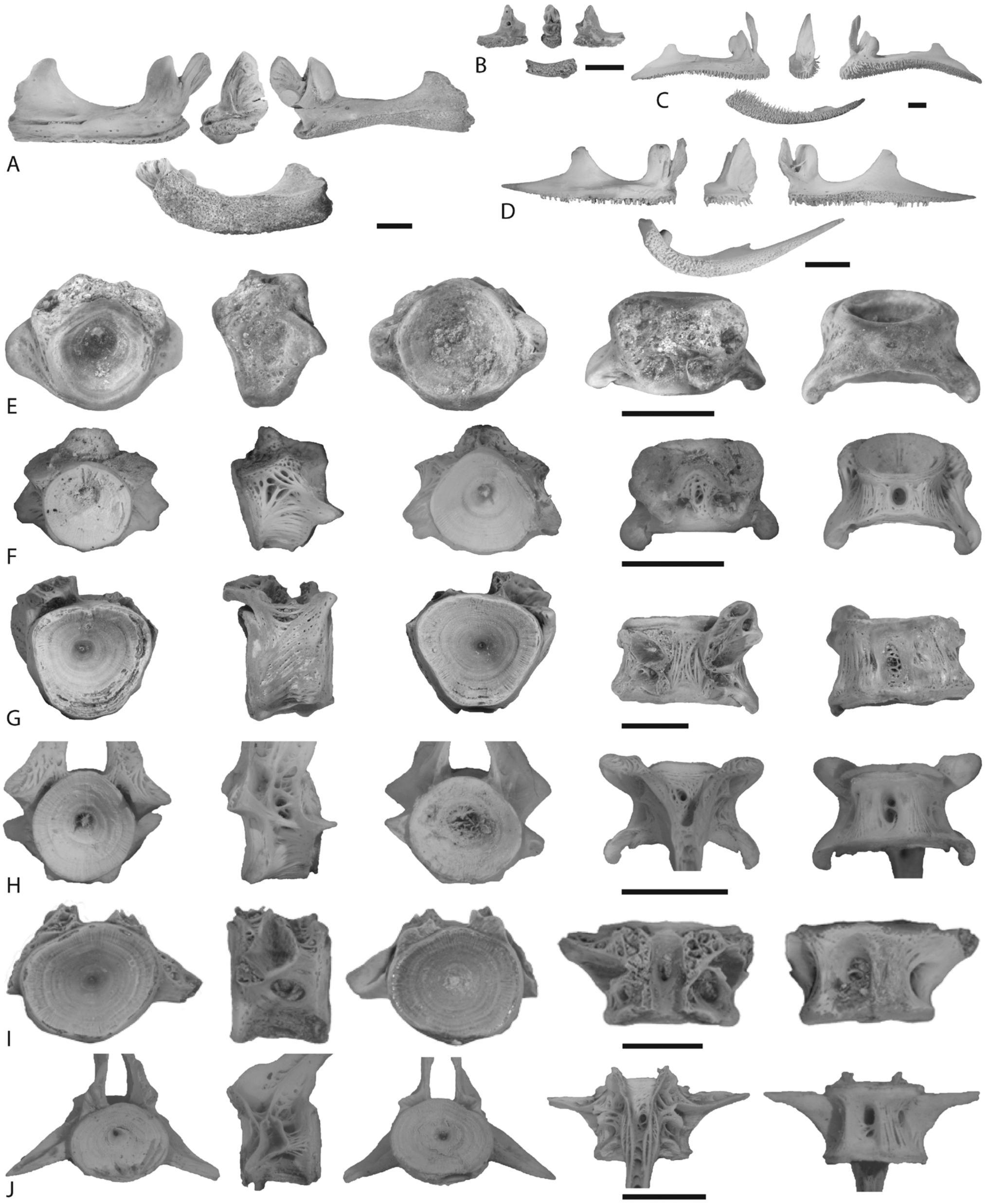
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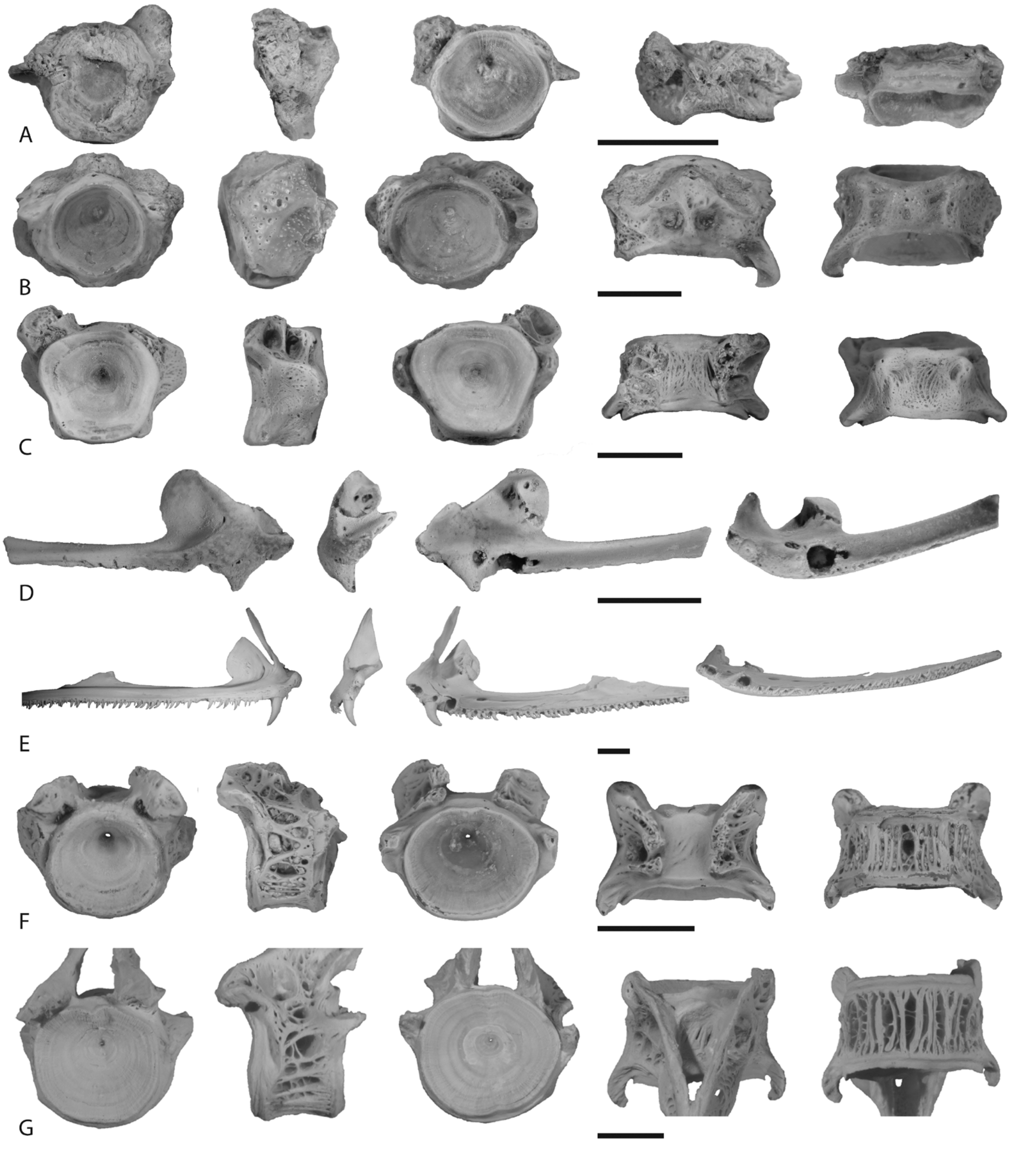
FIGURE 2.11. Wood Mountain Perciformes (**A**–**D**, **F**) and comparative (**E**, **G**) material. **A**, cf. *Pomoxis* pathologic abdominal centrum (ROM 64982); **B**, ?Percidae first centrum (ROM 65015); **C**, ?Percidae anterior abdominal centrum (ROM 65018); **D**–**G**, *Stizostedion* material: **D**, *Stizostedion* right premaxilla (CMN 54209); **E**, *Stizostedion vitreum* (UAMZ 8420) right premaxilla; **F**, *Stizostedion* anterior abdominal centrum (ROM 53651); **G**, *Stizostedion vitreum* (UAMZ 8421) anterior abdominal centrum. Premaxillae are presented, from left to right, in lateral, anterior, medial and ventromedial views. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.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APPENDIX 2.1. Comparative material examined. All of these specimens are dried skeletons, and each number represents an individual specimen.

Family Anguillidae: *Anguilla rostrata* Lesueur, 1817a – ROM R1721

Family Catostomidae: *Carpiodes carpio* (Rafinesque, 1820a) – KU 12732; *Carpiodes cyprinus* (Lesueur, 1817b) – CMN 77-183; *Catostomus catostomus* (Forster, 1773) – UAMZ F8558, F8582; *Ictiobus cyprinellus* (Valenciennes in Cuvier and Valenciennes, 1844) – KU 15337; *Moxostoma macrolepidotum* (Lesueur, 1817b) – ROM R7377

Family Centrarchidae: *Lepomis gibbosus* (Linnaeus, 1758) – CMN 73-236C; *Lepomis macrochirus* Rafinesque, 1819 – ROM R6210; *Micropterus dolomieui* Lacepède, 1802 – CMN 73-258, ROM R6125 (juvenile); *Pomoxis nigromaculatus* (Lesueur in Cuvier and Valenciennes, 1829) – CMN 76-075

Family Chanidae: *Chanos chanos* (Forskål, 1775) – UAMZ F8550

Family Cottidae: *Cottus bairdi* Girard, 1850 – ROM R6589; *Cottus cognatus* Richardson, 1836 – CMN 80-185; *Myoxocephalus octodecemspinosus* (Mitchill, 1814) – ROM R2430

Family Cyprinidae: *Campostoma anomalum* (Rafinesque, 1820b) – ROM R7890; *Chrosomus eos* Cope, 1861 – ROM R7897; *Clinostomus elongatus* (Kirtland, 1840a) – ROM R7754; *Cyprinella spiloptera* (Cope, 1867) – ROM R6823; *Cyprinus carpio* Linnaeus, 1758 – UAMZ F8557; *Hybognathus hankinsoni* Hubbs in Jordan, 1929 – ROM R2569; *Luxilus cornutus* (Mitchill, 1817) – ROM R6425; *Macrhybopsis storeriana* (Kirtland, 1844) – ROM R6385; *Nocomis biguttatus* (Kirtland, 1840a) – ROM R5358; *Notemigonus crysoleucas* (Mitchill, 1814) – ROM R7664; *Notropis atherinoides* Rafinesque, 1818c – ROM R2561; *Pimephales notatus* (Rafinesque, 1820b) –

ROM R7750; *Ptychocheilus oregonensis* (Richardson, 1836) – ROM R6513; *Semotilus atromaculatus* (Mitchill, 1818) – ROM R5885; *Semotilus margarita* (Cope, 1867) – CMN Z-668

Family Esocidae: *Esox lucius* Linnaeus, 1758 – UAMZ F8551, F8552; *Esox masquinongy* Mitchill, 1824 – ROM R2243; *Esox niger* Lesueur, 1818b – CMN 87-385

Family Fundulidae: *Fundulus heteroclitus* (Linnaeus, 1766) – ROM R3852

Family Hiodontidae: *Hiodon alosoides* (Rafinesque, 1819) – UAMZ F8556

Family Ictaluridae: *Ameiurus natalis* (Lesueur, 1819) – ROM R7245; *A. nebulosus* (Lesueur, 1819) – CMN 77-254; *Ictalurus punctatus* (Rafinesque, 1818d) – UAMZ F8553; *Noturus flavus* Rafinesque, 1818a – CMN 77-182, UAMZ 7527

Family Lotidae: *Lota lota* (Linnaeus, 1758) – CMN 85-603, ROM R1850

Family Moronidae: *Morone americana* (Gmelin, 1789) – ROM R6327; *Morone chrysops* (Rafinesque, 1820c) – ROM R6377; *Morone saxatilis* (Walbaum, 1792) – UAMZ F8554

Family Osmeridae: *Osmerus mordax* (Mitchill, 1814) – CMN Z-4079

Family Percidae: *Perca flavescens* (Mitchill, 1814) – UAMZ 4821, UMMZ 171120, 175905 (8 of 9), 175905 (9 of 9), 179978, 194309; *Stizostedion vitreum* (syn. *Sander vitreus*) (Mitchill, 1818) – UAMZ F8420, F8421

Family Percopsidae: *Percopsis omiscomaycus* (Walbaum, 1792) – ROM R6493

Family Salmonidae: *Coregonus clupeaformis* (Mitchill, 1818) – CMN 73-259b.; *Stenodus leucichthys* (Güldenstädt, 1772) – CMN Z4206

Family Scianidae: *Aplodinotus grunniens* Rafinesque, 1819 – CMN Z-275; *Rhinichthys cataractae* (Valenciennes in Cuvier and Valenciennes, 1842) – ROM R6592

Family Umbridae: *Umbra limi* (Kirtland, 1840b) – ROM R7818

CHAPTER 3

The late Eocene–early Oligocene ichthyofauna from the Eastend area of the Cypress Hills Formation, Saskatchewan, Canada.[*]

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INTRODUCTION

After the first discovery of vertebrate fossils in the Cypress Hills by McConnell in 1883 (McConnell, 1885) and their initial descriptions by Cope (1885; 1891) and Lambe (1908), fossils from the Cypress Hills Formation have been the basis of many publications. However, a full description of the ichthyofauna of the formation has never been published. This fauna is described here.

The Cypress Hills Formation was formally described by Williams and Dyer (1930), but the deposits were first studied by McConnell (1885), who attributed them to the lower Miocene, corresponding to the Oligocene in later terminology (Vonhof, 1969). The formation was then thought to represent a limited period of deposition during the Chadronian North American Land Mammal Age, based on the assumption that fossils collected from scattered localities of different stratigraphic levels derived from a single horizon (Storer and Bryant, 1993; Storer, 1996). This led to the establishment of the now abandoned “Cypress Hills Oligocene,” although the Chadronian has since been re-interpreted as representing the last Eocene land mammal age (Swisher and Prothero, 1990). Extensive biochronological work on Cypress Hills mammalian material later led to the recognition of several distinct local faunas, representing a near-continuous period of deposition of more than 28 million years, between the late Eocene Uintan and the early Miocene Hemingfordian (Storer and Bryant, 1993; Storer, 1996). To the north of the town of Eastend, Saskatchewan, deposits are biostratigraphically dated to the latest Eocene Chadronian (Calf Creek Local Fauna, Carnagh Local Fauna, Irish Spring Local Fauna, KSW Local Fauna, and Anxiety Butte Chadronian), the earliest Oligocene Orellan (Fossil Bush Local Fauna and Anxiety Butte Orellan), and the early Oligocene Whitneyan (Rodent Hill Local Fauna and Anxiety Butte Whitneyan) land mammal ages (Storer and Bryant, 1993; Storer, 1996; Bell, 2004). The Eastend area of the Cypress Hills Formation, sometimes referred to as the eastern area of the formation (Leckie and Cheel, 1989), is therefore composed of sediments deposited between approximately 37 and 30 Ma (Swisher and Prothero, 1990; Prothero, 1995). The Calf Creek Local Fauna is the most diverse of these local faunas, and best approximates the formerly recognised "Cypress Hills Oligocene" (Storer, 1996). It comprises about 75 mammalian species from more than 40 families, according to Storer (1996). The Calf Creek avifauna includes three families, each represented by a single monotypic genus erected based on Cypress Hills material (Weigel, 1963). The Calf Creek herpetofauna has also been described and comprises 13 families, all of which are extant (Holman, 1963; 1968; 1972). Holman (1972) noted the distinctly modern aspect of the Calf Creek herpetofauna, and of the amphibian fauna in particular, contrasting it to the mammalian taxa, none of which represent extant genera, and of which more than half of the 19 mammalian families then recognised are extinct. Petrified wood fragments have also been recovered, indicating the presence of six plant families in the local flora (Roy and Stewart, 1971).

According to Holman (1972), the Calf Creek herpetofauna suggests subtropical palaeoclimates with freezing temperatures rare or absent. This is mainly indicated by the presence of a relatively large boid snake, a crocodilian, and land tortoises (Holman, 1972). The six plant families recognised by Roy and Stewart (1971) represent a mix of temperate and warm-temperate taxa. Only one of these families, Pinaceae, still occurs in the area; the rest are limited to more southern and either more eastern or western parts of North America, or to eastern Asia (Roy and Stewart, 1971). The fossil assemblage as a whole, therefore, indicates that southern Saskatchewan climates were much warmer in the late Eocene and early Oligocene than at present.

In addition to climatic indications, the herpetofauna also suggests permanent water bodies through the presence of a soft-shelled turtle, an aquatic emydid turtle and a crocodilian (Holman, 1972). The presence of a sandpiper in the formation (Weigel, 1963) is consistent with this interpretation. However, the nearby presence of in situ nodular silcretes indicates strongly seasonal rainfall or arid conditions being prevalent at least locally in the interchannel zones of the floodplain (Leckie and Cheel, 1990). Silcretes could also indicate poor water drainage, and high but fluctuating pH environments, similar to conditions in a periodically flooded alkaline pan (Leckie and Cheel, 1990). That these nodules were found overlying lacustrine deposits and as fragments forming part of flood-deposited breccias (Leckie and Cheel, 1990) does, however, suggest that these arid conditions were not constant. At least part of the local vegetation was deciduous, as indicated by several taxa recovered among the petrified wood remains (Roy and Stewart, 1971), and the amphibian taxa attributed to *Ambystoma* and *Scaphiopus*, which are fossorial and associated with deciduous forests (Holman, 1972). Overall, the herpetofauna suggests a mix of habitats, including open woodland or shrubby grassland with loose soil (Holman, 1972). The dentition of the rodent assemblage from the early Oligocene Rodent Hill Locality (Whitneyan land mammal age) further indicates that grasses were not yet dominant in the area, based on the tooth crown of these taxa being lower than that of more recent forms (Bell, 2004).

Previous work on the fishes of the formation has been restricted to material referred to Lepisosteiformes (Lambe, 1908; Grande, 2010), Amiiformes (Cope, 1891; Ami, 1891; Lambe, 1908; Boreske, 1974; Grande and Bemis, 1998), and Siluriformes (Cope, 1891; Lambe, 1908; Lundberg, 1975). Material from the Cypress Hills Formation was used to erect *Lepidosteus longus* Lambe, 1908. This taxon was later considered a nomen dubium by Grande (2010), who referred to the material only as representing an indeterminate lepisosteiform. Similarly, amiiform material from the formation was named *Amia whiteavesiana* Cope, 1891, *A. macrospondyla* Cope 1891, and *A. exilis* Lambe, 1908. Boreske (1974) referred the *A. exilis* material to *A. scutata* Cope, 1871; while Ami (1891) mentioned the presence of *A. selwyniana* in the Cypress Hills collections. Grande and Bemis (1998) considered all of the Cypress Hills amiid material to be diagnostic only at the subfamilial level, and referred the material to an indeterminate amiine taxon. The siluriform fossils of the formation were named by Cope (1891) as three new species: *Rhineastes rhaeas* Cope, 1891, *Amiurus cancellatus* Cope, 1891 and *Amiurus maconnellii* Cope, 1891. However, Lundberg (1975) argued that the material was not diagnostic enough to form the basis of new taxa and attributed Cope's *Rhineastes* material to *Astephus* sp. and the other two taxa to *Ictalurus* sp., the subgenus *Ictalurus* recognised at the time having been raised to generic level since (Miller, 1986).

Geological Setting

The Cypress Hills Formation is represented by erosional remnants of fluvially deposited and weakly cemented gravels, conglomerates and sandstones, along with volcanic ashes, bentonite, silt, clay and marl (Vonhof, 1969; Leckie and Cheel, 1989; Leckie, 2006). The western part of the formation has relatively more large clasts, while average grain size is smaller in the eastern part of the formation (Vonhof, 1969; Leckie and Cheel, 1989; Leckie, 2006), in an area corresponding to where the fossils described here were recovered (Leckie and Cheel, 1989). In this area, lacustrine marlstones and fossil-bearing debris-flow deposits are interbedded with the deposits of braided channels up to nine metres deep, occasionally cutting into the lake deposits (Leckie and Cheel, 1989). The formation ranges in thickness between approximately 30 and 50 metres in the area north of Eastend (Vonhof, 1969, reported as 100 to 160 feet). These sediments represent the distal areas of a wide braidplain, with low-sinuosity rivers flowing north-northeast towards what is now the Hudson Bay (Leckie and Cheel, 1989; Leckie, 2006). Sediments were derived from the Rocky Mountains of western Montana, with tributaries coming from the Sweetgrass Hills, Highwood and Bearpaw Mountains, as indicated by the lithology of the Cypress Hills pebbles (Vonhof, 1969) and the proximal – distal eastward trend of relative clast sizes (Leckie and Cheel, 1989; Leckie, 2006). Several of the fossiliferous beds in the study area correspond to Leckie and Cheel's (1989) conglomeratic breccias and associated sandstones, which they interpreted as representing debris-flow deposits resulting from flooding episodes. According to Leckie and Cheel's

(1989) proposed depositional setting, the eastern parts of the formation would correspond to the most distal parts of the braidplains, where river channels would have represented a smaller proportion of the sedimentation than interchannel deposits. In these areas, lakes in alluvial flats, grasslands and open woodland would have accumulated skeletal material, which would become incorporated into debris-flow deposits caused by flash-flooding resulting from rare, torrential precipitation in the highlands (Leckie and Cheel, 1989).

MATERIALS AND METHODS

The fossils described here represent the combination of fish material recovered from 37 localities by several field expeditions between 1949 and 1972, through both surface-collecting and sediment dry-screening (Appendix 3.1). The majority of these localities are to the north and northwest of the town of Eastend, in Tp. 7 R. 21 (approximately latitude 49.525564, longitude -108.718057), Tp. 7 R. 22 (approximately latitude 49.525591, longitude -108.853864), and Tp. 8 R. 22 (approximately latitude 49.612941, longitude -108.853883), W. 3rd meridian. Additional localities are to the southwest of Eastend, in Tp. 3, R. 22, W 3rd meridian (approximately latitude 49.176126, longitude -108.833781), and to the northeast of Eastend, in Tp. 9, R. 20 (approximately latitude 49.700292, longitude -108.582649), W. 3rd meridian (Fig. 3.1). Some of the material included in this study was recovered from localities for which no precise geographical and stratigraphical information was recorded. Because of the complex stratigraphy of the Cypress Hills

Formation, and because of the lack of geographic and stratigraphic information for some of the localities, it is possible that some of the material originates from localities falling outside of the Chadronian to Whitneyan land mammal age time interval. However, all taxa reported are known from localities that are within the townships and ranges indicated above, representing this time period.

Material Examined

All of the fossil material reported here is curated in the Royal Ontario Museum, Toronto, Ontario, Canada (ROM). Extant comparative material (Appendix 3.2) is from the Canadian Museum of Nature, Ottawa, Ontario, Canada (CMN), ROM, University of Michigan Museum of Zoology, Ann Arbor, Michigan, U.S.A. (UMMZ), University of Kansas Natural History Museum, Lawrence, Kansas, U.S.A. (KU), and University of Alberta Museum of Zoology, Edmonton, Alberta, Canada (UAMZ). Fossil comparative material is from the University of Alberta Laboratory of Vertebrate Palaeontology, Edmonton, Alberta, Canada (UALVP).

Methods

Comparisons with the modern taxa listed in Appendix 3.2 and with articulated fossil specimens from the Green River Formation curated in the UALVP formed the basis of the identifications of the isolated fossils. Nelson's (2006) taxonomic system was followed. Wherever possible, taxonomic attributions were based on features interpreted to represent autapomorphies. In some cases, however, identifications had to be made based on general phenetic similarities. The material was coated in ammonium chloride prior to photographing. A Nikon DXM 1200C digital camera mounted on a Zeiss Discovery.V8 stereo microscope was used to photograph the specimens.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII Cope, 1887
Order LEPISOSTEIFORMES Hay, 1929
Family LEPISOSTEIDAE Cuvier, 1825
LEPISOSTEUS Lacépède, 1803
(Fig. 3.2A, B)

Material—Three complete scales (ROM 66987–66989), Fig. 3.2A; two fragmentary scales (ROM 67024, 67110); three abdominal centra (ROM 66990–66992), Fig. 3.2B.

Description—The scales are rhomboid and their external surfaces are covered in ganoin. Their edges are unserrated. The dorsal peg and anterodorsal process (sensu Grande, 2010) are variously developed in these specimens.

The centra are opisthocoelous, wider than high, and holospondylous. The dorsal surfaces of all centra are poorly preserved, with broken surfaces extending between anterior and posterior articular surfaces along their midlines. These broken surfaces presumably correspond to the area where the neural arches are fused to the centrum. Wide and stout parapophyses project from the lateral surfaces of the centra, bearing an articular pit for the pleural rib on their distal end. The ventral surface bears a pair of longitudinal parasagittal processes close to the midline of the centrum, extending for its full length. The surface of the bone is smooth; it is also slightly porous on the anterior and posterior articular surfaces.

Remarks—This material is not diagnostic enough to identify at the species level, as previously noted by Grande (2010). The shape and ganoin covering of the scales are characteristic of the Lepisosteidae. They lack serrations and surface ornamentations, which are present in *Atractosteus* (Grande, 2010); these are therefore attributed to *Lepisosteus*. The variable development of the dorsal peg and of the anterodorsal processes suggests that both flank and caudal scales are represented in the assemblage. The centra can also be attributed to the Lepisosteidae, as opisthocoelous centra are characteristic of these fishes (Grande, 2010). A number of extremely poorly preserved, conical teeth from the formation probably also represent lepisosteid material; however these are too worn to be diagnostic.

Order AMIIFORMES Hay, 1929 (sensu Grande and Bemis, 1998)
Suborder AMIOIDEA Bonaparte, 1832 (sensu Grande and Bemis, 1998)
Family AMIIDAE Bonaparte, 1832
Subfamily AMIINAE Bonaparte, 1838
(Fig. 3.2C–F)

Material—One partial maxilla (ROM 66920), Fig. 3.2C; one partial dentary (ROM 67051), Fig. 3.2D; 37 abdominal centra (ROM 66921–66923, 66965, 66970, 66971, 67013–67015, 67025, 67031–67034, 67052, 67063, 67064, 67073, 67094, 67111–67113, 67126, 67132, 67142, 67153–67155, 67168, 67170, 67172, 67182, 67190, 67199, 67202–67204), Fig. 3.2E; 10 caudal centra (ROM 66924, 66935, 66972, 67035, 67036, 67065, 67074, 67156, 67174, 67205), Fig. 3.2F.

Description—The maxilla and dentary are robust, and both have a single tooth row. Neither preserves articulated teeth. The tooth bases are oval, being wider medio-laterally than they are long antero-posteriorly.

The only articular surface preserved on the maxilla (ROM 66920, Fig. 3.2C) is the surface on which the supramaxilla attaches. This area is posterior to a slight supramaxillary notch, on the dorsal surface of the maxilla. Two maxillary foramina are preserved on the medial surface of the element, anterior to the supramaxillary notch. The anterior-most foramen is only partially preserved on the broken anterior surface of the element. The tooth bases increase in size anteriorly, towards the symphysis. The medial side of the element has a smooth surface, while the lateral side has shallow striations, predominantly oriented longitudinally.

The dentary (ROM 67051, Fig. 3.2D) is much smaller and more weathered than the maxilla. It is deeper and more incomplete posteriorly, tapering into a rounded and weathered symphyseal surface on its anterior end. The medial surface has a bony shelf extending longitudinally where the coronoid plates (sensu Grande and Bemis, 1998) would have articulated in life. The lateral surface of the element has a series of eight foramina, alternating in placement from adjacent to the ventral margin of the bone, to nearer to the tooth row. The bone surface is smooth on the medial side of the element. The lateral side is covered in shallow longitudinal striations and small pits, giving a fibrous appearance to the bone on this surface.

The centra are oval in end view, rectangular in lateral view, and have shallow articular surfaces at their anterior and posterior ends, with a centrally located notochordal foramen. Abdominal centra (Fig. 3.2E) are wider than they are high or long. Relatively shallow rectangular neural arch pits extend for the full length of the centrum on the dorsal surface. The lateral surface has fused parapophyses of variable lengths depending on the placement of the centrum along the vertebral series. The distal end of these parapophyses has an oval articular pit for the rib. A pair of narrow rectangular pits is present ventrally. These pits are smaller and closer to the midline than the neural arch pits, and represent the aortal facets for the articulation of a cartilaginous haemal process, as in *Amia calva* (Goodrich, 1958; Grande and Bemis, 1998). Caudal centra (Fig. 3.2F) are similar to the abdominal centra, but are typically slightly longer, and higher than wide. The caudal series also lacks parapophyses, and these centra have ventral articular pits for the haemal arch instead of the aortal facets. In all centra, the surface sculpturing is uniform and shallow, consisting of a network of thin, antero-posteriorly directed bony struts.

Remarks—The bony texture of the lateral surfaces of the maxilla and dentary, along with their tooth bases being wider than long, are characteristics consistent with those of the Amiidae. The attribution of the fossils to this family is additionally supported by the presence of the supramaxillary notch on the maxilla, and of the medial bony shelf of the dentary (Grande and Bemis, 1998).

The centra can be attributed to the Amiidae, based on the characteristic aortal facets in the abdominal series, shape of the neural arch articular pits, and surface sculpturing. Additionally, the fusion of the parapophyses to the centra allows these elements to be attributed to the subfamily Amiinae (Grande and Bemis, 1998). However, as noted by Grande and Bemis (1998), the Cypress Hills elements have no unique diagnostic that would allow them to be assigned to a genus.

Division TELEOSTEI Müller, 1846
Subdivision OSTEOGLOSSOMORPHA Greenwood, Rosen, Weitzman, and Myers, 1966
Order HIODONTIFORMES McAllister, 1968
Family HIODONTIDAE Valenciennes in Cuvier and Valenciennes, 1846
Aff. *HIODON* Lesueur, 1818
(Fig. 3.2G, H)

Material—Two abdominal centra (ROM 67133, 67200).

Description—These centra are approximately as high as they are long and have a centrally located notochordal foramen. The larger centrum (ROM 67200, Fig. 3.2G) is shorter and has a relatively much smaller notochordal foramen than the smaller centrum (ROM 67133, Fig. 3.2H). The articular surfaces at the anterior and posterior ends of the former are also distinctly triangular, having a wide and flat ventral margin, while the smaller centrum is more circular in end view. The dorsal surfaces bear a pair of small, characteristically rounded pits located close to the anterior end of the centra. These pits are separated by an hourglass-shaped bony ridge. The broken bases of the parapophyses, which are fused to the centrum, are visible on the ventral margin of the lateral surfaces in both centra, with a rib articular pit immediately posterior to these. The lateral surfaces also have an elongate accessory pit, immediately dorsal to the parapophyses and rib articular pits, extending for the full length of the centrum. The ventral surface is distinctively flat, featureless in the larger centrum (ROM 67200, Fig. 3.2G), but with an elongate pit extending along the midline of the smaller element (ROM 67133, Fig. 3.2H). The bone surfaces have limited texturing, most notable on the dorsal surfaces, which have shallow pitting in no clear orientation.

Remarks—The shallow, rounded, relatively small neural arch pits close to the anterior end of the centrum, fused parapophyses and rib articular pits posterior to the base of the parapophyses are characters supporting the attribution of these centra to the Hiodontidae. These centra are morphologically identical to those of *Hiodon* (Fig. 3.3A), the only extant genus of the Hiodontiformes, which still occurs in the area (Scott and Crossman, 1973). The Cypress Hills specimens can be differentiated from the Cretaceous hiodontid centra described by Brinkman and Neuman (2002) because the latter lack the accessory pit on the lateral surface, above the parapophysis. However, the detailed morphology of the centra of *Eohiodon* is currently unknown, therefore whether the Cypress Hills centra represent *Hiodon* or *Eohiodon* cannot be determined.

The elements probably represent juvenile individuals, based on the large relative sizes of the notochordal foramen and on their small overall sizes. However, given the small adult sizes of some hiodontids, especially Cretaceous taxa, this would have to be tested with a growth study similar to that of Newbrey et al. (2007), which would require access to a larger sample of centra. The triangular articular surfaces of the larger centrum (ROM 67200, Fig. 3.2G) indicate that it represents a centrum in a more anterior position along the vertebral series than the smaller centrum (ROM 67133, Fig. 3.2H).

Subdivision OSTARIOCLUPEOMORPHA Arratia, 1997 (= OTOCEPHALA Johnson and Patterson, 1996)

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

Order CYPRINIFORMES Bleeker, 1859

Family CATOSTOMIDAE Gill, 1862a

(Fig. 3.3B, F)

Material—Fifteen centra from the Weberian apparatus, 12 of which are the first centra of the vertebral series (ROM 66925, 66937, 66938, 66973, 66974, 67053, 67116, 67117, 67143, 67144, 67189, 67191), Fig. 3.3B; three represent the anterior part of the second vertebral centrum (ROM 66939, 66950, 67192), Fig. 3.3F.

Description—The first centra (Fig. 3.3B) are characteristically short relative to their height and width. In anterior view, the centrum is rectangular, being wider than high, and is essentially flat, although some centra have bulges along the outer margins of their ventro-lateral areas. The posterior end of the centrum is concave, much wider than the anterior articular surface, and is weakly keeled both dorsally and ventrally. The midline of the dorsal surface has an elongate pit, bordered by a pair of bony ridges. Lateral to these ridges is a pair of circular pits for articulation with the scaphium, which are larger than the median pit. The rest of the dorsal surface is either featureless or weakly pitted. Transverse processes extend from the area of the lateral surface at the widest point of the centrum, as seen in posterior view. The transverse process is oriented laterally, and its base is adjacent to the posterior end of the centrum. A shallow depression is present on the lateral surface, ventral to the base of the transverse process. The ventral surface has a very shallow transverse depression at mid-length of the centrum, bordered posteriorly by a slightly projecting ridge of bone.

All three specimens representing the second centrum of the Weberian apparatus (Fig. 3.3F) are incomplete posteriorly and only preserve the anterior articular surfaces and areas adjacent to them. The shape of the anterior end of the centrum approximates a diamond, having broad, wing-like lateral projections and being keeled both dorsally and ventrally. The dorsal keel is less sharp than the ventral keel. The dorsal side of these elements is characteristic in having two elongated articular pits for the neural arch, separated by a thin sheet of bone. The surface of the bone within these pits is different from all other surfaces in being rough, giving it a frosted appearance. The dorsal surfaces of the wing-like lateral projections at the anterior end of the centrum are more heavily pitted than the ventral surfaces. The ventral surface of the centra has a pair of small pits close to the anterior end of the centrum, which are separated by a thin, occasionally forked bony strut. Posterior to this area, a blunt keel of heavily pitted bone extends to the broken posterior end of the most complete element (ROM 67192). Aside from the articular pits for the neural arches and the under surface of the lateral wing-like projections, most bone surfaces have numerous pits, organized in no particular orientation.

Remarks—The first centra (Fig. 3.3B) have the disc-shape characteristic of cypriniform first centra, including both cyprinids and catostomids. They are more similar to catostomids in being wider than high, and in the dorso-lateral placement of the transverse processes. These features are seen in catostomid comparative material (Fig. 3.3C, D) but not in modern cyprinids (Fig. 3.3E), which have first centra that are higher than wide, with transverse processes located ventro-laterally. Therefore, the fossils are attributed to the Catostomidae based on these characteristics. A more precise identification of the fossils is impossible however, because the first centra of many modern catostomids have very similar morphologies.

The elements representing the anterior parts of the second vertebral centra (Fig. 3.3F) are similar to the second Weberian centra of catostomid (Fig. 3.3G) and cyprinine fishes (Fig. 3.3H). The anterior articular surfaces articulate to the posterior articular surfaces of the first centra in life, and the corresponding shapes of these surfaces in the fossils described here permit their attribution to the same catostomid fossil taxon. Weberian elements representing the second centrum of the vertebral series were also recovered from the Miocene Wood Mountain Formation of southern Saskatchewan (Chapter 2; Divay and Murray, 2013), where the articular surface at the posterior end of the centrum was distinctly smaller than the articular surface at the anterior end. It is not known whether or not the Cypress Hills Formation fossils also possess this character, because this part of the centrum is not preserved in these fossils.

Family CYPRINIDAE Bonaparte, 1832

Subfamily LEUCISCINAE Günther, 1868

Aff. *PTYCHOCHEILUS* (Richardson, 1836)

(Fig. 3.4A)

Material—Five abdominal centra (ROM 66926, 66976, 67139, 67193, 67194).

Description—These centra are approximately as high as they are wide or long. In end view, the centra are approximately circular, although their widest point is slightly ventral to the mid-height. The notochordal foramen is located centrally. The anterior and posterior articular surfaces are surrounded by a slightly projecting margin of smooth bone. The broken bases of the neural arch extend the full length of the centrum, on either side of a deep mid-dorsal pit. A deep accessory pit occupies the dorso-lateral surface of the centrum. Variably interconnected longitudinal bony struts form a bony network occupying the rest of the lateral surfaces. The characteristically triangular parapophyseal articular pit is adjacent to the anterior end of the centrum. This pit is delimited by a slightly projecting transverse bony ridge ventro-laterally, within this network of bony struts. The parapophyseal articular pit is restricted to the anterior part of the centrum, never extending its full length. The ventral surface of the centrum has a deep and elongate mid-ventral pit along the midline of the centrum. In some centra, the bony struts on either side of this pit are the same as those delimiting the ventral margin of the parapophyseal articular pits. In centra where this is not the case, both pairs of longitudinal struts are extensively interconnected with several transverse bony struts. The bony surfaces of these centra lack any characteristic texture.

Remarks—These centra have several cypriniform characteristics, including the presence of a median pit both dorsally and ventrally, the presence of a single accessory pit in the dorsal part of the lateral surface, as well as the characteristic depth of all of these pits, which all extend to the core of the centrum. However, the network of bony struts occupying the more ventral part of the lateral surface, and the parapophyseal articular pit being limited to the anterior part of the lateral surface, differentiates these centra from those of several other cypriniforms. These characteristics, as well as the distinctive triangular shape of the parapophyseal articular pits, are features seen in some leuciscine cypriniforms. However, most modern leuciscines are much smaller fishes than the taxon represented by the fossils, and several lack a mid-ventral pit, having a flat featureless bony surface on their ventral side instead. Within the Leuciscinae, the fossils most closely resemble *Ptychocheilus* centra (Fig. 3.4B), which are of similar size and possess the mid-ventral pit. However, the networks of bony struts seen in several areas of the fossil centra are more extensive than those seen in *Ptychocheilus*; therefore the fossils probably indicate the presence of a distinct, large leuciscine taxon with affinities to *Ptychocheilus*.

Family CATOSTOMIDAE Gill, 1862a or CYPRINIDAE Bonaparte, 1832

(Fig. 3.4C)

Material—Five first Weberian centra (ROM 66936, 66958, 66959, 67115, 67171).

Description—These first centra of the vertebral series are much shorter than they are high or wide. The anterior articular surface is essentially flat, but bulges slightly forward on its ventro-lateral margins. The posterior articular surfaces are distinctly concave. Both anterior and posterior articular surfaces are oval, being slightly higher than wide. The dorsal surface has a median ridge of bone, between a pair of circular pits for articulation with the scaphium. The lateral surface has a low bony ridge extending between the dorso-lateral and the ventro-lateral areas of the centrum, connecting to the bases of the transverse processes. These transverse processes are clearly oriented ventro-laterally. The ventral surface has a median flat bony surface, bordered by low bony ridges. This flat bony surface is between a pair of small circular pits. All surfaces of the centrum lack clear texturing, aside from the mid-dorsal ridge, which is variously porous, depending on specimens.

Remarks—These distinctive, disc-like first centra are characteristic of the first Weberian centrum of both catostomids and cyprinids. However, the catostomid comparative material (Fig. 3.3C, D) either has transverse processes fused to the dorso-lateral margin of the centrum, or very short, indistinct transverse processes. The ventro-laterally oriented transverse processes of the fossils are more similar to those of cyprinine cyprinids (Fig. 3.3E). Catostomids occur in North America from the Eocene (Cavender, 1998)—and possibly as early as the Paleocene (Wilson, 1980)—onwards. However, the only cyprinid subfamily reliably known to occur in North America is the Leuciscinae, first appearing in Oligocene deposits (Cavender, 1998). Most modern leuciscines are much smaller than the fossil, and their transverse processes, although similar to those of the fossils in being fused to the centrum ventrally, are different in that they project laterally, rather than ventrolaterally. In addition, some leuciscines, such as *Ptychocheilus*, also differ in that, although their first centrum is also disc-like, it is slightly longer than the fossils. Cyprinine cyprinids (Fig. 3.3E) share all characteristics seen in the fossil centra, but are not reliably known to occur in North America (Cavender, 1998). Therefore, the fossils either indicate the presence of cyprinines in North America, or the presence of an indeterminate catostomid or leuciscine taxon distinct to those described above, with a cyprinine-like morphology of the first centrum. Similar fossils were found in the Miocene Wood Mountain Formation of Saskatchewan, together with second Weberian centra of a distinctively cyprinine-like morphology, which led to the same conclusion (Chapter 2; Divay and Murray, 2013).

Indet. cypriniform centra

(Fig. 3.4D, E; 5A)

Material—Seventeen abdominal centra (ROM 66966, 66975, 66993, 67018, 67044, 67066, 67076, 67096, 67118, 67134, 67135, 67157, 67173, 67175, 67179, 67201, 67206), Fig. 3.4D, E; one compound ural centrum (ROM 66964), Fig. 3.5A.

Description—The abdominal centra (Fig. 3.4D, E) are approximately as high as they are wide, and their length is shorter or subequal to their height. Depending on the position of the centra along the vertebral series, the articular surfaces on their anterior and posterior ends are either wider and flatter ventrally with a slightly dorsal notochordal foramen, as in anterior abdominal centra, or circular with a central notochordal foramen, as in more posterior abdominal centra. A very deep, elongate pit extends between anterior and posterior ends of the centrum along its midline both dorsally and ventrally. The dorsal pit is bordered by the broken bases of the neural arch, which also extend for the full length of the centrum. The parapophyseal articular pits are characteristically large and deep, occupying the ventral half of the lateral surface. These pits are approximately rectangular, extending the full length of the centrum, and sometimes preserve the base of the parapophysis in articulation with the centrum, as in ROM 67018 (Fig. 3.4E). The dorsal half of the lateral surface has a deep, rectangular accessory pit that is slightly smaller than the parapophyseal articular pit. It is usually bisected by a single ridge of bone connecting the base of the parapophysis to that of the neural spine, but some low, interconnected bony ridges are also sometimes present within this pit. The surfaces of these centra generally lack bone texturing, although some superficial pitting is sometimes present on the anterior and posterior parts of the bony ridge that separates the accessory pit from the parapophyseal articular pit.

The ural centrum (Fig. 3.5A) is long, but does not preserve the uroneural or hypural. The long axis of the centrum is angled dorsally compared to the articular surface at the anterior end of the centrum. In anterior view, the centrum is oval, being slightly higher than it is wide, and has a centrally located notochordal foramen. The posterior part of the centrum is laterally compressed and oval in cross-section, being higher than wide. The dorsal surface preserves the broken bases of the neural arch adjacent to the anterior articular surface. These broken bases extend posteriorly as bony ridges. The midline of the dorsal surface is essentially flat, with some pitting in its anterior region and shallow furrows beside the bases of the neural arch. The dorso-lateral margins of the element have deep elongated pits adjacent to the articular surface at the anterior end of the centrum. The lateral surfaces have sinuous plications and some pitting. The ventral surface has a deep articular pit occupying its entire width in the anterior region, for articulation with the parhypural and first hypural. The ventral surface is poorly preserved posterior to this pit. All bone surfaces are smooth and lack any characteristic texture.

Remarks—The morphology of the abdominal centra is clearly different from that of leuciscine cyprinids, including those described above, but is similar to both catostomids (Fig. 3.4F) and cyprinines (Fig. 3.4G), which cannot be distinguished based on disarticulated abdominal centra. It is likely that these abdominal centra were derived from the two cypriniform taxa represented by the more diagnostic first and second centra described above. In any case, these abdominal centra do not definitely indicate the presence of additional cypriniform fishes in the Cypress Hills Formation.

The compound ural centrum (Fig. 3.5A) is recognisable as such based on its dorsally angled long axis, when compared to the articular surface of its anterior end, as well as the mid-ventral articular surface for articulation with the parhypural and first hypural. The pitting and plications of the lateral surface and the elongated pits on the dorso-lateral margins correspond to the morphology of modern leuciscines and catostomids (Fig. 3.5B). It is additionally similar to these two taxa by its length, which is much longer than in cyprinine cyprinids. However, none of the preserved features allow the centrum to be unambiguously attributed to either the Catostomidae or the Leuciscinae; it is therefore left as Cypriniformes indet.

Order SILURIFORMES Hay, 1929 (sensu Fink and Fink, 1996)

Family ICTALURIDAE Bleeker, 1863

ASTEPHUS Cope, 1873

Taxon A

(Figs. 3.5C–G, 3.6A–C)

Material—One dentary (ROM 67077), Fig. 3.5C; one basioccipital (ROM 67054), Fig. 3.5D; 13 dorsal fin spines (ROM 66957, 66977, 66994–66998, 67097, 67158, 67159, 67195, 67207, 67208), Fig. 3.5E; 107 pectoral fin spines (ROM 66927–66930, 66940–66948, 66951, 66960–66962, 66967–66969, 66978–66981, 66985, 66999–67007, 67012, 67019–67021, 67026–67028, 67037–67040, 67045–67048, 67055, 67056, 67067–67069, 67078–67087, 67098–67105, 67119–67121, 67127–67131, 67136, 67140, 67145–67148, 67160–67164, 67169, 67176, 67177, 67181, 67183–67187, 67190, 67196, 67197, 67209–67212,), Fig. 3.5F; one first centrum of the vertebral series (ROM 67106), Fig. 3.5G; one fragment of a centrum from the compound vertebra of the Weberian apparatus (ROM 67088), corresponding to the left side of the posterior-most part of the element, Fig. 3.6A; one anterior post-Weberian abdominal centrum (ROM 67089), Fig. 3.6B; 21 more posterior abdominal centra (ROM 66931, 66932, 66949, 66952, 66963, 67008–67010, 67022, 67029, 67041, 67049, 67057–67059, 67070, 67090, 67107, 67165, 67166, 67213), Fig. 3.6C.

Description—The dentary (ROM 67077, Fig. 3.5C) is large, robust, well-preserved anteriorly but incomplete posteriorly. The tooth-bearing surface is slightly wider near the symphysis, narrowing posteriorly. The tooth bases are small, numerous, and are not oriented in rows. The symphyseal surface has a relatively flat medial margin; it bulges anteriorly to form a low symphyseal process that is directed anteriorly. The symphyseal surface has three grooves extending radially from the dorso-medial area; the most medial of these is deeper and almost vertical, dividing the symphysis into a wide anterior surface and a narrower medial one. There is a sharp antero-ventral crest that tapers anteriorly. It bifurcates near the symphysis and joins the medial and anterior margins of the symphyseal surface, forming a triangular depression in between these crests that corresponds to the deep groove of the symphyseal surface. A medial shelf projecting from the medial margin of the dentary supports the tooth pad. The medial surface of the dentary has very shallow longitudinal plications extending radially from the dorsal region adjacent to the symphysis. There are four mandibular foramina on the lateral surface of the dentary; the distance between these increases posteriorly. The surface texturing of the dentary is deepest on its lateral surface, where it forms a series of imbricated V-shaped ridges, the apexes of which occur at the foramina.

The robust basioccipital (ROM 67054, Fig. 3.5D) is weathered and incomplete both anteriorly and dorsally, but preserves part of the posterior articular surface and most of the ventral and ventro-lateral surfaces. The posterior articular surface is angular, being markedly flattened ventrally. The posterior part of the dorsal surface has a robust, projecting median ridge, flanked by wide, heavily weathered facets. The more anterior part of the element is thinner and narrower, with a very low median ridge. Shallow fossae are present on the lateral surfaces, adjacent to the posterior articular surface. Also adjacent to the posterior articular surface, the ventral surface has a deep mid-ventral pit that is oval, being slightly longer than wide. This mid-ventral pit is flanked by a pair of shallower, more elongate pits. Most of the bony surfaces of the element are markedly fibrous in texture, apart from a band of smooth bone including the lateral fossae and the ventral surface in between them. Where present, these bony fibres are oriented longitudinally.

The proximal bases of the dorsal fin spines (Fig. 3.5E) are almost in line with the spine shaft. The lateral condyles do not extend laterally beyond the triangular base. A longitudinal ridge originates on the dorsal side of the basal foramen and extends the full length of the spine on its anterior edge, thinning distally. On the proximal posterior edge, a median furrow extends from the basal foramen, enclosing a similar longitudinal ridge. The furrow narrows and disappears distally, the longitudinal ridge becoming the only structure on the posterior edge of the distal spine. Both anterior and posterior ridges have small, bump-like, finely spaced tubercles along their full lengths. Sinuous striations, oriented longitudinally, occur along the spine shaft, with numerous pits visible in the grooves between these striations.

The proximal end of the pectoral fin spines (Fig. 3.5F) have a deep, wide and elongate basal recess on their posterior surface. There is also a well-defined basal recess on the anterior surface, between the bases of the ventral process and of the dorsal articulating process; it is shorter, narrower and shallower than the posterior basal recess. The proximal surface of the ventral process forms a line with that of the dorsal articular process. The characteristic bone texture also seen on the dorsal fin spines occurs on all surfaces of the pectoral spines apart from the articular surfaces and within the basal recess. This texture is more marked in larger specimens. The spine shaft is oval in cross-section, with a furrow extending from the basal recess on the proximal part of its posterior surface. Minute serrations are visible on a small ridge on the dorsal side of this furrow. Distally, the posterior furrow closes and the ridge becomes more robust, occupying the midline of the posterior edge of the spine for the remainder of its distal portion. A similar ridge extends along the anterior edge of the spine; it is similarly finely serrated. None of the spines recovered are complete, but the best-preserved specimens show an increase of the thickness of these ridges distally, and correspondingly larger serrations on the distal spine.

The first centrum of the Weberian apparatus (ROM 67106, Fig. 3.5G) is higher than wide, and wider than long. In anterior view, the centrum is somewhat angular and pentagonal. The external margin of the posterior end of the centrum is poorly preserved. The notochordal foramen is located dorsally. Where it is preserved, the area adjacent to the articular surfaces has a slightly projecting margin of smooth bone. A pair of large circular pits for articulation with the scaphium is present on the dorsal surface of the centrum. Apart from the smooth areas immediately adjacent to the articular surfaces, the lateral surfaces are fibrous in texture, and lack any accessory pitting. The bony fibres are predominantly oriented longitudinally, but are interconnected with transverse fibres. The ventral surface has a median depression with a central pit formed by the particularly loose arrangement of the bony fibres in that area. As in extant catfishes, a pair of parasagittal processes borders this mid-ventral depression, projecting ventrally from the surface of the centrum, and the distal end of the best preserved process curves posteriorly. The latero-posterior surfaces of the processes have grooves connected to articular pits on the ventral surface of the centrum, for articulation with the compound vertebra of the Weberian apparatus. These ventral articular pits are lateral and immediately adjacent to the process bases.

The centrum of the compound vertebra of the Weberian apparatus (ROM 67088, Fig. 3.6A) is very fragmentary, preserving less than half of the posterior articular surface, and the adjacent left lateral and dorsal surfaces. The posterior end of the centrum is nearly flat, with a shallow radial bulge extending between the area of the notochordal foramen and the ventro-lateral margin of the element. Although the notochordal foramen is not preserved, the growth rings on the posterior articular surface indicate that it was located dorsally. The dorsal surface of the element is broken and abraded where the neural arch would have been fused in life. The lateral surface of the element is essentially flat and featureless, and is angled toward the midline, indicating that the complete element would be wider at its posterior end than anteriorly. Additionally, as in extant ictalurids, the ventral surface is strongly keeled, and curves gently dorsally in its more anterior part, indicating that the element would not be as high anteriorly as it is at its posterior articular surface.

The anterior post-Weberian abdominal centrum (ROM 67089, Fig. 3.6B) is characteristic in being relatively shorter than the more posterior centra, and in having markedly less angular articular surfaces at its anterior and posterior ends, with a dorsally located notochordal foramen. Unlike in more posterior abdominal centra, the bases of the neural arch and of the transverse processes are fused, forming a complex, and the transverse processes are also located more dorsally in this centrum than in more posterior positions along the vertebral series. The centrum is slightly higher than wide, and much wider than long. In anterior view, the centrum is oval; it is nearly circular in posterior view, being slightly wider ventrally than the anterior end. Both anterior and posterior articular surfaces are surrounded by a margin of smooth bone. The dorsal surface of the centrum has a pair of low longitudinal ridges delimiting a narrow, elongate mid-dorsal pit. These ridges are flanked by a pair of pits that are not as elongate as the median one. The broken bases of the neural arch-transverse process complex project from the dorso-lateral margin of the centrum, immediately lateral to these pits. These are parallel and adjacent to the articular surfaces in both their anterior and posterior areas. In between, they are connected by median longitudinal ridges and lateral ridges flaring out posteriorly. There is no other pitting on the centrum apart from an elongated, oval mid-ventral pit. The bone texture is fibrous, especially on the lateral and ventral surfaces. These bony fibres are mostly parallel to the articular surfaces, but are densely interconnected.

The abdominal centra (Fig. 3.6C) have shallow, hexagonal anterior and posterior ends, which become deeper and more circular in more posterior centra, as in modern ictalurids. The notochordal foramen is central to the articular surfaces. The broken bases of the neural arch extend for the full length of the centrum on its dorsal side. An elongate mid-dorsal pit extends for the full length of the centrum in between these neural arch bases. Some centra have a low longitudinal bony ridge within this dorsal pit. There is a pair of elongate pits lateral to the neural arch bases, separating these from the bases of the parapophyses. As in the dorsal pit, the paired dorso-lateral pits have low longitudinal bony fibres within them in some specimens. The bases of the parapophyses are robustly fused to the centra, projecting from their lateral surfaces; none of the elements preserve more than the broken bases of their parapophyses. Immediately ventral to the parapophyseal base is an elongate pit. The ventral side of the centrum is flattened, and the ventro-lateral part projects from the surface of some centra. Ventral and ventro-lateral bony surfaces are fibrous, with most bony fibres being oriented longitudinally, but these are variably interconnected. In some centra, this fibrous texture is very deep, resulting in several elongated pits on the ventral and ventro-lateral surfaces.

Remarks—Based on the descriptions and material figured by Lundberg (1975;fig. 1), the dentary and fin spines can be identified as *Astephus*. The shape of the symphysis, anterior tapering of the antero-ventral crest, first lateral foramen being away from the symphysis, and the lateral ridges forming imbricated V-shapes originating at the lateral foramina are features supporting this attribution. The fin spines correspond to Lundberg's (1975) description in having very fine serrations that are slightly larger on the posterior edge and little more than tubercles on the anterior edge. Other features that support this attribution include the slightly projecting ridge that support these serrations, and the longitudinal sinuous striations that extend along the full length of the spine shaft. These spines and the dentary are attributed to a single taxon on the basis of the maximal sizes they reach, which are clearly larger than the maximal size of the other ictalurid material found in the formation. Some of the centra also reach considerably large sizes; the centra are therefore included here. Additionally, the centra correspond in size and general morphology to Cope's (1891) description of Cypress Hills *Astephus* material, which he had originally attributed to *Rhineastes*.

Lundberg (1975) recognised the presence of two ictalurids in the Cypress Hills Formation, among which he identified *Astephus* based on the bone texture of a pectoral spine and on the structure of a basioccipital. Unfortunately, the basioccipital described above is too poorly preserved to be compared to Lundberg's (17975) observations. Unlike here, elements referable to *Astephus* only corresponded to the smaller ictalurid of the formation in Lundberg's (1975) material. The larger Cypress Hills ictalurid was referred to *Ictalurus* by Lundberg (1975) on the basis of its large size and pectoral spine morphology. In our material, the larger of the two Cypress Hills ictalurids is clearly identifiable as *Astephus*, based on the dentary. The dentary of *Ictalurus* is different in that the symphysis is much wider than high, convex dorsally and concave ventrally, and in that the dentary lacks an antero-ventral crest and lateral ridges altogether. The larger pectoral spines are also easily distinguished from those of *Ictalurus* based on their deep and long anterior basal recess and posterior median furrow extending from the basal recess on the proximal part of the spine shaft. Neither of these characteristics is seen in any extant ictalurid genus, so that these appear to be characters of *Astephus*. However, because Lundberg's (1975) material was not re-examined, the possibility of the presence of a large *Ictalurus* in the formation, alongside the large *Astephus* taxon A, cannot be excluded.

ASTEPHUS Cope, 1873

Taxon B

(Fig. 3.6D)

Material—Twelve pectoral fin spines (ROM 66953–66955, 67050, 67091, 67108, 67122–67125, 67149, 67188).

Description—The pectoral fin spine bases have a long, wide and deep posterior basal recess. They also have a well-defined, smaller anterior basal recess, between the bases of their ventral and dorsal articular processes. The proximal edge of the dorsal articular process forms a line with that of the ventral process. The spine shaft is oval in cross-section, and very compressed laterally. The anterior edge of the spine has a median ridge with fine, bump-like tubercles. Proximally, the posterior edge of the spine has a furrow, in line with the posterior basal recess of the spine; this furrow narrows and disappears distally. The posterior edge of the spine also has very large, recurved median serrations, proximally originating along the midline of the posterior furrow. The bone surface is flat within the basal recesses and posterior furrow; it has a multitude of bumps giving it a frosted appearance on articular surfaces. All other surfaces of the spine have shallow striations, which are longitudinally oriented on the spine shaft.

Remarks—The presence of two ictalurids in the Cypress Hills Formation can be recognised from the two different pectoral spine morphologies recovered in the formation. Those of *Astephus* taxon B differ from taxon A in their smaller maximal size, in their much larger posterior serrations, and in the origination of these serrations in the midline of the posterior furrow, rather than on a ridge on the dorsal side of the posterior basal recess, as in taxon A. However, details of their morphologies suggest that they are closely related. Both morphologies have an anterior basal recess and a proximal furrow on their posterior edge, which are features absent from all extant ictalurid comparative material and seem to be characteristic of *Astephus*. The smaller Cypress Hills ictalurid material was therefore attributed to that genus as well.

That both Cypress Hills ictalurids represent a single genus may explain why diagnostic differences are difficult to establish in the centra and dorsal fin spines recovered. Ictalurid centra are diagnostic to the generic level, at least within the extant ictalurids (Chapter 2; Divay and Murray, 2013). However, as Lundberg (1975) noted, the Cypress Hills ictalurid centra cannot be grouped into clearly separate morphologies representing different taxa. It is here proposed that this is because the Cypress Hills taxa are congeneric. If this is the case, some of the smaller centra described as belonging to *Astephus* taxon A above probably represent the centra of *Astephus* taxon B. The dorsal fin spines of both *Astephus* taxa recognised here may be similarly indistinguishable.

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

Order SALMONIFORMES Bleeker, 1859 (sensu Greenwood, Rosen, Weitzman, and Myers, 1966)

Indeterminate salmoniform abdominal centra

(Fig. 3.6E)

Material—Thirteen abdominal centra (ROM 66933, 66982, 66986, 67011, 67060, 67071, 67092, 67093, 67137, 67150, 67151, 67167, 67191).

Description—These centra are approximately circular in end view with a centrally located notochordal foramen. All are shorter than high or wide, and several are wedge-shaped in side view, being shorter dorsally than ventrally. The articular surfaces at their anterior and posterior ends are surrounded by a slightly projecting margin of smooth bone. The neural arch pits and parapophyseal articular pits are long, extending the full length of the centrum from anterior to posterior articular surfaces. These are characteristic and similar to one another in being bisected longitudinally by low bony ridges, sometimes giving the impression that the centra have an unusually large number of narrow, slit-like pits. The bisecting longitudinal bony ridges are variously developed in different centra, with some of the wedge-shaped centra apparently lacking them altogether in their neural arch pits, although this may be the result of poor preservation. In centra where these are most developed, the bisecting ridges are recognizable from surfaces between articular pits by their texture, because these ridges are smoother than the surfaces separating articular pits from one another. In the better-preserved centra, both neural arch pits and parapophyseal articular pits exhibit a slight ridge along their inside margin, extending towards the core of the centrum. This gives the articular pits a slight hourglass shape. Accessory pits are generally absent, although shallow triangular pits are sometimes present close to articular pits. When present, these accessory pits are limited to the areas immediately adjacent to the anterior or posterior ends of the centrum. The bone texture is never fibrous or spongy. The bone surface of the better-preserved specimens has minute and shallow depressions, giving the bone a frosted appearance everywhere except the articular surfaces.

Remarks—These centra have several salmoniform characters, such as their overall spool-like shape, and their autogenous neural arch and parapophyses. The ridges seen extending towards the core of these centra along the inside margins of their articular pits are also present in salmoniform fishes (Chapter 2; Divay and Murray, 2013). All of these characters are seen in more recent taxa, such as extant and Miocene *Esox* (Chapter 2; Divay and Murray, 2013), and as early as Late Cretaceous relatives (Brinkman and Neuman, 2002). However the Cypress Hills centra are of unique morphology, distinct from those of all of the comparative material examined, most notably because of the longitudinal ridges bisecting the neural arch and parapophyseal articular pits. Given their unique morphologies, these elements probably represent a previously unknown taxon related to this order, and are therefore left as indeterminate Salmoniformes.

Superorder ACANTHOMORPHA Rosen, 1973 (sensu Stiassny, 1986)
Order PERCOPSIFORMES Berg, 1940 (sensu Springer and Orrell, 2004)
Aff. AMBLYOPSIDAE Bonaparte, 1846
(Figs. 3.6F, H; 3.7B)

Material—One complete first centrum (ROM 67042), Fig. 3.6F; one fragmentary first centrum (ROM 67109); one abdominal centrum (ROM 67043), Fig. 3.6H; five caudal centra (ROM 67061, 67062, 67072, 67214, 67215), Fig. 3.7B.

Description—The two first centra (Fig. 3.6F) have a tripartite anterior articular surface for articulation with the basioccipital and the exoccipitals. The most complete fossil (ROM 67042) further indicates that these first centra are unusually long compared to those of other acanthomorph fishes, including percopsiforms. The anterior and posterior articular surfaces are deep, surrounded by a narrow margin of smooth bone, and the notochordal foramen is located centrally. The anterior surface for articulation with the basioccipital is approximately circular. The antero-lateral facets for articulation with the exoccipitals are not in contact with one another, so that they are widely separated above the surface for articulation with the basioccipital. These facets are oval, being slightly wider than high, and are slightly smaller than the surface for articulation with the basioccipital. The plane of contact between the first centrum and the exoccipitals is approximately the same as the one between the centrum and the basioccipital. The posterior end of the centrum is taller than wide and slightly wider ventrally than dorsally, with lateral postzygapophyses. The surface of the centrum between the bases of the fused neural arches is flat. The bases of the fused neural arch extend between the medial margin of the antero-lateral articular facets and the posterior third of the centrum, where bony struts project laterally from them, forming the lateral margin of the postzygapophyses. The lateral surface has a depression beneath the area where the neural arch base and the postzygapophyses connect. A trench extends posterior to this depression, towards the ventral side of the posterior articular surface of the centrum. The ventral surface is hourglass-shaped, being narrowest beneath the depressions on the lateral surfaces of the centrum. The bone texture is an intricate network of struts and shallow pits giving a spongy appearance to all surfaces. The pits are weakly arranged in rows that are primarily oriented longitudinally.

The abdominal centrum (Fig. 3.6H) is elongate, being much longer than high, and is as high as it is wide. In end view, the centrum approximates a hexagon, with flattened dorsal and ventral sides. The centrum is deeply amphicoelous, with a central notochordal foramen, and a slightly projecting margin of smooth bone surrounds the anterior and posterior articular surfaces. The dorsal surface of the centrum is flat except for a narrow, deep and elongate mid-dorsal pit along the midline of the centrum. This mid-dorsal pit is mostly restricted to the posterior half of the dorsal surface, and is surrounded by very shallow pitting on either side, with the pits showing no particular arrangement. The broken neural arch bases are fused to the centrum, extending for its full length. Their lateral surfaces are superficially pitted. The dorsal half of the lateral surface of the centrum has a deep accessory pit. Below this is a bony strut extending the full length of the centrum at mid-height. This bony strut has pitting in its anterior and posterior parts, and on the right side of the centrum, it is sub-divided into two at mid-length, separated by a deep pit. The lateral bony strut has broken projections in its anterior portion. Below the bony strut, a deep accessory pit is present, with low bony struts bisecting it at mid-length. The ventral surface of the centrum has a deep longitudinal mid-ventral pit between bony struts that form the ventro-lateral margins of the centrum. These bony struts are superficially pitted.

Caudal and abdominal centra are similar in being longer than wide, and in the shape of the ends of the centrum, although these are less angular in the caudal elements (Fig. 3.7B). Caudal centra also have long mid-dorsal and mid-ventral pits that are deep, with low bony struts oriented both longitudinally and transversally. The broken bases of the fused neural and haemal arches extend for the full length of the centrum. The lateral surfaces have several longitudinal bony struts with limited interconnections between them. These struts are either parallel or extend radially from an area adjacent to the anterior end of the centrum at mid-height.

Remarks—The morphology of the first centra (Fig. 3.6F) described here is unique to percopsiform fishes (Fig. 3.6G) among the comparative material examined. Percopsiform characters of these centra include their fused neural arches, the large, near-circular facets for articulation with the exoccipitals and how these are widely flared laterally (Murray, 1994). Within the Percopsiformes, the length of these first centra and the articular plane of the facets for articulation with the exoccipitals being similar to that of the surface for articulation with the basioccipital are features most similar to the condition seen in the Amblyopsidae (Murray, 1994:fig. V-10). Abdominal centra (Fig. 3.6H) are characteristic of those of percopsiform fishes (Fig. 3.7A) in their length and in the longitudinal bony struts projecting from their lateral surfaces at their anterior end. The caudal centra described here (Fig. 3.7B) are similar to those of percopsiforms (Fig. 3.7C) in having many longitudinal bony struts on their lateral surfaces, extending radially from the anterior region of the centrum in some centra. All of these elements are attributed to a single percopsiform taxon because of their consistent sizes, percopsiform characters, and the specifically amblyopsid characters of the first centra.

Percopsiform fishes have a relatively long fossil history that includes freshwater forms in the North American Western Interior as early as the early

Paleocene *Mcconichthys* of Montana (Grande, 1988) and the middle Paleocene *Massamorichthys* (Murray, 1996) and *Lateopisciculus* (Murray and Wilson, 1996) from Alberta. The diversity and range of North American freshwater percopsiform fishes increased in the Eocene and Oligocene (e.g., Green River Formation, Grande, 1984), and the combined distribution of extant taxa is wide-ranging, extending throughout Canada, west into Alaska, southwest into the Pacific drainage, and south to the Missouri Basin in the United States (Scott and Crossman, 1973; Murray, 1994).

However, fossil amblyopsids are unknown, and most extant forms are cavefishes whose distribution is currently limited to disjunct areas east and south of the central United States (Murray, 1994). These discontinuous areas are thought to reflect the survival of populations in Pleistocene periglacial refugia, possibly representing the relict ranges of a family previously more widespread to the north of its current range (Niemiller et al., 2012). Furthermore, in spite of the absence of fossil evidence, the family is thought to be relatively old, with molecular clock estimates placing the ancestor to the Amblyopsidae in the Eocene (Dillman et al., 2011). Therefore, if the material described here represents an amblyopsid fish, as the anatomy of the first centrum suggests, the Cypress Hills percopsiform would lend important support to the hypotheses that the family was much older and wider ranging than the previous lack of fossil evidence seemed to indicate.

PERCOMORPHA Rosen, 1973

Order PERCIFORMES Bleeker, 1859

(Fig. 3.7D, E)

Material—Two abdominal centra (ROM 67023, 67141).

Description—These centra are shorter than high. In anterior view, the centrum is higher than wide, while in posterior view, it is approximately as high as it is wide. The centrum is distinctly flattened dorsally and ventrally in anterior view, and is more weakly flattened laterally. In posterior view, the centrum is also angular and similarly flattened dorsally and ventrally, but it is much wider than the anterior end. It flares out laterally at a point slightly dorsal to its mid-height, giving the articular surface an overall hexagonal shape. The notochordal foramen is slightly dorsal in both anterior and posterior views. The median region of the dorsal surface of the centrum has loosely arranged longitudinal bony fibres. This region is bordered by flat, featureless bone, and the broken bases of the neural arch. Posteriorly, the neural arch bases flare out laterally, connecting to the dorsal postzygapophyses at the widest point of the posterior end of the centrum. A large, rectangular mid-ventral pit occupies the entire ventral surface of the centrum. The more posterior centrum (ROM 67141, Fig. 3.7E) has rectangular rib articular pits on the dorso-lateral margin of the centrum, adjacent to the anterior end of the centrum. There is no accessory pitting, but the lateral surfaces have a complex bony texture of interconnected struts giving the centrum a spongy appearance. These struts are more robust in the area dorsal to the postzygapophyses; they are more loosely arranged ventral to that area.

Remarks—These centra are very similar to the centrarchid abdominal centra described below. However, they are clearly distinctive in their large mid-ventral pit. The fossils are most similar to percid anterior abdominal centra (Fig. 3.7F) in their general morphology and in the presence of this mid-ventral pit. However, a precise taxonomic attribution is impossible based on abdominal centra alone. The Centrarchidae and the Percidae have very similar centra, but these families are distinguished by features of the first centrum. As none of the perciform first centra described below match these elements in their bone texture, their taxonomic affinities remain obscure at present. Should these be percid centra, they would predate the earliest reliable occurrence of the family in North America, which is in the Miocene Wood Mountain Formation of southern Saskatchewan (Murray and Divay, 2011; Divay and Murray, 2013; Chapter 2). If they represent a centrarchid fish, they probably represent a taxon distinct from the one described below, given their morphological peculiarities.

Family indeterminate

MIOPLOSUS Cope, 1877

(Fig. 3.7G, 3.8D, E)

Material— One anterior-most abdominal centrum (ROM 67095), Fig. 3.7G; four more posterior abdominal centra (ROM 67016, 67017, 67075, 67114), Fig. 3.8D, E.

Description— The anterior-most abdominal centrum is relatively weathered but preserves enough of its original surfaces to be described. It is deeply amphicoelous, taller than wide, with a slightly dorsal notochordal foramen. The centrum is rectangular in anterior view, being taller than wide. The posterior end of the centrum is much smaller and slightly less angular, only being flattened dorsally. An elongate pit extends for the full length of the centrum along the midline of the dorsal surface, bisected in its middle by a narrow, low, longitudinal bony strut. The broken base of the neural arch forms two pairs of elongate ridges, so that each side is formed by two ridges that extend the full length of the centrum and are joined posteriorly. The medial edge of the neural arch borders the dorsal pit; the lateral surface forms the dorso-lateral margin of the centrum. The neural arch base delimits a triangular pit restricted to the anterior part of the centrum, wider anteriorly, enclosing loose bony fibres. The lateral surface of the centrum has a single narrow pit at mid height, extending the full length of the centrum. The ventral surface is poorly preserved, but seems to have several elongate pits. The bone texture of this element is characteristically fibrous, with most surfaces dominated by the longitudinally arranged edges of sheet-like structures of bone extending radially from the notochordal area of the centrum.

The abdominal centra are approximately as wide or wider than they are high and long. The ends of the centrum are oval and flattened both dorsally and ventrally, with a central notochordal foramen. In larger centra (Fig. 3.8D), low ridges connect the foramen to the outer margins of the articular surfaces both dorsally and ventrally. This ridge is most conspicuous on the dorsal side of the posterior articular surface, where it forms a notch on the outer margin of the articular surface. The ridge is less developed or absent in small abdominal centra (Fig. 3.8E). A slightly projecting margin of smooth bone surrounds the articular surfaces on the ends of the centrum. The dorsal surface of the centrum has an elongate, slit-like pit along the midline, encasing a network of thin and low bony ridges. The broken bases of the fused neural arch border this pit, extending the full length of the centrum. A pair of shallow accessory pits restricted to the posterior half of the centrum is adjacent to the neural arch bases, on the dorso-lateral surface of the centrum. The ventral part of the lateral surface has a large but shallow rib articular pit, the anterior margins of which are formed by characteristically short parapophyses. The rib articular pit is wider anteriorly, and is slightly anterior in placement. A large rectangular trench occupies most of the ventral surface; it extends the full length of the centrum along its midline and has a deeper, round pit approximately in its centre. Most surfaces of this centrum are fibrous in texture, with bony fibres primarily oriented longitudinally. However, the bone within the rib articular pits and the ventral trench is noticeably smoother, only being slightly porous or plicated.

Remarks—The anterior-most abdominal centrum is notable in that the anterior articular surface is much larger than the posterior articular surface. This is a very rare condition in the comparative material examined, only seen in some of the Weberian centra of ostariophysans and in the anterior-most abdominal centra of *Mioplosus* (Fig. 3.8A). In this genus, the articular surface at the anterior end of anterior-most centra extends ventrally beyond the rest of the ventral surface, as in the Cypress Hills fossil. Furthermore, the Cypress Hills specimen has fused neural arches projecting anteriorly from the centrum, which correspond to the anterior part of the neural arch forming dorsal prezygapophyses in *Mioplosus*. The triangular pits lateral to the neural arch base at the anterior end of the centrum, elongate accessory pits on the lateral surface, and deeply fibrous bony texture also support this attribution. The more posterior abdominal centra have remarkably small parapophyses anterior to the rib articular pits, which are unique to *Mioplosus* (Fig. 3.8 B, C) among the acanthomorph material examined. Additionally, the Cypress Hills fossils have shallow and triangular rib articular pits, accessory pits on the dorso-lateral side of the centra and a fibrous surface texture that is deeper in larger specimens, which are all features consistent with the morphology of *Mioplosus*.

Mioplosus occur in late Paleocene to late middle Eocene Green River Formation deposits, where thousands of specimens have been recovered, mainly from Fossil Lake (Grande, 2001). The considerable sizes of some of the Cypress Hills centra (e.g., ROM 67075, Fig. 3.8D) are also consistent with previous reports of *Mioplosus* specimens reaching at least 420 mm (Grande, 2001) and possibly up to 510 mm in length (Grande, 1984). The taxonomic affinities of *Mioplosus* are uncertain, with authors placing the genus within the Percidae (e.g., Cope, 1877; Woodward, 1901; Grande, 1984), the Percichthyidae (Cavender, 1986) or in the Moronoidei (sensu Smith and Craig, 2007), as a relative of latids (Whitlock, 2010); Bruner (2011) excludes *Mioplosus* from the Percidae and does not group it with any other family. Considering this and the unique morphology of the Cypress Hills abdominal centra among observed acanthomorphs, it is here included as a perciform of uncertain affinity, as in Bruner (2011).

Family ?MORONIDAE Jordan, 1923

(Fig. 3.8F)

Material—Two abdominal centra (ROM 67152, 67180).

Description—The height, width and length of these centra are approximately equal. The ends of the centra are circular with a central notochordal foramen, and the anterior and posterior articular surfaces are surrounded by a slightly projecting margin of smooth bone. The broken bases of the neural arch extend for the entire length of the centrum. These are more robustly fused to the centrum at their anterior and posterior areas, forming a bony bridge above the centrum at mid-length. In between the neural arch bases, the dorsal surface of the centrum is fibrous, with bony fibres more loosely arranged at mid-length than in the more robust areas adjacent to the anterior and posterior ends of the centrum. The parapophyses are characteristically broad, and originate close to the anterior end of the centrum. The anterior edges of the parapophyses are fused to the centrum at mid-height, while the posterior edges originate on the ventro-lateral margins. The lateral sides of the centrum are more robust at mid-height, but otherwise bear no characteristic feature. The ventral surface has a pair of robust bony ridges delimiting an elongate, oval mid-ventral depression that extends for the full length of the centrum. The bone surface within the ventral depression is fibrous, with more loosely arranged fibres towards its centre. The lateral surfaces of the centrum are covered by longitudinal rows of shallow pits, except on the parapophyses, where bony fibres are more clearly defined and parallel to the long axis of the transverse process.

Remarks—The morphology of these centra is identical to that of centra from the mid-Miocene Wood Mountain Formation of Saskatchewan tentatively attributed to the Moronidae by Divay and Murray (2013; Chapter

2). The fossils possess all characteristics of moronid abdominal centra (Fig. 3.8G), including a fibrous dorsal surface, a more robust attachment of the neural arches in the anterior and posterior parts of the centrum, broad wing-like parapophyses, and a mid-ventral depression bordered by a pair of ridges. However, the moronid comparative material differs in that it is relatively longer, and in details of lateral surface texture. The attribution of the specimens to the Moronidae therefore remains tentative. If this attribution is correct, these fossils represent the earliest evidence of the family in North America.

Family CENTRARCHIDAE Gill, 1862b

(Figs. 3.9A, B, D)

Material—Two first centra (ROM 66956, 6718), Fig. 3.9A, B; three abdominal centra (ROM 66934, 66983, 66984), Fig. 3.9D.

Description—The first centra are recognisable as such from their tripartite anterior articular surfaces. These centra are slightly longer dorsally than ventrally, giving them a slight wedge shape in lateral view. The anterior articular surface for the basioccipital is keeled dorsally and broadly rounded ventrally; the posterior end of the centrum is circular. The notochordal foramen is slightly dorsal in both anterior and posterior views. The paired facets for articulation with the exoccipitals are widely joined medially, and occupy the anterior portion of the dorsal surface. Posterior to these, the dorsal surface has a pair of rounded pits for articulation with the autogenous neural arch, separated by an hourglass-shaped longitudinal bony ridge. The facets for articulation with the exoccipitals project from the lateral surfaces of the centrum and connect to widely flared dorsal postzygapophyses by a bony ridge on the dorso-lateral margin of the centrum. The lateral side has one or two accessory pits immediately beneath this bony ridge, and both centra have a single, asymmetric, rounded accessory pit on their right ventro-lateral margin. Additionally, the larger centrum (Fig. 3.9A) is different from the smaller centrum (Fig. 3.9B) in that the latter also has a mid-ventral pit along the midline, adjacent to the posterior end of the centrum. The bone texture of the lateral and ventral surfaces is fibrous, apart from a narrow margin of smooth bone adjacent to the articular surfaces. Bony fibres are predominantly oriented longitudinally, but some are extensively interconnected, giving the bone a spongy appearance.

The abdominal centra (Fig. 3.9D) are approximately as high as they are wide, and are shorter than high. In anterior view, the centrum is distinctly narrower and slightly more angular than it is when viewed in posterior view. The notochordal foramen is centrally located. Dorsally, between the fused neural arch bases, the centra have a network of loosely arranged bony struts surrounded by a flat and featureless surface. The broken bases of the neural arch extend for the full length of the centrum. The neural arch bases extend anteriorly to fuse to dorsal, hook-like prezygapophyses in at least one of these centra, ROM 66983 (Fig. 3.9D); the others are not well enough preserved to determine whether or not they also possess this characteristic. Posterior dorsal postzygapophyses are widely flared, fusing to the dorso-lateral margin of the centrum in an area corresponding to the widest point of the posterior end of the centrum. All surfaces ventral to the pre- and postzygapophyses are covered by a network of bony struts. These struts are mostly oriented longitudinally, but are also interconnected, giving the bone surface a spongy appearance.

Remarks—These centra resemble those of centrarchid and percid fishes, which are morphologically very similar. However, the first centra (Fig. 3.9A, B) can be attributed to the Centrarchidae (Fig. 3.9C) based on the wide median connection of the paired facets for articulation with the exoccipitals, whereas these are separated in the Percidae. The abdominal centra (Fig. 3.9D) are attributed to the same taxon as the first centra based on their centrarchid morphology (Fig. 3.9E) and because their bone texture is similar to that of the first centra, primarily in the longitudinal orientation of the bony struts on most of the surfaces of the centra. A more precise taxonomic attribution is impossible, because of the lack of other distinctive features, such as pitting, which could be used to distinguish various centrarchid taxa.

DISCUSSION

The fishes of the Cypress Hills Formation represent a diverse ichthyofauna with at least fourteen different fish taxa identified. The ichthyofauna is similar to the herpetofauna in its modern aspect, as the only taxon likely to represent an extinct family is the indeterminate salmoniform. However, this fish is morphologically distinctive, and probably indicates the presence of a previously unrecognised archaic group in the Paleogene fluvial environments of North America.

The amblyopsid-like percopsiform is an interesting component to the fauna, especially if it represents the first fossil occurrence of the

Amblyopsidae. This would indicate that the family was much more widespread during the Eocene-Oligocene transition than at present.

Other groups of Cypress Hills fishes have fossil histories dating back to the Eocene Green River Formation or earlier, such as lepisosteids, amiids, hiodontids, catostomids, ictalurids, and perciforms (Grande, 2001). The absence of well-represented groups from the Green River Formation, such as osteoglossids, paraclupeids and clupeids, can either indicate that these were absent because the local environment was unsuitable, or because these taxa were latitudinally restricted to the south of the Cypress Hills Formation. Alternatively, it may indicate that the transition to a more modern ichthyofauna from a previously clupeomorph-rich one occurred between the deposition of the Green River and Cypress Hills formations. The Cypress Hills ichthyofauna is one of the oldest assemblages documenting fish diversity in the North American Western Interior after the onset of increased seasonality between the middle and late Eocene. This period is one to which widespread mammalian faunal turnovers have been attributed (Storer, 1996). If, as hypothesized above, the ichthyofaunal turnover occurred at the same time, this increased seasonality may also have been the driving force for the establishment of the more modern Cypress Hills fish fauna.

Other freshwater fish faunas of similar age include the slightly older Clarno Formation (Cavender, 1968) and the Eocene–Oligocene John Day Formation (Cavender, 1998), both from Oregon, as well as the Florissant Formation of Colorado (Veatch and Meyer, 2008). However, the work on fishes of these formations is relatively limited, and these assemblages appear to be much less diverse, which may be because they were deposited by floodplain lakes that typically represent few environments. Cavender (1968) reports amiid, hiodontid, siluriform and catostomid material from the Clarno Formation. The Florissant Beds have amiids, catostomids, ictalurids and percopsiforms (Cope, 1878; 1884). The John Day Formation is notable in preserving the first North American record of the Cyprinidae (Cavender, 1998), and its Eocene–Oligocene deposition corresponds to the age of the Cypress Hills leuciscine described here. The latitude of the Cypress Hills ichthyofauna is also significant because it represents the most northern of these assemblages, providing a reference for future studies documenting latitudinal influences on the fish diversities of the time.

Palaeoclimatic Reconstruction

Previous studies had suggested much warmer, warm-temperate to subtropical, climates during the deposition of the Cypress Hills Formation, based on the plants (Roy and Stewart, 1971) and the reptiles (Holman, 1972) of the formation. The Cypress Hills herpetofauna, in particular, suggested that freezing temperatures were rare or absent in Eocene–Oligocene southern Saskatchewan (Holman, 1972). The distributions of modern relatives of the Cypress Hills fishes are consistent with these palaeoclimatic reconstructions, suggesting that the ranges of these fishes shifted with changing climates. Therefore, the ichthyofauna of the formation can be used to refine these palaeoclimatic reconstructions.

The modern relatives of several of the fishes represented in the assemblage would no longer be found at such high latitudes, having shifted their ranges south or southeast. For example, both *Lepisosteus* and *Amia* are almost entirely absent from Canada, and are only infrequently found in Canadian waters east of the Great Lakes and in the Great Lake drainages (Scott and Crossman, 1973). Furthermore, cold water taxa that are common in modern Saskatchewan waters, such as salmoniforms, are entirely absent from the Cypress Hills Formation. Salmoniforms are relatively large fishes with robust skeletal elements, and their absence from the fossil sample is most likely to reflect their true absence from the source community, rather than taphonomic or collecting bias. According to Scott and Crossman (1973), the modern range of salmonids east of the Rocky Mountains is restricted to north of 40°N; their absence from the Cypress Hills Formation, therefore, suggests that the temperatures of southern Saskatchewan during the latest Eocene were similar to those of lower latitudes today. The Hiodontidae are a family of boreal fishes that only occurs north of the Gulf coast of the United States, but both extant species are sometimes found in the fresh waters of Louisiana (Douglas, 1974). Therefore, the ichthyofaunal composition of the Cypress Hills Formation suggests palaeotemperatures similar to those of the Gulf coast.

This interpretation is corroborated by the large sizes reached by some of the Cypress Hills ictalurid material. Currently, Ictaluridae occur from Canada to Guatemala, and the largest genera are *Ictalurus* and *Pylodictis*, reaching 1.6 metres (Nelson, 2006). Species of *Ictalurus* occur in Canada as far west as Manitoba, but their maximal length is significantly less in that area (Scott and Crossman, 1973) than in more southern populations. Both genera reach their maximal sizes in the southeast United States, such as in the state of Louisiana (Douglas, 1974).

Therefore, the palaeoclimatic indications of the fish fauna of the Cypress Hills Formation are consistent with those of the herpetofauna (Holman, 1972) and flora (Roy and Stewart, 1971). The late Eocene–early Oligocene temperatures of southern Saskatchewan were probably much warmer than at present and unlikely to fall below freezing, similar to current conditions in the southern United States.

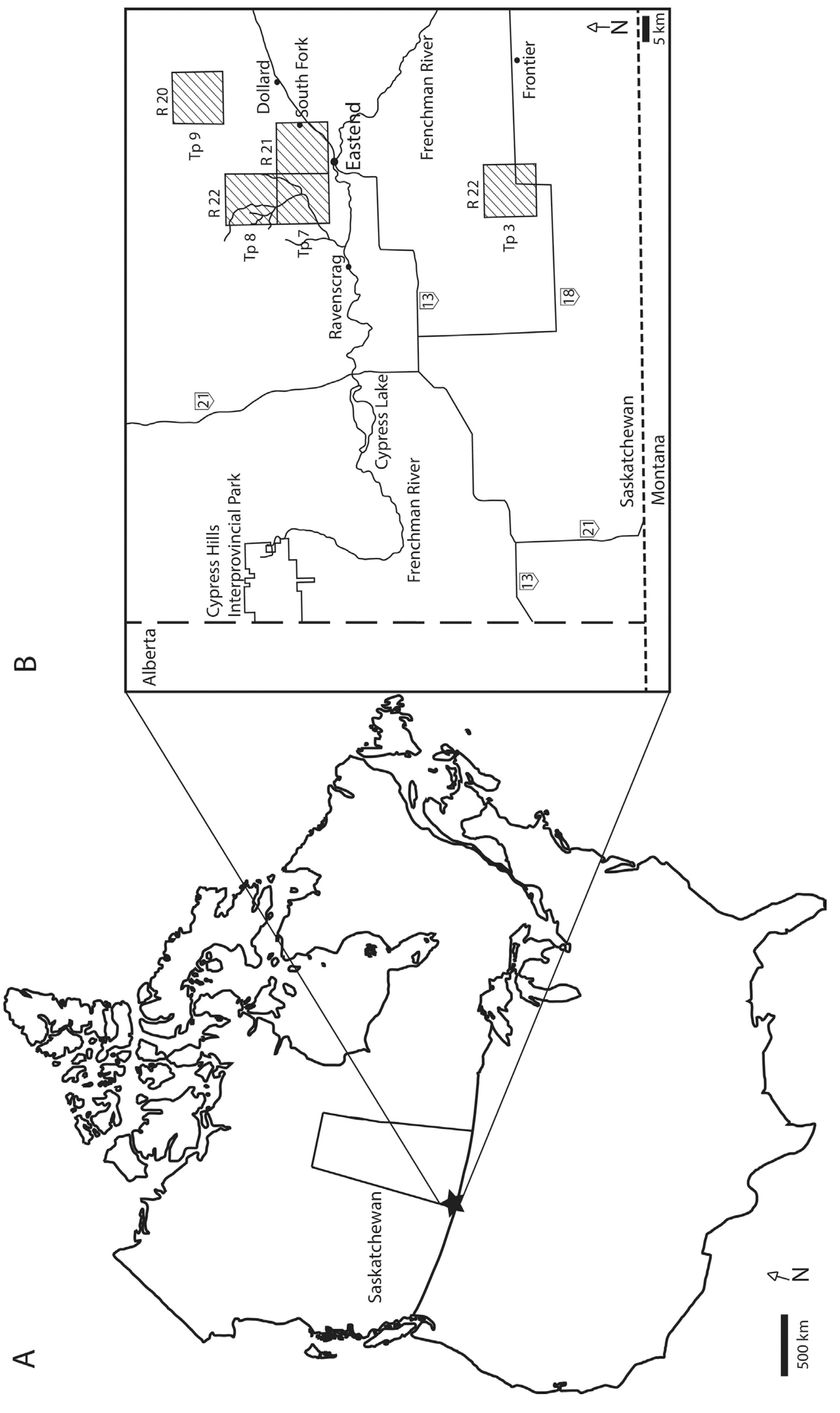
Palaeoenvironmental Reconstruction

The Cypress Hills Formation ichthyofauna indicates a lowland fluvial environment consistent with the braided river floodplain environment suggested by the sedimentary geology of the formation (Leckie and Cheel, 1989; Leckie, 2006). The presence of silcretes forming in situ in some layers and silcrete fragments forming part of the flood-deposited breccias that bear many of the fossils of the formation had been interpreted by Leckie and Cheel (1990) as evidence of strongly seasonal rainfalls and locally arid conditions. The abundance of ictalurid material representing small individuals is consistent with this interpretation, suggesting that many of the fossil localities were shallow backwater ponds. In these environments, smaller individuals of taxa resistant to anoxic conditions would be most common, especially those that tend not to migrate back to river channels during the dry season, as is the case with most catfishes (Welcomme, 1973). Much of the ictalurid material recovered is heavily weathered, as Lundberg (1975) also noted, which may indicate that this material was exposed for a length of time before being buried in a flooding event, or repeated periods of reworking and redeposition, resulting in abrasion in several stages of the burial process. This could indicate that these shallow ponds were not permanent, resulting in the death of many of these individuals as the pools dried out, and leading to the exposure of the skeletal elements on the floodplain prior to permanent burial.

However, lacustrine deposits, flood deposits and palaeochannels (Leckie and Cheel, 1989) all indicate that arid conditions were not constant, or they were localised, and the fish fauna also indicates the presence of deep-water environments nearby. The large sizes reached by some of the fishes of the formation, especially *Mioplosus* and *Astephus* taxon A, are clear indications that not all waters were shallow during deposition. The largest extant ictalurids, *Ictalurus* and *Pylodictis*, tend to favour deep river-channel environments (Scott and Crossman, 1973; Douglas 1974); therefore, the size attained by much of the larger Cypress Hills *Astephus* material could indicate long-lasting similar environments in the vicinity. This corroborates Holman's (1972) suggestion of permanent water bodies based on the herpetofauna of the formation, and Leckie and Cheel's (1989) description of a nine-metre deep river channel in the eastern Cypress Hills Formation.

Although the predominant shallow backwaters were probably hypoxic, as indicated by the abundance of catfish and bowfin material, the fauna as a whole indicates that well-oxygenated environments were also available. Cypriniforms, percopsiforms and centrarchids would probably have tracked the oxygenated waters by seasonally migrating between the floodplain backwaters and the river channels, as modern relatives do today (Welcomme, 1973). This could explain their relative rarity compared to small ictalurids. Abundant aquatic vegetation was also probably available, as indicated by the presence of lepisosteids, amiids, cypriniforms and centrarchids, all of which rely on vegetation as cover to capture prey, evade predators, and/or to spawn (Scott and Crossman, 1973). All of these characteristics are typical of modern seasonal floodplains (Welcomme, 1973), suggesting that the formation was deposited in such an environment.

FIGURE 3.1. Locality map for the Eastend area of the Cypress Hills Formation. **A**, Location of the Cypress Hills Formation (marked with a star) relative to Saskatchewan, Canada, and the contiguous United States; **B**, Enlarged locality map showing the areas of provenance of the fossils included in this study. Most localities sampled are from the crosshatched township and range land divisions indicated. All ranges west of the Third Meridian.


A
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Interprovincial Park
Frenchman River
Cypress Lake
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Ravenscrag
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Tp 8
Tp 7
R 22
R 21
Tp 9
R 20
Dollard
South Fork
Eastend
Frenchman River
Tp 3
R 22
18
Frontier
13
21
Saskatchewan
Montana
N
5 km

FIGURE 3.2. Cypress Hills Formation fish material. **A**, **B**, Cypress Hills Formation *Lepisosteus* material: **A**, scale (ROM 66987) in lateral and medial views; **B**, abdominal centrum (ROM 66990); **C**–**F**, Cypress Hills Formation Amiinae material: **C**, Amiinae right maxilla (ROM 66920) in lateral, ventral, dorsal, and medial views; **D**, Amiinae right dentary (ROM 67051) in lateral, dorsal, symphyseal, ventral, and medial views; **E**, Amiinae abdominal centrum (ROM 67013); **F**, Amiinae caudal centrum (ROM 67035); **G**, **H**, Cypress Hills Formation aff. *Hiodon* material: **G**, anterior abdominal centrum (ROM 67200); **H**, posterior abdominal centrum (ROM 67133). Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

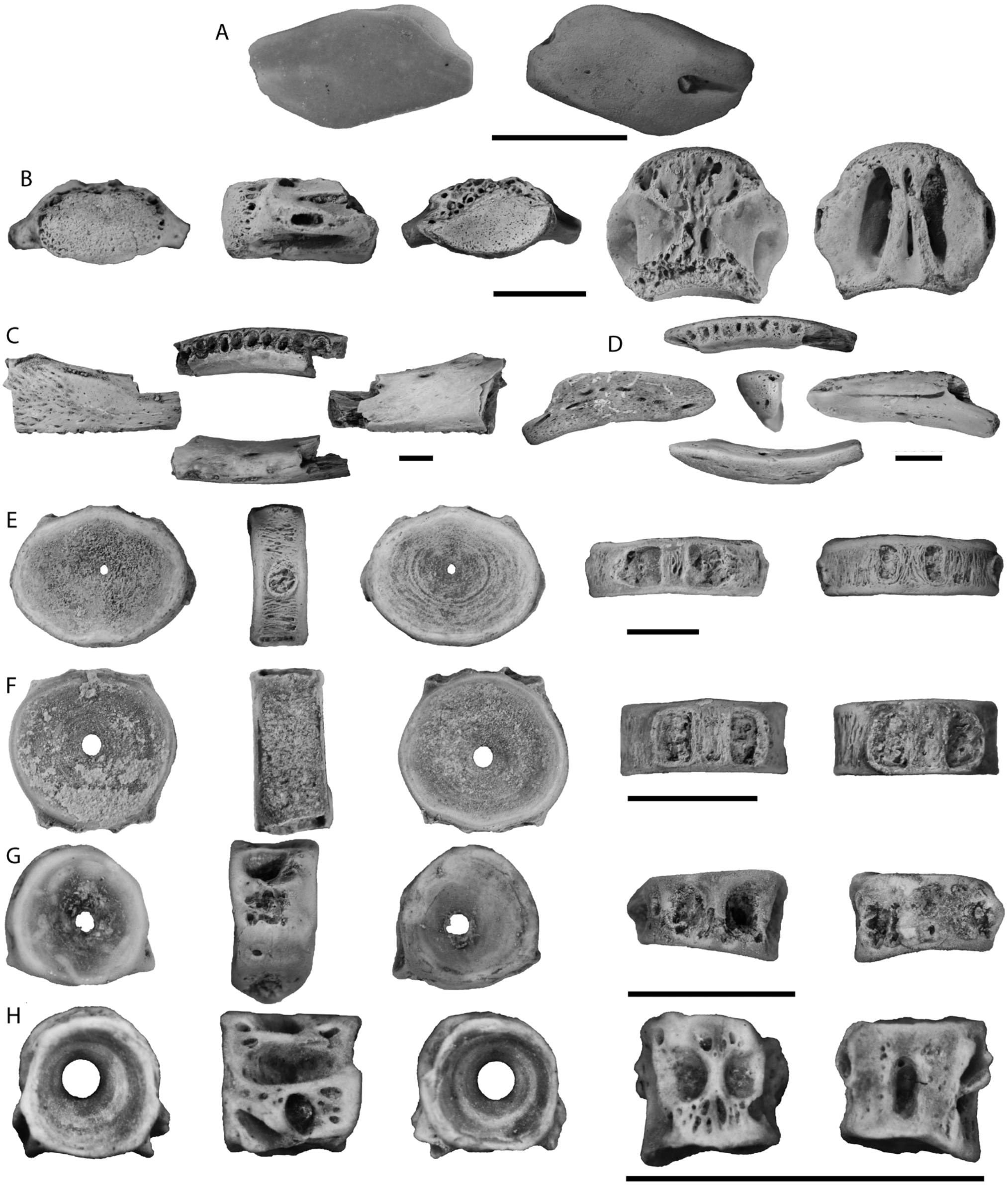
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FIGURE 3.3. Cypress Hills Formation (**B**, **F**) and comparative material (**A**, **C**–**E**, **G**, **H**). **A**, *Hiodon alosoides* (UAMZ F8556) abdominal centrum; **B**, Cypress Hills Catostomidae first Weberian centrum (ROM 66973); **C**, *Catostomus catostomus* (UAMZ F8582) first Weberian centrum; **D**, *Carpiodes carpio* (KU 12732) first Weberian centrum; **E**, *Cyprinus carpio* (UAMZ F8557) first Weberian centrum; **F**, anterior fragment of a Weberian apparatus corresponding to the second centrum of the vertebral series (ROM 67192); **G**, *Catostomus catostomus* (UAMZ F8582) second centrum of the Weberian apparatus; **H,** *Cyprinus carpio* (UAMZ F8557) Weberian apparatus second centrum. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

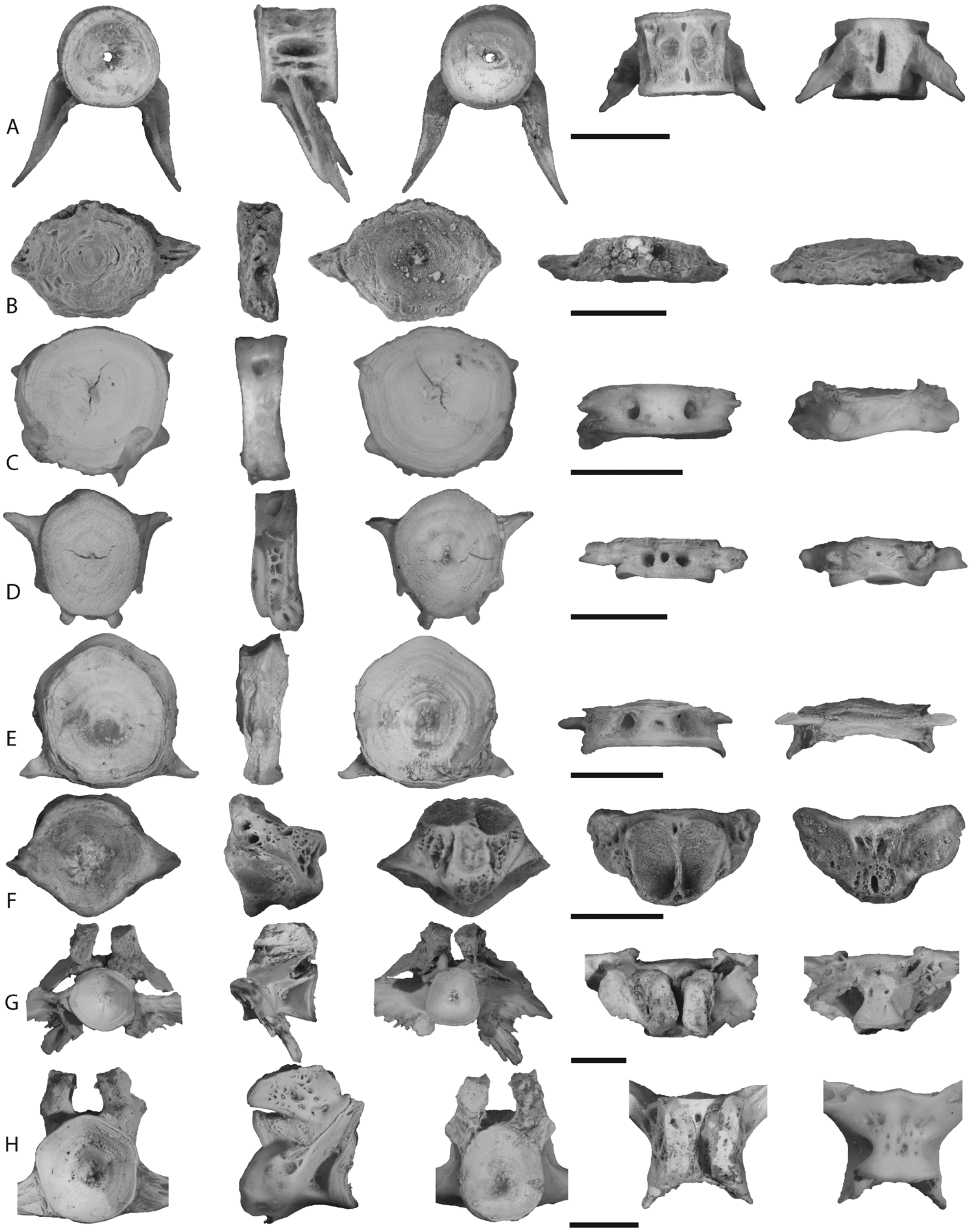
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FIGURE 3.4. Cypress Hills Formation (**A**, **C**–**E**) and comparative cypriniform material (**B**. **F**, G). **A**, Cypress Hills Formation leuciscine aff. *Ptychocheilus* abdominal centrum (ROM 66976); **B** *Ptychocheilus oregonensis* (ROM R6513) abdominal centrum; **C**, indeterminate cypriniform taxon first Weberian centrum (ROM 67115); **D**, **E**, abdominal centra of an indeterminate Cypress Hills Formation cypriniform belonging either to the Catostomidae or the Cyprininae: **D**, abdominal centrum preserved without articulated parapophyses (ROM 67201); **E**, abdominal centrum preserving the base of the parapophysis (ROM 67018); **F**, *Carpiodes carpio* (KU 12732) abdominal centrum without parapophyses; **G**, *Cyprinus carpio* (UAMZ F8557) abdominal centrum shown with the bases of the parapophyses articulated within the parapophyseal articular pits, as for the Cypress Hills Formation cypriniform centrum shown in Fig. 3.4E. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

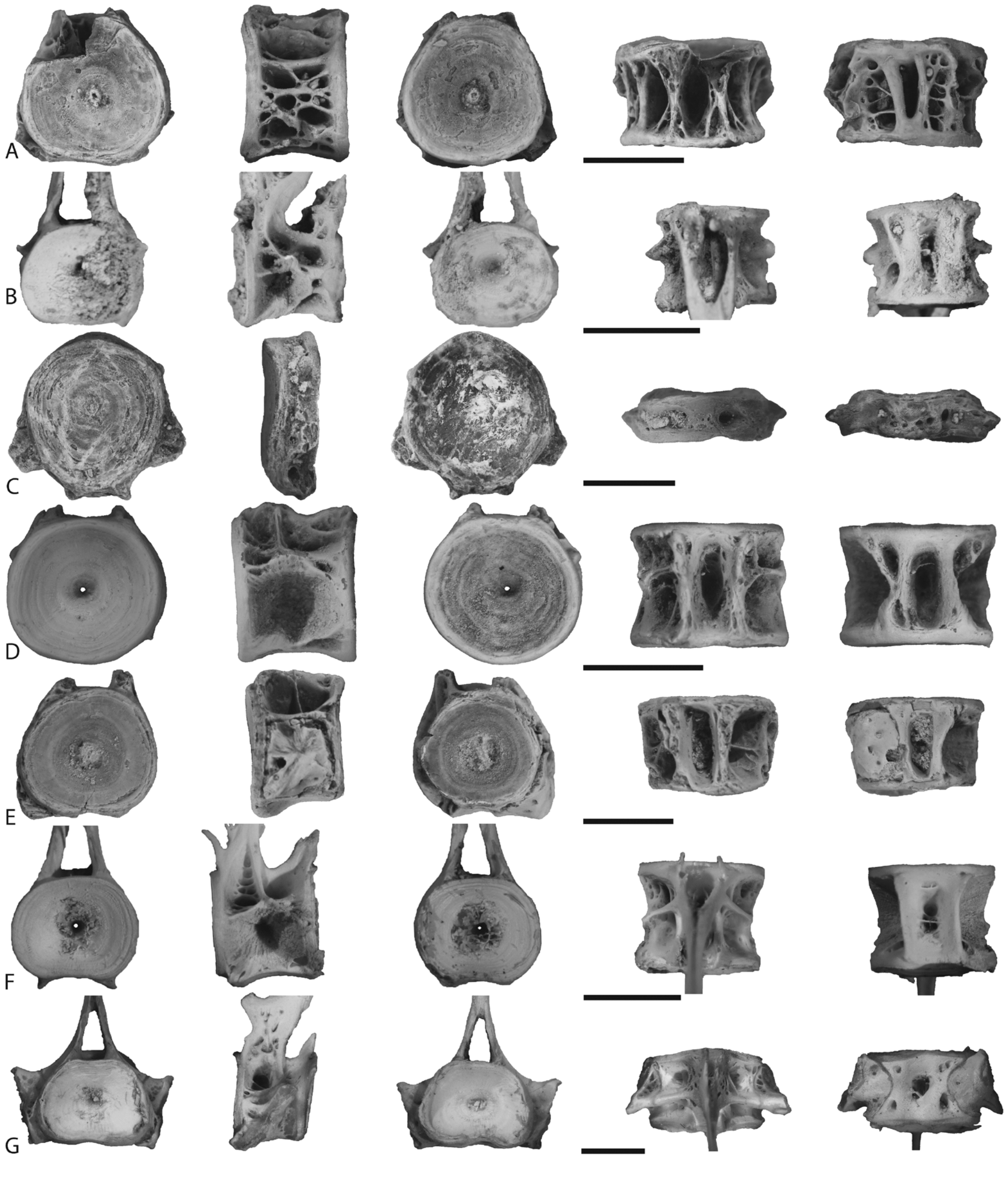
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FIGURE 3.5. Cypress Hills Formation (**A**, **C**–**G**) and comparative material (**B**). **A**, indeterminate Cypress Hills cypriniform ural centrum (ROM 66964); **B**, *Catostomus catostomus* (UAMZ F8582) ural centrum; **C**–**G**, Cypress Hills Formation *Astephus* taxon A material: **C**, dentary (ROM 67077) in lateral, symphyseal, medial, dorsal and ventral views; **D**, basioccipital (ROM 67054); **E**, dorsal fin spine (ROM 66994); **F**, pectoral fin spine (ROM 66978); **G**, first Weberian centrum (ROM 67106). The basioccipital and centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Fin spines are presented in anterior, lateral and posterior views. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

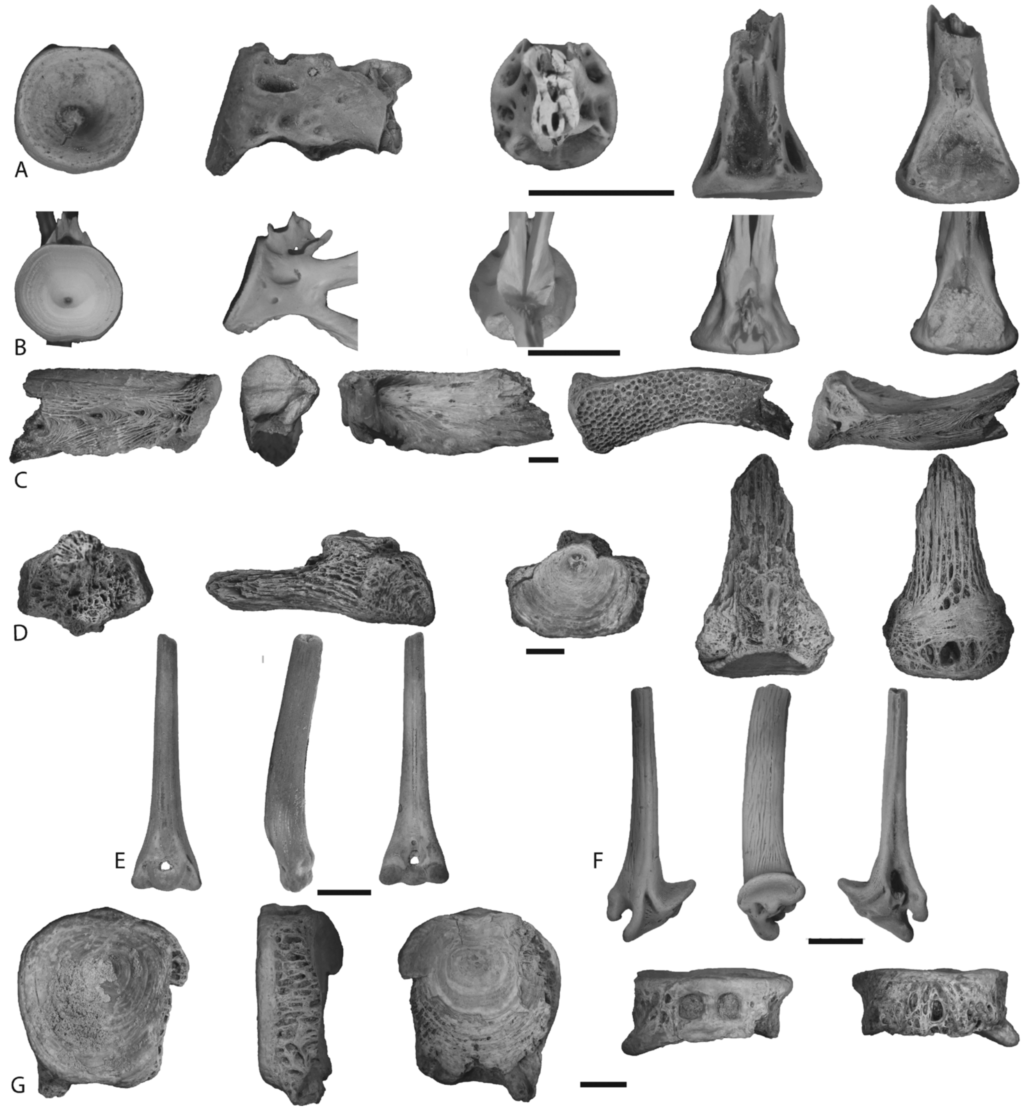
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FIGURE 3.6. Cypress Hills Formation (**A**–**F**, **H**) and comparative ostariophysan material (**G**). **A**–**C**, Cypress Hills Formation *Astephus* taxon A material: **A**, posterior fragment of a Weberian apparatus (ROM 67088); **B**, anterior abdominal centrum (ROM 67089), immediately behind the Weberian apparatus in the vertebral series; **C**, abdominal centrum (ROM 67022); **D**, pectoral fin spine (ROM 67122) of Cypress Hills Formation *Astephus* taxon B in anterior, lateral and posterior views; **E**, indeterminate salmoniform abdominal centrum (ROM 67191); **F**, Cypress Hills Formation aff. Amblyopsidae percopsiform first centrum of the vertebral series (ROM 67042); **G**, *Percopsis omiscomaycus* (ROM R6493) first centrum; **H,** aff. Amblyopsidae percopsiform abdominal centrum (ROM 67043). The centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.


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FIGURE 3.7. Cypress Hills Formation (**B**, **D**, **E**, **G**) and comparative acanthomorph material (**A**, **C**, **F**). **A**, *Percopsis omiscomaycus* (ROM R6493) abdominal centrum; **B**, aff. Amblyopsidae percopsiform caudal centrum (ROM 67061); **C**, *Percopsis omiscomaycus* (ROM R6493) caudal centrum; **D**, indeterminate perciform anterior abdominal centrum (ROM 67023); **E**, indeterminate perciform posterior abdominal centrum (ROM 67141); **F**, *Perca flavescens* (UMMZ194309-S1) abdominal centrum; **G**, Cypress Hills *Mioplosus* anterior-most abdominal centrum (ROM 67095). Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

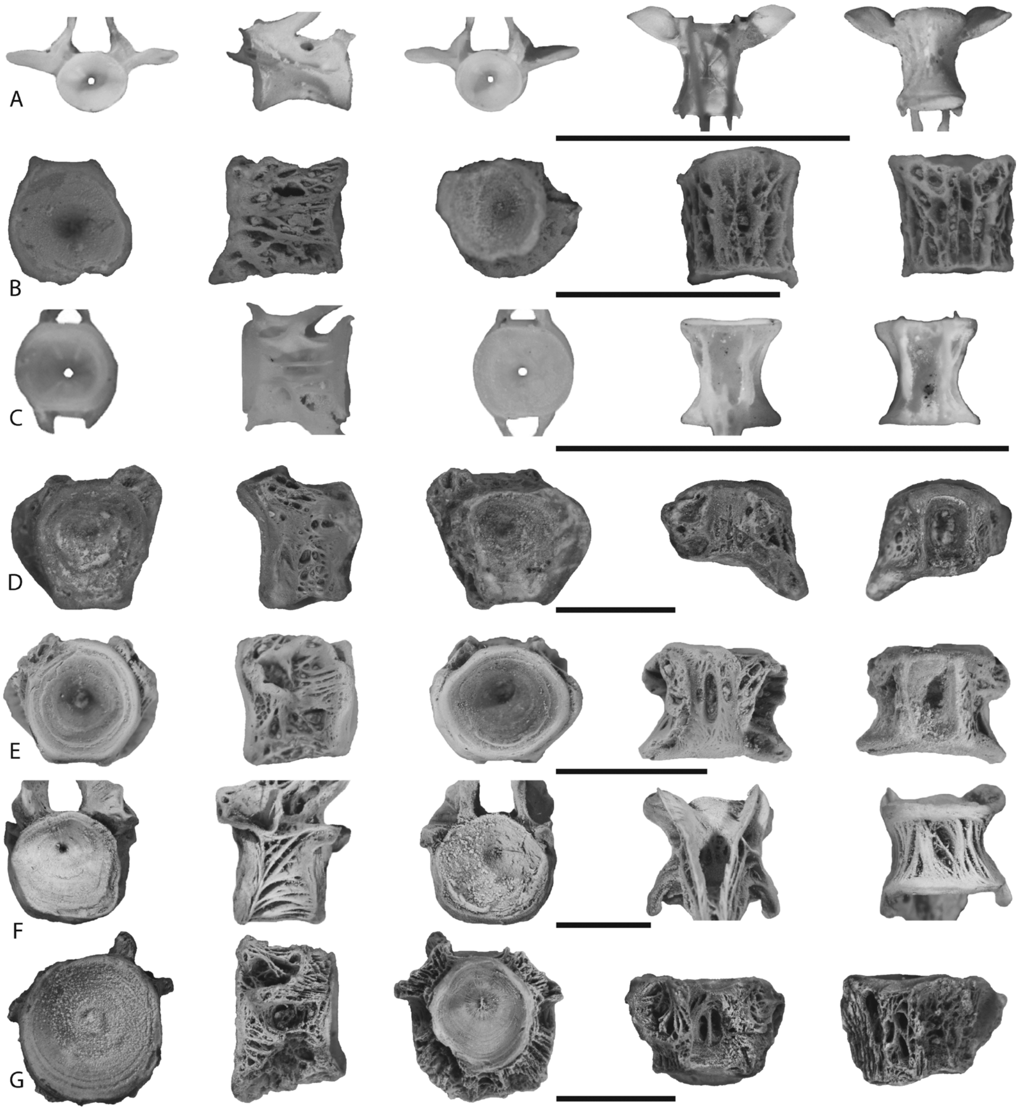
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FIGURE 3.8. Cypress Hills Formation (**D**–**F**) and comparative perciform material (**A**–**C**, **G**). **A**, left lateral view of the first four abdominal centra of a large articulated Green River Formation *Mioplosus* (UALVP 24234); **B**, posterior abdominal centra of the same Green River Formation *Mioplosus* (UALVP 24234); **C**, abdominal centra of a smaller articulated Green River Formation *Mioplosus* (UALVP 17828) in left lateral view; **D**, Cypress Hills Formation *Mioplosus* large abdominal centrum (ROM 67075); **E**, Cypress Hills Formation *Mioplosus* small abdominal centrum (ROM 67114); Cypress Hills Formation possible moronid abdominal centrum (ROM 67180); **D**; *Morone saxatilis* (UAMZ F8554) abdominal centrum. Isolated centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

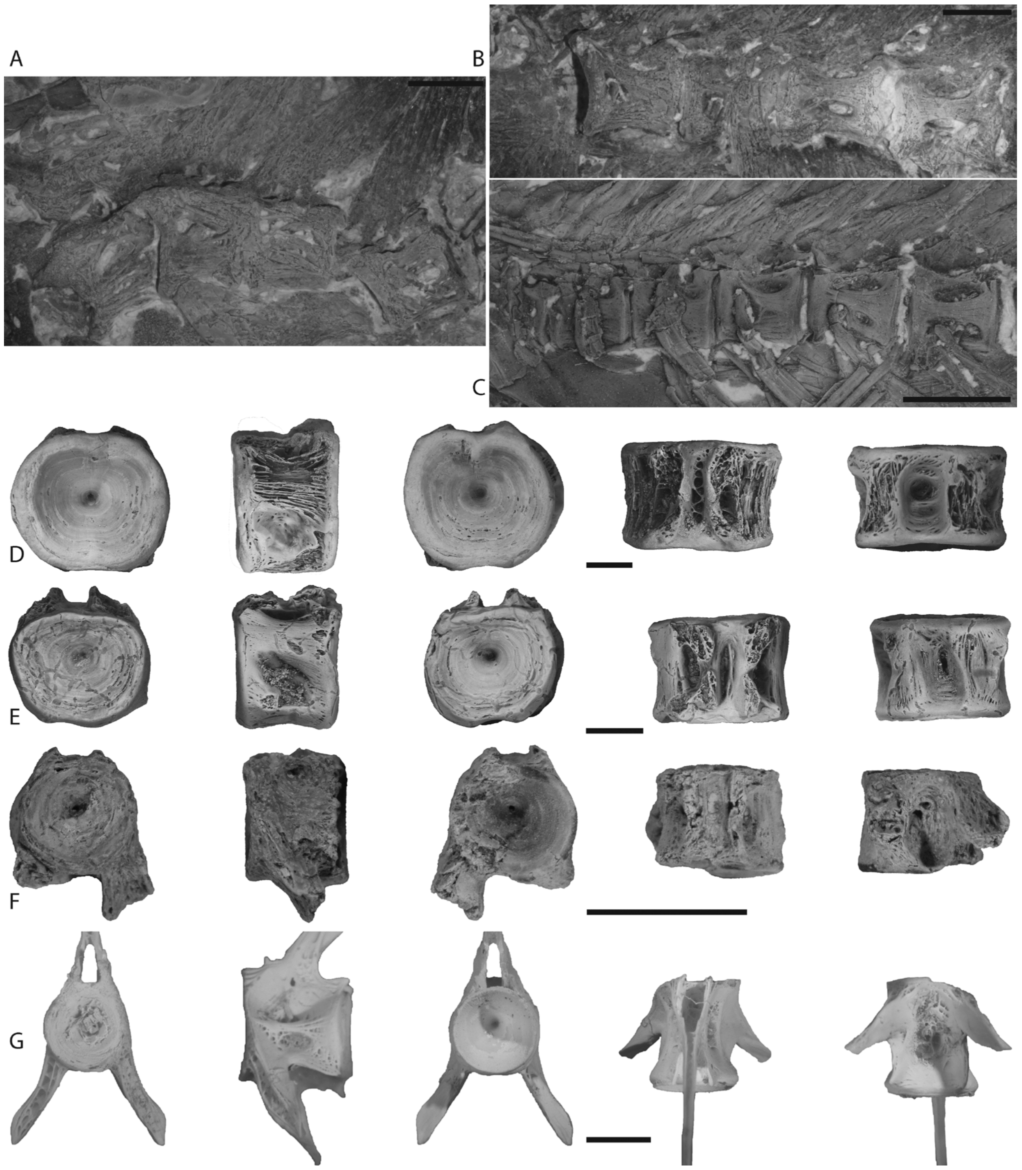
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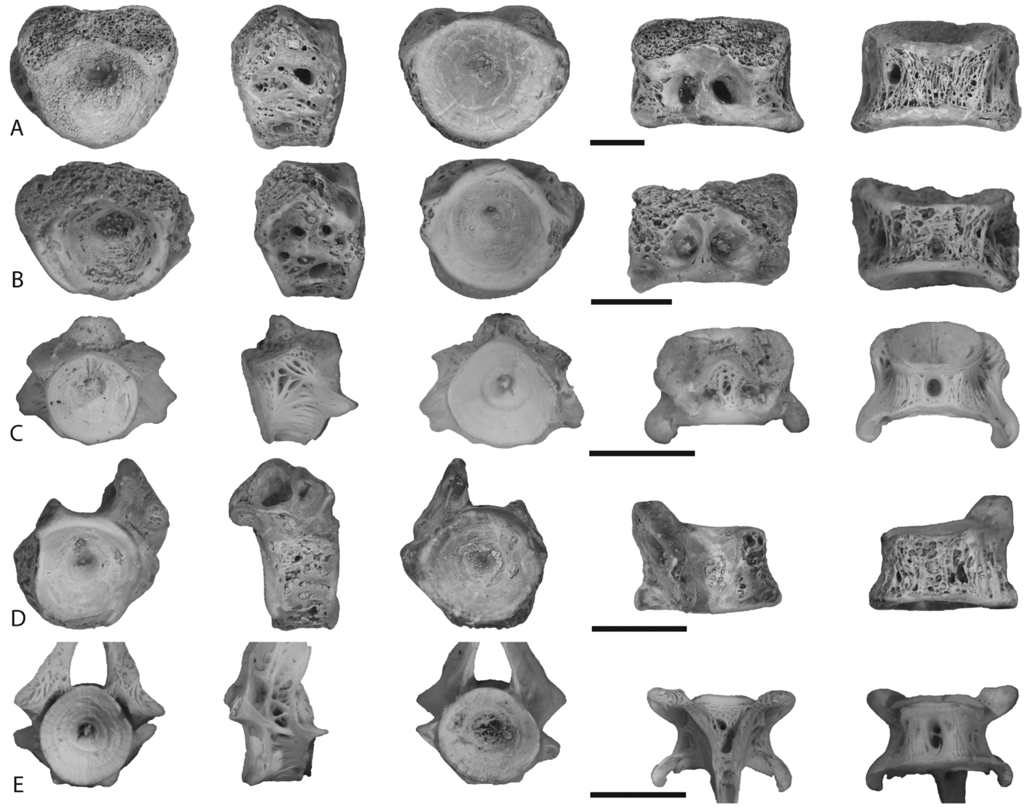
FIGURE 3.9. Cypress Hills Formation (**A**, **B**, **D**) and comparative perciform material (**C**, **E**). **A**, Centrarchidae large first centrum (ROM 67198); **B**, Centrarchidae small first centrum (ROM 66956); **C**, *Pomoxis nigromaculatus* (CMN 76-075) first centrum; **D**, Centrarchidae abdominal centrum (ROM 66983); **E**, *Pomoxis nigromaculatus* (CMN 76-075) abdominal centrum. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.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APPENDIX 3.1. Locality information for all of the material included in this study:

1. L41, Herman Pirson's Hill, southeast ¼ of southeast ¼ of Sec.4 Tp.8 Rg.22—Specimens ROM 66920–66934.
2. L40, Russell Hill 1949, Eastend Sk.—Specimens ROM 66935–66949.
3. Russell Hill on east side of Conglomerate Creek, northeast ¼ of Sec.4 Tp.8 Rg.22 Cypress Hills Oligocene (Sternberg and party 1949)—Specimens ROM 66950–66956.
4. L40, Small Tooth Locality Cypress Hills, Sk.—Specimens ROM 66957, 66958
5. L37, A573, Rodent Hill Cypress Hills, Sk.—Specimens ROM 66959—66964.
9. Found on Knowles and slopes of northeast side of Conglomerate Creek, ½ way between Stewarts and Whiles (not on Russell Hill) Cypress Hills, Sk. (Sternberg and party 1949)—Specimens ROM 66965–66969.
10. Calf Creek near Hunter Quarry, southwest ¼ of Sec.8 Tp.8 Rg.22—Specimens ROM 66970–66984.
11. Cypress Hills, Hornell and Weare 1949, Calf Creek Stewart Ranch—Specimens ROM 66985, 66986.
12. Calf Creek, Sec.7 Tp.8 Rg.22, W 3rd M, Collected by R. D. Weigel and J. A. Holman, 1967—Specimens ROM 66987–67011.
13. Ref. GE 67-4, Dollard, 985-475 Hanson Ranch, Eastend, '67 party, 19-VI-67—Specimen ROM 67012.

14. ’68 Party 12-VI-68, surface coll. from road cuts south of Hanson Ranch turnoff Eastend Sk.—Specimens ROM 67013–67023.
15. Small quarry across the valley from Hunter Quarry, Sec.5 Tp.8 Rg.22, surface collected, 15-V-68.—Specimens ROM 67024–67029.
16. Ref. Ge-8-68, Calf Creek Area, surface collected, 18-VI-68.—Specimens ROM 67030–67043.
17. Ref. 6E8-68 Small Tooth Quarry, Calf Creek, Hanson Ranch, 20-VI-68—Specimens ROM 67044–67050.
18. Various Outcrops N1/2 Sec.32 Tp.7 Rg.22 S1/2 Sec.5 Tp.8 Rg.22 Hanson ranch Eastend Sk., ’68 party, 25 and 26-VI-68, surface collected.—Specimens ROM 67051–67062.
19. 27-VI-68 North edge of Sec.32 Tp.7 Rg.22 Hanson Ranch—Specimens ROM 67063–67072.
20. ’68 Field Party, 28-VI-68, Hanson Ranch north edge of Sec.32 Tp.7 Rg.22, south edge of Sec.5 Tp.8 Rg.22—Specimens ROM 67073–67092.
21. ’68 party, surface collected, North side of coulee, northwest corner of Sec.32 Tp.7 Rg.22 Cypress Hills—Specimen ROM 67093.
22. Cypress Hills, Sk. 1968 Field Party, vicinity of Hanson Brothers Ranch, north west of Eastend, detailed locality not recorded—Specimens ROM 67094–67109.
23. 1968 party, surface collected, west of center of Sec.3 Tp.8 Rg.22, “Fairly high”—Specimens ROM 67110–67125.

24. Gyrmov, 26-VI-71, Dollard Street, Sec.7 Tp.8 Rg.22—Specimens ROM 67126–67131.
25. Collected by G. Gyrmov 26-VI-71, sec. 7, Tp. 8, Rg. 22 Dollard St. Cypress Hills, Sk.—Specimens ROM 67132–67137.
26. Sec.18 Tp.8 Rg.22, collected by G. Gyrmov, 26-VI-71—Specimens ROM 67138–67141.
27. Gyrmov, 28-VI-71, Dollard Street, Sec.16 Tp.3 Rg.22—Specimens ROM 67142–67152.
28. Sec.4 Tp.8 Rg.22, collected by Gyrmov, 19-VI-71, Cypress Hills, Sk.—Specimens ROM 67153–67167.
29. Tillie July 8/71 Sec.16 Tp.9 Rg.20 South edge of section at road cut—Specimens ROM 67168, 67169.
30. Sec.16 Tp.9 Rg.20, southern edge of Sec.16 at road cut. Collected by R Tillie and staff, July 8 ’71. Cypress Hills, Sk.—Specimens ROM 67170, 67171.
31. Sect.5 Tp.8 Rg.22, Cypress Hills, Sk. Collected by R. Tillie and staff July 9, 1971.—Specimens ROM 67172, 67173.
32. Sec.16 Tp.8 Rg.22. Collected by R. Tillie and staff 1971, Cypress Hills, SK.—Specimens ROM 67174–67177.
33. Cypress Hills, Sk. Pickings from concentrate, 1972. West side of Calf Creek, collected by Michael Torsgok and Roger Kidlark.—Specimens ROM 67178–67180.
34. Small Bones Quarry southeast ¼ of Sec.7 Tp.8 Rg.22—Specimen ROM 67181.

35. G. Gyrmov and D. Fisk. Cypress Hills, Sk. Sec.6 Tp.8 Rg.22, on the Dollard sheet.—Specimens ROM 67182–67188.
36. Entrance to Hanson’s Ranch and to the right side on his driveway, Cypress Hills, Sk.—Specimens ROM 67189–67191.
37. East side of trail next to HQ north of quarry, Cypress Hills—Specimen ROM 67190.
38. ¼ mile south on east side of Calf Creek campsite, Cypress Hills, Sk.—Specimens ROM 67191–67197.
39. ¼ mile north on east side of Calf Creek campsite, Cypress Hills, Sk.—Specimen ROM 67198.
40. Cypress Hills, Sk.—Specimens ROM 67199–67201.
41. Cypress Hills.—Specimens ROM 67202–67215.

APPENDIX 3.2. Comparative material examined. All of these specimens are dried skeletons, and each number represents an individual specimen.

Family Anguillidae: *Anguilla rostrata* Lesueur, 1817a – ROM R1721

Family Catostomidae: *Carpiodes carpio* (Rafinesque, 1820a) – KU 12732; *Carpiodes cyprinus* (Lesueur, 1817b) – CMN 77-183; *Catostomus catostomus* (Forster, 1773) – UAMZ F8558, F8582; *Ictiobus cyprinellus* (Valenciennes in Cuvier and Valenciennes, 1844) – KU 15337; *Moxostoma macrolepidotum* (Lesueur, 1817b) – ROM R7377

Family Centrarchidae: *Lepomis gibbosus* (Linnaeus, 1758) – CMN 73-236C; *Lepomis macrochirus* Rafinesque, 1819 – ROM R6210; *Micropterus dolomieui* Lacepède, 1802 – CMN 73-258, ROM R6125 (juvenile); *Pomoxis nigromaculatus* (Lesueur in Cuvier and Valenciennes, 1829) – CMN 76-075

Family Chanidae: *Chanos chanos* (Forskål, 1775) – UAMZ F8550

Family Cottidae: *Cottus bairdi* Girard, 1850 – ROM R6589; *Cottus cognatus* Richardson, 1836 – CMN 80-185; *Myoxocephalus octodecemspinosus* (Mitchill, 1814) – ROM R2430

Family Cyprinidae: *Campostoma anomalum* (Rafinesque, 1820b) – ROM R7890; *Chrosomus eos* Cope, 1861 – ROM R7897; *Clinostomus elongatus* (Kirtland, 1840a) – ROM R7754; *Cyprinella spiloptera* (Cope, 1867) – ROM R6823; *Cyprinus carpio* Linnaeus, 1758 – UAMZ F8557; *Hybognathus hankinsoni* Hubbs in Jordan, 1929 – ROM R2569; *Luxilus cornutus* (Mitchill, 1817) – ROM R6425; *Macrhybopsis storeriana* (Kirtland, 1844) – ROM R6385; *Nocomis biguttatus* (Kirtland, 1840a) – ROM R5358; *Notemigonus crysoleucas* (Mitchill, 1814) – ROM R7664; *Notropis atherinoides* Rafinesque, 1818a – ROM R2561; *Pimephales notatus* (Rafinesque, 1820b) –

ROM R7750; *Ptychocheilus oregonensis* (Richardson, 1836) – ROM R6513; *Semotilus atromaculatus* (Mitchill, 1818) – ROM R5885; *Semotilus margarita* (Cope, 1867) – CMN Z-668

Family Esocidae: *Esox lucius* Linnaeus, 1758 – UAMZ F8551, F8552; *Esox masquinongy* Mitchill, 1824 – ROM R2243; *Esox niger* Lesueur, 1818b – CMN 87-385

Family Fundulidae: *Fundulus heteroclitus* (Linnaeus, 1766) – ROM R3852

Family Hiodontidae: *Hiodon alosoides* (Rafinesque, 1819) – UAMZ F8556

Family Ictaluridae: *Ameiurus natalis* (Lesueur, 1819) – ROM R7245; *A. nebulosus* (Lesueur, 1819) – CMN 77-254; *Ictalurus punctatus* (Rafinesque, 1818b) – UAMZ F8553; *Noturus flavus* Rafinesque, 1818c – CMN 77-182, UAMZ 7527

Family Lotidae: *Lota lota* (Linnaeus, 1758) – CMN 85-603, ROM R1850

Family Moronidae: *Morone americana* (Gmelin, 1789) – ROM R6327; *Morone chrysops* (Rafinesque, 1820c) – ROM R6377; *Morone saxatilis* (Walbaum, 1792) – UAMZ F8554

Family Osmeridae: *Osmerus mordax* (Mitchill, 1814) – CMN Z-4079

Family Percidae: *Perca flavescens* (Mitchill, 1814) – UAMZ 4821, UMMZ 171120, 175905 (8 of 9), 175905 (9 of 9), 179978, 194309; *Stizostedion vitreum* (syn. *Sander vitreus*) (Mitchill, 1818) – UAMZ F8420, F8421

Family Percopsidae: *Percopsis omiscomaycus* (Walbaum, 1792) – ROM R6493

Family Salmonidae: *Coregonus clupeaformis* (Mitchill, 1818) – CMN 73-259b.; *Stenodus leucichthys* (Güldenstädt, 1772) – CMN Z4206

Family Scianidae: *Aplodinotus grunniens* Rafinesque, 1819 – CMN Z-275; *Rhinichthys cataractae* (Valenciennes in Cuvier and Valenciennes, 1842) – ROM R6592

Family Umbridae: *Umbra limi* (Kirtland, 1840b) – ROM R7818

CHAPTER 4

The fishes of the Farson Cutoff Fishbed, Bridger Formation (Eocene), greater Green River Basin, Wyoming, U. S. A.*

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INTRODUCTION

The Bridger Formation was first named by Hayden (1873), and covers wide areas of the greater Green River and Washakie Basins of southwestern Wyoming (Bradley, 1964). It was deposited in the early middle Eocene Bridgerian North American Land Mammal Age (NALMA), overlying the Green River Formation (Roehler, 1993). This time period corresponds to approximately 51 to 47 Ma (Smith et al., 2008). The predominantly fluvial Bridger Formation gradually covered the lacustrine Green River Formation from the north to the south of the basin during this period, corresponding to the last stages of the infilling of Lake Gosiute and to a period of increased volcanic activity to the west (Roehler, 1993; Smith et al., 2008). This resulted in the replacement of Lake Gosiute by a large floodplain with little relief, occasionally covered by short-lived shallow lakes (Bradley, 1964).

Extensive work has been carried out on the abundant fossils of the Bridger Formation, especially focusing on the biostratigraphy and biochronology of its mammalian fauna (Matthew, 1909; Wood, 1934; Gunnell et al., 2009). The herpetofauna of the formation has also been studied, with emphasis on crocodilian and especially the locally abundant turtle material. The taxonomic diversity of this material has been documented (Hay, 1908; Gaffney, 1972), and the taphonomy of some specific Bridger Formation turtle localities has been studied (Gilmore, 1945; Zonneveld, 1994; Brand et al., 2000). Other localities of the formation have also been studied taphonomically (Murphey, 2001; Murphey et al. 2001). The diverse palaeobotany of the greater Green River Basin has been studied and intensively sampled through both leaf impressions from lacustrine sediments (Wilf, 2000) and fluvially deposited petrified woods (Boonchai and Manchester, 2012).

These diverse lines of evidence have allowed relatively detailed and reliable palaeoclimatic and palaeoenvironmental reconstructions of the deposition of greater Green River Basin sediments. Evaporites of the Green River Formation immediately underlying the Bridger Formation indicate that the initial depositional period occurred in a relatively arid, hydrologically closed basin, where conditions may have been alkaline and/or saline (Smith et al., 2008). However, the early Bridgerian and the deposition of the Bridger Formation coincide with a return to a hydrologically open system, draining to the south or southwest (Smith et al., 2008). This interpretation is consistent with the palaeobotany of the Bridger Formation, which indicates subtropical climates (Boonchai and Manchester, 2012), and numerous forest swamp deposits (Roehler, 1993), which indicate relatively wet conditions. Reptilian and mammalian faunas also corroborate the reconstruction of the Bridgerian depositional environment as a warm, moist, closed forest environment (Gunnell and Bartels, 1994), with some evidence of warming climates during the Bridgerian based on the diversification of the herpetofauna (Walker, 1999). Ecological diversity analysis of the Bridger mammals further suggests that, although the area was constantly covered in tropical to subtropical forests, these became more densely canopied toward the mid-Bridgerian before returning to more open forests at the end of that age (Townsend, 2004). Bridgerian mammals also suggest an increase of environmental regionalism during the depositional period (Townsend, 2004).

The fish material from the formation is locally abundant, and is mostly preserved as disarticulated elements (Murphey, 2001). This material is usually reported as comprising lepisosteid, amiid and unidentified teleost material (e.g., Gunnell and Bartels, 1994; Buchheim et al., 2000), although identified teleosts, such as the clupeid *Knightia*, have also been recovered (Boonchai and Manchester, 2012). Several fish taxa have been erected based on Bridger Formation material. The lepisosteids *Atractosteus atrox* (Leidy, 1873) and *Atractosteus simplex* (Leidy, 1873), as well as the osteoglossid *Phareodus acutus* Leidy, 1873 were named on the basis of disarticulated material from the formation. Several more lepisosteid species were named by Marsh (1871) and Leidy (1873), but are now regarded as invalid (nomina dubia) because their holotype material is not considered to be diagnostic (Grande, 2010). The ictalurid catfishes *Astephus antiquus* (Leidy, 1873), *Astephus calvus* (Cope, 1873) and the ariid catfishes *Rhineastes peltatus* Cope, 1872 and *Rhineastes smithi* Cope, 1872 were also named based on Bridger material. Several amiid species were named from isolated fossils of the Bridger Formation by Marsh (1871), Cope (1873), and Leidy (1873). However, these taxa are considered invalid by Grande and Bemis (1998) because their holotype material is only diagnostic to subfamily level. Aside from these initial descriptions, the fish material from the formation is relatively poorly known, especially when compared to that of the underlying Green River Formation (e. g., Grande, 1984).

The present study focuses on a single locality preserving abundant and mostly disarticulated fish material, representing an assemblage of very low taxonomic diversity. This type of preservation allows the description of a wide variety of elements of these fishes, including three-dimensional details not preserved in articulated specimens from the Green River Formation. The low taxonomic diversity of this site is also interpreted as a palaeoecological indicator, and palaeoenvironmental considerations regarding both the depositional environment and the environmental tolerances of these fishes are proposed.

Geological Setting

The Bridger Formation has a full thickness of approximately 640 meters (reported as 2,100 feet), and is mostly composed of reworked volcaniclastic sediments deposited as tuffaceous sandstones and mudstones with some conglomerates, limestones, shales, siltstones, carbonaceous shales and carbonaceous siltstones also present (Roehler, 1993). These tuffs resulted from increased volcanic activity in a region extending west from the Yellowstone Park area across to the Pacific coast from the mid-Eocene to the end of the epoch (Roehler, 1993). The episodic introduction of volcanic particles in the basin probably led to the wide-ranging accumulation rates of sediments during this time, corresponding to the final infilling of Lake Gosiute in the southern parts of the Green River Basin (Roehler, 1993; Smith et al., 2008). Much of the formation was deposited in fluvial environments, but lacustrine, playa, paludal, and marginal mudflat depositional environments were also present (Roehler, 1993). Lithostratigraphic structures suggest that the lower Bridger Formation was deposited by alternating sequences of shallow widespread lakes forming limestones being suddenly infilled by volcaniclastics, and resulting in temporary fluvial-lacustrine systems (Buchheim et al., 2000). The silt and mudstones deposited in these fluvial-lacustrine systems (Buchheim et al., 2000) and in basin fills of the area (Roehler, 1993) correspond to the combination of white siltstones and grey-brown mudstones of the member where the material examined here was recovered.

MATERIALS AND METHODS

The material described here was recovered from University of California Museum of Paleontology (UCMP) locality UCMP V96246, a site known as the Farson Cutoff Fishbed, west of the town of Farson (approximately latitude 42.10994, longitude -109.451294), Sweetwater County, Wyoming, in the Bridger Basin of the greater Green River Basin (Fig. 4.1). This material was collected over several field expeditions led by M. T. Greenwald and J. H. Hutchison, both in August 1976, and by L. Macdonald in June 1977.

Material Examined

All of the material reported here from the Bridger Formation is curated in the University of California Museum of Paleontology (UCMP), Berkeley, California, U. S. A. Comparative Recent material (Appendix 4.1) is from the Canadian Museum of Nature (CMN), Ottawa, Ontario, Canada, the University of Kansas Natural History Museum (KU), Lawrence, Kansas, U. S. A., the Royal Ontario Museum (ROM), Toronto, Ontario, Canada, the University of Alberta Museum of Zoology (UAMZ), Edmonton, Alberta, Canada, and the University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Michigan,

U. S. A. Comparative fossil material from the Cypress Hills Formation is from the collections of the ROM (see Chapter 3; Divay and Murray, in press).

Methods

The isolated Bridger Formation fossils were identified through comparisons with modern taxa and with similarly isolated fossils from the Cypress Hills Formation (Chapter 3; Divay and Murray, in press). Nelson's (2006) taxonomic system was followed. Wherever possible, taxonomic attributions were based on features interpreted to represent autapomorphies. In some cases, however, identifications had to be made based on general phenetic similarities. The material was coated in ammonium chloride prior to photographing using a Nikon DXM 1200C digital camera mounted on a Zeiss Discovery.V8 stereo microscope.

Determining the Longevity and Growth Characteristics of *Astephus*— Post-Weberian abdominal centra and first modified centra of the Weberian apparatus were used to determine the longevity and growth characteristics of the Bridger Formation *Astephus*. These were then compared to the same elements from *Astephus* material from the late Eocene–early Oligocene Cypress Hills Formation of Saskatchewan, Canada, described by Divay and Murray (in press; Chapter 3). The Cypress Hills Formation *Astephus* material was hypothesized to represent two different species of widely different adult sizes: the large *Astephus* taxon A and the smaller *Astephus* taxon B (Chapter 3; Divay and Murray, in press). This hypothesis was based on differences in the morphology of pectoral fin spines in the assemblage, which corresponded to two distinct size classes. However, all centra of the Cypress Hills Formation assemblage had similar morphologies.

All Cypress Hills Formation centra well-enough preserved for growth annuli to be counted were included in the comparisons here (n = 20, ROM 66932, 66949, 66952, 66963, 67008, 67009, 67022, 67029, 67041, 67049, 67057-67059, 67070, 67089, 67090, 67106, 67107, 67165, 67166). The same number of centra was randomly selected from the Bridger Formation sample (n = 20, UCMP V193532-V193551). Longevity and growth characteristics were used to compare these taxa as they lack discrete characters to differentiate the centra of these presumed congeneric ictalurid species.

Growth annuli can be used to determine reliable age assignments from several bones in a variety of fishes; such age assignments then allow the comparison of the amount of growth of different individuals over a set period of time. Fossil centra have been used for this purpose in several fish families, including the Amiidae (Brinkman et al., 2014), the Hiodontidae (Newbrey et al., 2007), and the Esocidae (Newbrey et al., 2008). Determining growth characteristics was shown to be useful in determining the presence of a greater taxonomic diversity than could be determined through morphology alone in some taxa (e.g., Newbrey et al., 2007; Brinkman et al., 2014). As in these previous studies, it was here assumed that growth cessation marks were annular and represented by circular depressions following ridges on the anterior and posterior articular surfaces of centra. The first annulus was assigned to age one, although it may or may not directly correspond to age one in a particular species; however, this can only be determined with a sample of already-known age. Longevity was therefore determined based on the absolute number of these circular growth marks. In addition to longevity, size was measured at the fifth annulus as a radial distance from the notochordal foramen to determine relative amount of growth at a set age. Radial distances were all measured laterally, to standardize the orientation of these measurements, and rounded to the nearest 0.01 mm. Samples were statistically compared by testing for differences in the maximum number of growth annuli and in the radial distances at annulus 5 using two-tailed t-tests assuming unequal variances. Bonferroni corrections were applied to the 0.05 α-level of statistical significance in order to limit the probability of type I errors (false positives), which could be increased by the repeated use of t-tests.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII Cope, 1887
Order LEPISOSTEIFORMES Hay, 1929
Family LEPISOSTEIDAE Cuvier, 1825
Gen. et sp. indet.
(Fig. 4.2A, B)

Material—One lacrimomaxillary bone (UCMP V193426), Fig. 4.2A; one abdominal centrum (UCMP V193296), Fig. 4.2B.

Description—The lacrimomaxillary bone (Fig. 4.2A) is rectangular, being longer than wide. The ventro-lateral margin of the bone has a series of small conical teeth. There is a single row of larger, longitudinally striated teeth medial to the smaller ones. The medial side of the element is elongated and slightly concave. The dorso-lateral surface is ornamented with tubercules.

The opisthocoelous, holospondylous centrum (Fig. 4.2B) is wider than high, and longer than wide. The broken bases of the fused neural arches extend between the articular surfaces on the anterior and posterior ends of the centrum, along the midline of the dorsal surface. Parapophyses project from the lateral surfaces, extending for the full length of the centrum, but are broken distally. The ventral surface bears a pair of longitudinal parasagittal processes close to the midline, extending for the full length of the centrum. All bone surfaces are smooth.

Remarks—Bones forming the lateral margins of much of the upper jaw of lepisosteid gars are here called lacrimomaxillaries, following Grande's (2010) terminology. The centrum is characteristic of lepisosteiforms in being opisthocoelous, and the lacrimomaxillary is similar to that of both *Atractosteus* and *Lepisosteus*. *Atractosteus* is known to occur in the Bridger Formation (Leidy, 1873), while *Lepisosteus* has been recovered from the underlying Green River Formation (Grande, 2010). The elements described here may represent one or both of these genera, but are not diagnostic enough for these to be differentiated. This material is therefore left as Lepisosteidae indeterminate.

Division TELEOSTEI Müller, 1846

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

Order OSTEOGLOSSIFORMES Berg, 1940

Family OSTEOGLOSSIDAE Bonaparte, 1832

Subfamily OSTEOGLOSSINAE Bonaparte, 1832

PHAREODUS Leidy, 1873

(Figs. 4.2C–I, 4.3A–E)

Material—Seven premaxillae (UCMP V193263–V193265, V193418–V193420, V198895), Fig. 4.2C; 20 maxillae (UCMP V193213, V193271–V193282, V193421–V193425, V193431, V198896), Fig. 4.2D–F; 11 dentaries (UCMP V193266–V193270, V193413–V193417, V198897), Fig. 4.2G; five anterior basibranchial toothplates (UCMP V193214, V193215, V193429, V193430, V198894), Fig. 4.2H; one tooth-bearing pharyngeal element probably representing the posterior basibranchial toothplate (UCMP V193262), Fig. 4.2I; one basioccipital (UCMP V198901), Fig. 4.3A; four basioccipitals preserved articulated with the first centrum of the vertebral series (UCMP V193295, V193336–V193338), Fig. 4.3B; seven first centra of the vertebral series (UCMP V193339–V193342, V193600, V193601, V193236) Fig. 4.3C; 68 abdominal centra (UCMP V193237–V193239, V193298–V193311, V193343–V193358, V193383–V193387, V193602–V193628, V198907 [2 specimens], V198911), Fig. 4.3D, E.

Description—The premaxillae (Fig. 4.2C) bear evidence of up to nine large conical teeth. The anterior teeth are slightly smaller than those in more posterior positions. All teeth are relatively wide for most of their length, and are capped with a short, narrow, translucent pointed tip. The bases of the teeth project slightly from the alveolar process and have shallow longitudinal striations, which the tooth crowns lack. The alveolar process of the premaxilla projects medially from the tooth-bearing area, forming a bony shelf. There is a dorsal groove on the posterior part of the alveolar process, where the anterior process of the maxilla articulates with the premaxilla. The premaxilla has a wide ascending process anteriorly, which is taller posteriorly than anteriorly. The surface for the articulation of the premaxilla with the nasal is located on the medial side of the ascending process and approximates a cone, the apex of which is at the base of the process.

None of the recovered maxillae is complete, but the morphology of the bone can be mostly determined. There is a rod-like anterior process with a short ventral keel for articulation with the dorsal posterior groove of the premaxilla (Fig. 4.2D). This anterior process is angled slightly dorsally and medially compared to the rest of the maxilla. A well-defined bony bulge on the dorsal surface of the maxilla is positioned anteriorly, where the bone is in contact with the antorbital, at the base of the anterior process and immediately anterior to the alveolar process. Maxillary teeth are similar to those of the premaxilla (Fig. 4.2E); however, the teeth on the maxilla are consistently slightly smaller than those on an equivalent-sized premaxilla, and are slightly posteriorly inclined. These teeth become smaller and closer together posteriorly (Fig. 4.2F). The medial surface of the maxilla is convex anteriorly, becoming flat then concave towards its posterior part, while the lateral surface remains convex for the full length of the bone. Posterior to the tooth row, the maxilla widens dorso-ventrally into a vertical sheet of bone.

Dentary teeth are different from those of the premaxilla and maxilla in being wider medio-laterally than antero-posteriorly (Fig. 4.2G). They are identical to premaxillary teeth in all other respects. The dentary is wider at the symphysis, narrowing posteriorly. The symphysis is convex, with more porous bone than other surfaces of the dentary, and triangular, being wider dorsally than ventrally. The dentary has a sharp antero-ventral crest that tapers anteriorly towards the symphysis. There is a large mental foramen on the lateral surface of the dentary, and a more posterior foramen that is closer to the tooth row. Two shallow longitudinal striations originate close to this second foramen. The rest of the lateral side of the dentary has a rough surface with some pitting, which may be due to poor preservation. The medial surface is smoother, with a shallow but wide trench over most of its ventral half.

The dorsal tooth-bearing surface of the anterior basibranchial toothplate is convex, bearing teeth similar to those of the premaxilla in single rows on both of its lateral sides (Fig. 4.2H). In between these are a multitude of shorter and narrower teeth arranged randomly, which lack the terminal pointed cap of the lateral teeth. The ventral side of the tooth plate is concave, and all of the exposed surfaces are featureless.

The probable posterior basibranchial is oval, with a tooth-bearing surface over approximately half of its circumference (Fig. 4.2I). These teeth are arranged in two alternating rows, are more recurved than any other teeth described here, and are capped by the same sharp, narrow tip as premaxillary teeth. Pharyngeal teeth also lack the slightly projecting tooth bases seen in the teeth of other elements. The lateral surface of the element has shallow pits and striations arranged radially.

The posterior articular surface of the basioccipital approximates a hexagon, with flattened dorsal and ventral sides (Fig. 4.3A). Ventral to this articular surface, there is a posterior bony projection that is rectangular in cross section. Several basioccipitals were recovered still in articulation with the first centrum of the vertebral series (Fig. 4.3B), showing that this bony projection cups the ventral surface of the first centrum, articulating with it in two deep ventral pits. A thin bony ridge extends for most of the dorsal side of the basioccipital, bifurcating posteriorly to form a notch in the area adjacent to the posterior articular surface. The dorsal ridge is flanked by two pairs of pits, the anterior pair being much longer than the posterior. The posterior dorsal pits are rounded, with shallow radial striations. The ventral half of the lateral surface has a triangular fossa tapering anteriorly, with some longitudinal bone fibres extending through it and along its edges. On the lateral surface, the area between the posterior articular surface and the posterior dorsal pits is also fibrous in texture. The medial ventral surface is deeply fibrous, with fibres oriented longitudinally, and more robust lateral sides. All other bone surfaces are flat and featureless.

The articular surfaces at the anterior and posterior ends of the first centrum (Fig. 4.3C) are oval to triangular, being higher than wide, and usually slightly wider dorsally than ventrally. The notochordal foramen is located either centrally or slightly ventrally. The centrum has a pair of large, rounded neural arch pits on its dorsal surface, separated by an hourglass-shaped bony surface that is less deeply fibrous in texture than the other surfaces of the centrum. The ventral side has very deep pits articulating with the posterior projection of the basioccipital. These ventral articular pits are closer together than the neural arch pits, with the pits separated only by a thin sheet of bone posteriorly. Aside from the surface separating the neural arch pits and a thin margin of slightly projecting smooth bone around the articular surfaces, all surfaces of the centrum are deeply fibrous, with most fibres oriented longitudinally.

Abdominal centra have a central notochordal foramen and somewhat flattened dorsal and ventral margins in end view. Anterior centra (Fig. 4.3D) are wider than high, and higher than long. The more posterior centra gradually become more circular in end view, and these centra also become gradually longer. The articular surfaces at both anterior and posterior ends of the centrum are surrounded by a thin margin of smooth bone. On the dorsal surface, deep rectangular neural arch pits extend for the full length of the centrum in most specimens. However, neural arches are sometimes fused to the centrum, especially in more posterior positions along the vertebral series (Fig. 4.3E). A mid-dorsal pit separates the neural arch bases in centra where these are fused. The centrum has rib articular pits adjacent to the articular surface at its posterior end, similar to the condition seen in some hiodontids, such as *Hiodon*. These pits are positioned laterally in anterior abdominal centra, gradually becoming more ventral in posterior centra. Anterior abdominal centra lack parapophyses, but these are large and fused to the lateral surface of the centrum in more posterior positions of the vertebral series. In the first few centra with parapophyses, these are restricted to the anterior margin of the rib articular pit, gradually extending along the ventral margin of this pit in more posterior centra. The ventro-lateral margin of the centrum has deep pits adjacent to the ventral margin of the parapophyses. These pits are separated by a wide bony surface in anterior centra, which becomes narrower and hourglass-shaped in more posterior centra. In posterior-most abdominal centra, this ventral bony surface becomes more fibrous in texture, with an elongate mid-ventral pit. Most surfaces of the centrum are formed by longitudinally arranged bone fibres that are most visible on the dorsal, ventral, and dorso-lateral surfaces. Centra become more deeply fibrous in texture in posterior positions, and the centra of smaller individuals are also more fibrous than those of larger ones.

Remarks—Two valid species of *Phareodus* are known from North America (Li et al., 1997). These are *P. encaustus* and *P. testis*, both of which are known to occur in the Bridger Formation (Grande, 1984). The two species are mainly differentiated based on meristic characters, position of the mouth corner relative to the orbit, and different relative sizes of some skull bones (Li et al., 1997) that have not been recovered from the Farson Cutoff Fishbed. Differences between the number of teeth on the maxillae and dentaries of *P. encaustus* and *P. testis* (Li et al., 1997) could potentially be used to identify the taxon or taxa present in this locality; however, the material described here is too incomplete for precise tooth counts. Additionally, according to Li (1994), both *P. encaustus* and *P. testis* have seven to nine premaxillary teeth, which corresponds to the premaxillae described above. Therefore the material described here corresponds to previous descriptions of both species of *Phareodus*, and could indicate the presence of either—or both—in the Farson Cutoff Fishbed locality.

Subdivision OSTARIOCLUPEOMORPHA (= OTOCEPHALA) Arratia, 1997

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

Family ICTALURIDAE Bleeker, 1863

ASTEPHUS Cope, 1873

(Figs. 4.3F–I, 4.4, 4.5)

Material—Thirty dentaries (UCMP V193216, V193284–V193294, V193432–V193446, V198898–V198900), Fig. 4.3F; five articulars (UCMP V193409–V193412, V193447), Fig. 4.3G; one post-temporal (UCMP V193297), Fig. 4.3H; 58 basioccipitals (UCMP V193217–V193221, V193314, V193396–V193407, V193563–V193599, V198902–V198904), Fig.3I); one fragmentary cleithrum (UCMP V193283), Fig. 4.4A; 10 pectoral fin spines (UCMP V193208, V193408, V193448–V193455), Fig. 4.4B, C; 22 first Weberian centra of the vertebral series (UCMP V193222–V193224, V193378–V193380, V193388, V193552–V193557, V198906 [4 specimens], V198908 [5 specimens]), Fig. 4.4D; one first Weberian centrum preserved articulated with the centrum of the complex vertebra of the Weberian apparatus (UCMP V193388), Fig. 4.4E; 35 centra of the complex vertebra of the Weberian apparatus (UCMP V193209–V193212, V193390–V193395, V193456–V193478, V198909 [2 specimens]), Fig. 4.4F; one complex vertebra on the Weberian apparatus preserved in articulation with the first post-Weberian centrum (UCMP V193389), Fig. 4.4G; seven first post-Weberian centra (UCMP V193381, V193382, V193558–V193562), Fig. 4.4H; 119 abdominal centra (UCMP V193225–V193235, V193312, V193313, V193359–V193377, V193479–V193551, V198905 [9 specimens], V198909, V198910 [3 specimens]), Fig. 4.5A, B.

Description—The numerous tooth bases of the dentaries (Fig. 4.3F) are small, and not oriented in rows. The tooth-bearing surface is wider towards the symphysis and narrows slightly posteriorly. The symphyseal surface has a groove originating in its dorso-medial corner that separates the symphysis into a wide anterior surface and a narrower posterior one. The dentary has a sharp antero-ventral crest that tapers and bifurcates anteriorly, joining with the anterior and posterior margins of the symphyseal surface to form a triangular depression adjacent to the symphysis. The teeth are borne on a shelf that is widest by the symphysis, projecting from the medial margin of the dentary. The medial surface of the dentary has shallow longitudinal plications extending radially from the symphyseal area, with those on the ventral margin developed into a more pronounced bulge posteriorly. The lateral surface of the dentary has a row of foramina; the distance separating successive foramina increases posteriorly. The bone texture is more pronounced on the lateral surface of the dentary than on the medial surface. The ventral half of the lateral surface has relatively deep, imbricated, v-shaped ridges, the apexes of which are at the foramina.

The posterior articular surface of the articular (Fig. 4.3G) projects from the dorsal surface of the bone, and is deeply concave. The coranoid process forms a prominent dorsal projection in the anterior part of the articular, where it is in contact with the dentary. The medial surface of this bone is covered with bumps in no particular orientation while the lateral surface is deeply fibrous, with primarily longitudinal bone fibres.

The post-temporal (Fig. 4.3H) has a thin, rounded lateral projection. The bone is much thicker in its mid-section, but the medial projection is broken, and little more detail is preserved. The bone texture is deeply fibrous, especially on the dorso-lateral surface, where fibres are mostly oriented longitudinally, with numerous interconnections between them.

The basioccipital (Fig. 4.3I) has a pentagonal to hexagonal posterior articular surface and central notochordal foramen. The dorsal surface has a pair of narrow ridges extending for the full length of the bone close to its midline, which separate two paired pits on the dorso-lateral margin of the basioccipital. The pair of pits closest to the posterior articular surface is more angular while the anterior paired pits have curved margins and are more elongated. The lateral surfaces of the basioccipital have shallow fossae on their ventral half, close to the posterior articular surface. The ventral surface has a large, deep, circular mid-ventral pit, surrounded by smooth projecting bone extending between the ventral margins of the lateral fossae. These surfaces of smooth bone extend anteriorly on the ventro-lateral margins of the basioccipital. All other surfaces on the ventral and lateral sides of the bone are deeply fibrous in texture, with bony fibres primarily oriented longitudinally.

The poor preservation of the cleithrum (Fig. 4.4A) does not allow a detailed description of this bone. However, apart from articular surfaces, the bone shows the characteristic deeply fibrous texture seen in *Astephus*, with bone fibres that are oriented mostly longitudinally.

The pectoral fin spines (Fig. 4.4B) have a wide basal recess on their posterior surface, which narrows distally into a shallower posterior furrow. The anterior surface also has a well-defined basal recess, between the bases of the ventral process and of the dorsal articulating process. It is shorter, narrower and shallower than the posterior basal recess. The proximal surface of the dorsal articulating process forms a line with that of the ventral process. Anterior and posterior edges of the distal spine have ridges that are covered with small, bump-like serrations. On the posterior edge of the spine, this ridge originates within the posterior furrow, becoming more robust distally, where the furrow closes. Distal spine fragments (Fig. 4.4C) bear larger recurved serrations on their posterior edge. Bone surfaces are flat at the spine base, and longitudinally fibrous along the spine shaft. This spine shaft is oval in cross section.

The first Weberian centrum (Fig. 4.4D) is slightly higher than wide, and clearly wider than long. The articular surfaces at the anterior and posterior ends of the centrum are surrounded by a slightly projecting margin of smooth bone, and the notochordal foramen is located dorsally. The dorsal surface of the centrum has a pair of rounded pits for articulation with the scaphium; these pits are located close to the midline and separated by a narrow ridge of smooth bone. The ventral surface has a large mid-ventral pit flanked by paired parasagittal processes. The distal ends of these processes curve posteriorly. In specimens where these processes are best preserved, their posterior surface is grooved longitudinally, and this groove originates on the lateral side of the process base. The anterior margin of this groove extends to the ventro-lateral margin of the centrum as a bony fibre. One first centrum is preserved in articulation with the complex vertebra of the Weberian apparatus (sensu Chardon et al., 2003), showing that the ventral processes articulate with the ventral keels of the Weberian (Fig. 4.4E). All surfaces of the centrum are deeply fibrous in texture, the bony fibres being predominantly longitudinal with some interconnections between them.

The robust complex vertebra of the Weberian apparatus (Fig. 4.4E–G) has deep anterior and posterior articular surfaces that are slightly higher than wide, with a dorsal notochordal foramen. The elongate centrum of the complex vertebra is formed by the fusion of centra two to four in all catfishes (Chadron et al., 2003), and several Bridger Formation specimens are incompletely preserved, showing the notochordal canal expanding and retracting between these fused centra. There is a deep ventral trench extending for the full length of the apparatus, bordered by sharp ventral keels. On their anterior end, these keels have shallow grooves for the articulation with the first centrum of the vertebral series. The posterior end of each ventral keel has slight projections and grooves for articulation with the first centrum after the apparatus, as can be seen where the apparatus is preserved in articulation with the first centrum posterior to it (Fig. 4.4G). The narrowest point of the Weberian is slightly posterior to the articular surface at its anterior end, the bone then widens again, and the posterior articular surface is slightly wider than the anterior articular surface. The neural arch and parapophysis complex flares widely in its posterior area, and its dorsal surface has plications extending laterally from the midline of the centrum, while its ventral surface is flat and featureless (Fig. 4.4F). The anterior and posterior ends of the apparatus are weakly fibrous, and bony fibres are also visible within the ventral trench. Lateral surfaces are not as fibrous, and are mostly flat.

Abdominal centra (Figs. 4.4H; 4.5A, B) are higher and wider than long, and the articular surfaces at their anterior and posterior ends are surrounded by a slightly projecting margin of smooth bone. Anterior abdominal centra (Figs. 4.4H; 4.5A) are higher than wide, have hexagonal articular surfaces, and a dorsally located notochordal foramen. Additionally, the anterior end of the first non-Weberian centrum (Fig. 4.4H) has a flat, uneven articular surface with dorsal and ventral anterior projections on its midline, which articulate with the complex vertebra of the Weberian apparatus. In more posterior centra (Fig. 4.5B), the width and height of each centrum are approximately equal, anterior and posterior ends are less angular, and the notochordal foramen is located centrally. All abdominal centra have an elongate mid-dorsal pit that is bordered by the bases of the neural arches. The mid-dorsal pit and neural arch bases all extend the full length of the centrum. There is a pair of pits on the dorso-lateral margin of the centrum, lateral to the neural arch bases. Robust parapophyses fuse to the centrum on the lateral margin of these pits. In anterior abdominal centra, these parapophyses are on the dorso-lateral margin of the centrum, and are connected to the neural arch bases by a bony ridge that is adjacent and parallel to the anterior end of the centrum. The parapophyses are more lateral in placement and unconnected to neural arch bases in more posterior centra. The lateral surface of the centrum has an elongate pit ventral to the base of the parapophyses. The ventral surface has an elongate mid-ventral pit that is flanked by projecting longitudinal ridges in anterior centra. These ridges and the ventral pit become progressively smaller in more posterior centra. All bone surfaces are fibrous in texture, with bony fibres predominantly oriented longitudinally, but with some interconnections between them.

Remarks—The morphology of the pectoral fin spines and the surface texture of the dentaries closely correspond to the Bridger Formation *Astephus* material described by Lundberg (1975). The fibrous surface texture of most elements is characteristic of the genus, according to Lundberg (1975), and allows the identification of the articular, the post-temporal and the cleithrum fragments. The dentaries described here are also nearly identical to the large

Astephus taxon A material from the Cypress Hills Formation of Saskatchewan described by Divay and Murray (in press; Chapter 3), although the Canadian material is much larger.

That the pectoral fin spine fragments described here either have small, bump-like serrations or larger, recurved posterior serrations could indicate that these represent two different taxa. The material tentatively attributed to *Rhineastes smithi* by Lundberg (1975), after the initial identification by Cope (1872), also includes fin spines with larger posterior serrations. However, the rest of the material is consistent with a single genus being present in the Farson Cutoff Fishbed, and larger serrations are only observed on distal spine fragments. Therefore, larger serrations on distal spine fragments probably indicate that serrations increase in size distally, rather than indicate two different taxa with different spine morphologies in this locality. Centra of modern ictalurids are diagnostic to generic level (Chapter 2; Divay and Murray, 2013), and the centra described here are also consistent with a single genus being present in the locality. Furthermore, the morphology of these centra is also similar to that of fossils recovered in the Cypress Hills Formation (Chapter 3; Divay and Murray, in press).

Several plate-like tooth-bearing elements have also been recovered, and may represent fragments of other tooth-bearing bones, such as vomers, but these are very poorly preserved. These are covered with small tooth bases in no particular orientation, similar to those of the dentaries, and therefore probably represent the same taxon as the rest of the material described here.

ANALYSIS OF LONGEVITY AND GROWTH IN *ASTEPHUS*

Results—The longevity of *Astephus* individuals, as approximated by the total number of growth annuli on fossil centra, is similar in all specimens of both the Bridger and Cypress Hills formations (Fig. 4.6). The Bridger Formation *Astephus* centra have a maximum of 14 annuli ($\bar{x} = 8.8$, sample variance = 5.64), while those from the Cypress Hills have a maximum of 18 annuli ($\bar{x} = 8.2$, sample variance = 16.33). The numbers of annuli in centra from both samples were not found to be statistically different ($t = 0.586$, d.f. = 31, $p = 0.562$; Bonferroni-corrected α-level = 0.0125; Table 4.1). The largest difference in longevity was found to be between the partitioned data hypothesized to represent Divay and Murray's (in press; Chapter 3) *Astephus* taxon A and taxon B from the Cypress Hills Formation, although this difference was not found to be statistically significant ($t = 2.37$, d.f. = 13, $p = 0.034$; Bonferroni-corrected α-level = 0.0125). When compared to the Bridger Formation, both data partitions representing taxon A and taxon B had less significant differences in longevity ($t = 1.36$, d.f. = 8, $p = 0.211$ and $t = 1.74$, d.f. = 19, $p = 0.097$, respectively; Bonferroni-corrected α-level = 0.0125).

All Bridger Formation specimens had radial distances at annulus 5 between 2.13–3 mm. However, the Cypress Hills *Astephus* centra had much more variable radial distances at annulus 5, ranging from 2 to 6 mm. These clearly plot into two distinct groups (Fig. 4.6): one varies between 5–6 mm, distinct from both the rest of the Cypress Hills sample and the Bridger sample, while the other ranges between 2–3.33 mm. Differences between the measurements of the Bridger and Cypress Hills formation samples were found to be significant ($t = 2.92$, d.f. =31, $p = 0.004$; Bonferroni-corrected α-level =

0.0125), but, when compared to one another, differences between the hypothesized taxon A and taxon B from the Cypress Hills were found to be much more significant ($t = 15.91$, d.f. = 14, $p < 0.001$; Bonferroni-corrected α-level = 0.0125). The measurements from the Bridger Formation specimens are entirely overlapped by those representing the hypothesized Cypress Hills Formation taxon B sub-sample, and differences between these are not significant ($t = 0.34$, d.f. = 16, $p = 0.739$; Bonferroni-corrected α-level = 0.0125). Measurements from the Cypress Hills Formation taxon A sub-sample were found to be significantly different from those of the Bridger Formation ($t = 19.34$, d.f. = 7, $p < 0.001$; Bonferroni-corrected α-level = 0.0125).

Interpretations—That the maximum numbers of annuli in specimens from both the Bridger and Cypress Hills formations are not significantly different, vary comparably and overlap without forming distinct groups is here interpreted as evidence that all *Astephus* taxa included in the samples had similar longevities. Therefore, any variation in the sizes of the specimens results from different growth rates over their similar lifespans, rather than a uniform rate of growth but different ages at time of death. This interpretation is reinforced by the lack of a correspondence between the maximum longevities and the maximum radial distances: the oldest individual in the Bridger Formation sample had 14 annuli, but did not have a particularly large radial distance at annulus 5 (2.73 mm). Similarly, the oldest individual in the Cypress Hills sample had 18 annuli, but a radial distance at annulus 5 of 3.13 mm. Furthermore, the largest radial distances measured from both the Bridger and Cypress Hills formations samples do not correspond to the centra with the largest numbers of annuli (3 mm for 9 annuli and 6 mm for 15 annuli, respectively).

The Bridger Formation *Astephus* has a similar radial distance at annulus 5 as do the *Astephus* individuals with the smaller set of measurements from the Cypress Hills Formation, which is here interpreted as evidence that the individuals in the Bridger Formation and the smaller individuals in the Cypress Hills Formation had similar growth rates. The greater variation in the radial distances of these Cypress Hills measurements may indicate a greater variation in the growth rate of these individuals, or may result from the greater weathering of these specimens, leading to measurement errors. The group of Cypress Hills specimens with significantly larger radial distances at annulus 5 indicate that these individuals had much faster growth rates prior to annulus 5 than others included in this study, whether from the Cypress Hills or Bridger formations. Therefore, this result supports Divay and Murray's (in press; Chapter 3) hypothesis that two species of *Astephus* were present during the deposition of the Cypress Hills Formation, the larger one of which (*Astephus* taxon A) had a faster growth rate than the smaller taxon (*Astephus* taxon B). The Bridger Formation *Astephus* taxon had similar growth rates as the Cypress Hills *Astephus* taxon B.

DISCUSSION

The Farson Cutoff Fishbed locality is notably poor in fish diversity, with only three taxa represented: Lepisosteidae, *Phareodus*, and *Astephus*. All are also represented in the underlying Green River Formation (Grande, 1984), which is considered to have been deposited in similarly tropical to subtropical climates (Roehler, 1993). Therefore, the taxonomic composition of this assemblage is consistent with previous palaeoclimatic reconstructions based on the sedimentology, palaeobotany, reptilian and mammalian faunas of the Bridger Formation.

Because both large and small fossils were recovered from the site, the low taxonomic diversity of the locality is unlikely to result from either a taphonomic or a collection bias against other fishes that would have been present in the source community. It therefore probably indicates that the community itself was species-poor. Considering the species richness of the immediately underlying Green River Formation (Grande, 1984), the Farson Cutoff Fishbed locality was unlikely to be hydrologically inaccessible to other fish taxa, and its low taxonomic diversity is more likely to reflect local environmental conditions instead.

Although palaeobotanical and faunal evidence suggest relatively wet conditions throughout most of the deposition of the Bridger Formation, a somewhat saline depositional environment should be considered because of the increased environmental regionalism shown by Townsend (2004), combined with the evidence of aridity in the underlying Green River Formation (Smith et al., 2008). Saline conditions would severely restrict the taxonomic diversity of the local ichthyofauna, and would be expected to result in such a species-poor assemblage. Lepisosteids occur in fresh, brackish, and marine waters (Scott and Crossman, 1973). However, although some catfishes, such as ariids (Nelson, 2006), and the osteoglossid *Brychaetus* (Arambourg, 1952) can occur in marine environments, both *Phareodus* and *Astephus*, are freshwater taxa (Grande, 1984). The Farson Cutoff Fishbed assemblage is therefore unlikely to reflect saline conditions.

Lepisosteids (Scott and Crossman, 1973), osteoglossids and catfishes (Welcomme, 1979) are all commonly found in the backwaters of the lateral floodplains. These environments are typically hypoxic and would therefore be expected to only have fishes capable of surviving in anoxic conditions. Both *Atractosteus* and *Lepisosteus* are capable of air-breathing, and tolerate warm, oxygen-poor waters, in which most other fishes cannot survive (Grande, 2010; Scott and Crossman, 1973). Although *Astephus* is an extinct genus, many catfishes are resistant enough to anoxic conditions to spend the dry season on the floodplain without migrating back to oxygenated channel waters (Welcomme, 1979), and *Astephus* has been found in environments interpreted as hypoxic backwaters (Chapter 3; Divay and Murray, in press). Modern osteoglossids are also typically tolerant of low oxygen conditions and are commonly found in backwaters (Welcomme, 1979); therefore, *Phareodus* may also have been tolerant of such conditions.

Freshwater environments are usually saturated with oxygen (normoxic) through photosynthesis of aquatic vegetation and water turbulence facilitating exchanges with the atmosphere (Davenport and Sayer, 1993). The anoxic environment indicated by the fishes of the Farson Cutoff Fishbed may indicate little photosynthetic activity, which could be due to turbid waters, and is typically the result of high temperatures, high organic loading and stagnant waters (Davenport and Sayer, 1993). However, stagnant waters would not be expected to preserve almost entirely disarticulated material, as is the case here. It is noteworthy that some centra were preserved in articulation with others or with basioccipitals, and that the Farson Cutoff Fishbed collection includes a partially articulated catfish skull (Divay, pers. obs.), which could not be obtained to be described here. Partial articulation may indicate that the material was not preserved as lag deposits, like other microvertebrate sites (e.g., Chapter 2; Divay and Murray, 2013), and the preservation of the material in fine sediments precludes the burial of these elements during seasonal, high-energy flooding episodes. At present, the taphonomy of the locality cannot be reconstructed without more details on its sedimentology, and the ichthyofauna remains the best evidence for reconstructing the depositional environment.

The Farson Cutoff Fishbed assemblage is therefore consistent with a stagnant, hypoxic, lateral floodplain depositional environment. This interpretation is consistent with the Bridger Formation being deposited by a fluvio-lacustrine system with frequent water level changes, as suggested by Buchheim et al. (2000). In such a system, low-oxygen backwaters only sustaining fishes tolerant of hypoxic conditions would be susceptible to become isolated from channel waters by a lowering of the water level and / or a sudden influx of volcanic sediments. Such shallow backwaters would then be infilled, preserving low diversity fish assemblages biased towards taxa tolerant of hypoxic conditions.

FIGURE 4.1. Locality map for the Farson Cutoff Fishbed, locality UCMP V96246, of the Bridger Formation, Wyoming. **A**. Location of the Bridger Formation (marked with a star) relative to Wyoming and the contiguous United States. **B**. Enlarged locality map showing the greater Green River Basin (dotted line), Sweetwater county (dashed line), and the Farson Cutoff Fishbed (star) relative to the borders of Wyoming, Idaho, Utah, and Colorado.

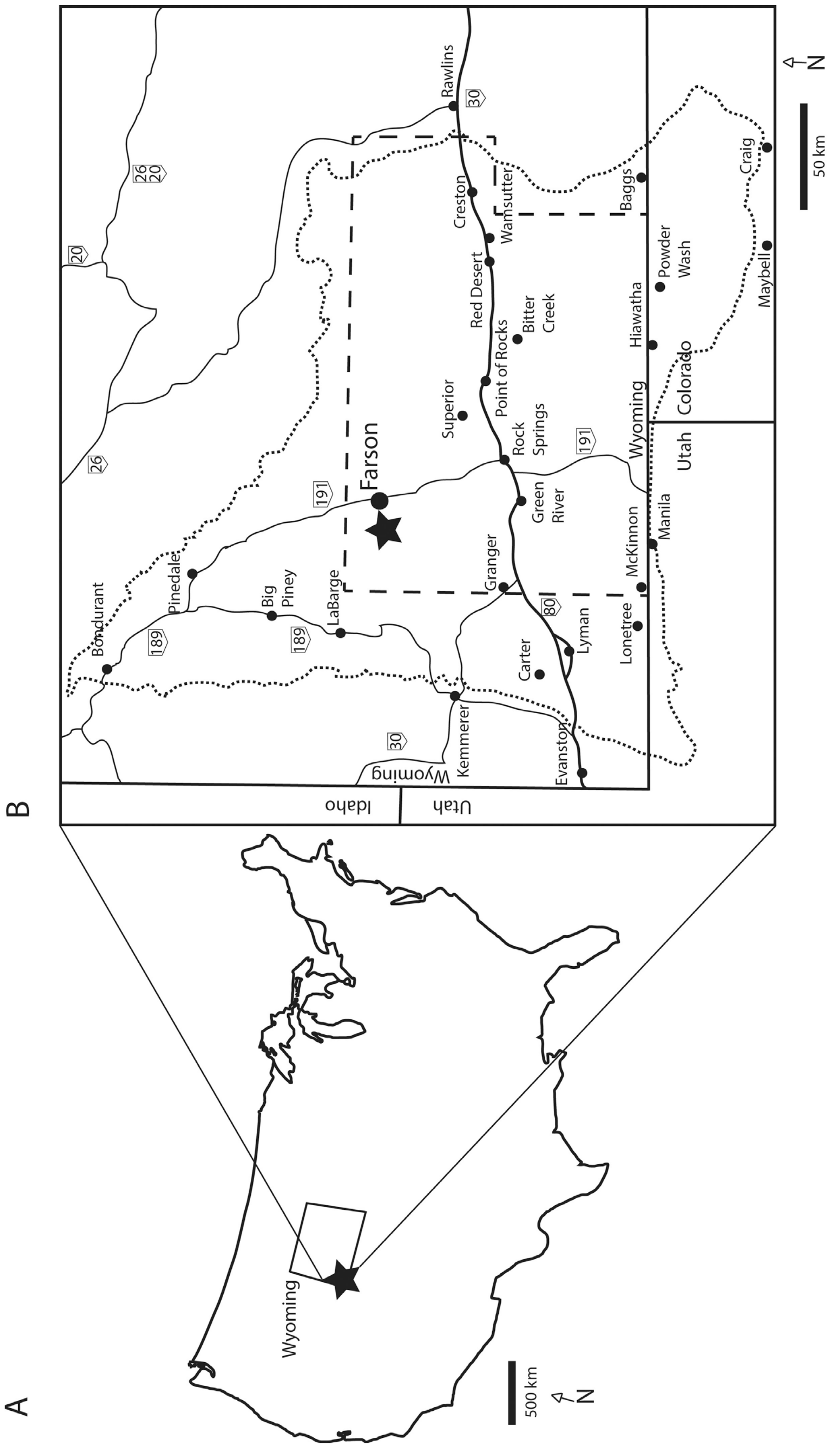

A
Wyoming
500 km
N
B
Idaho
Utah
Wyoming
Bondurant
Pinedale
Big Piney
LaBarge
Kemmerer
Evanston
Carter
Lyman
Lonetree
Granger
McKinnon
Manila
Green River
Farson
Rock Springs
Superior
Point of Rocks
Bitter Creek
Red Desert
Wamsutter
Creston
Rawlins
Baggs
Hiawatha
Powder Wash
Maybell
Craig
Wyoming
Colorado
Utah
26
20
26 20
189
189
191
191
30
30
80
50 km
N

FIGURE 4.2. Bridger Formation fish material. **A**, **B**, Bridger Formation indeterminate lepisosteid material: **A**, right lacrimomaxillar (UCMP V193426) in lateral, dorsal, medial and ventral views; **B**, abdominal centrum (UCMP V193296) in anterior, lateral, posterior, dorsal and ventral views. **C**–**I**, Bridger Formation *Phareodus* material: **C**, premaxilla (UCMP V198895) in lateral, medial, dorsal and ventral views; **D**, anterior fragment of a maxilla (UCMP 193271) in medial, lateral, ventral, and dorsal views; **E**, fragment of a maxilla representing the middle part of the bone (UCMP V198896) in lateral, medial, and ventral views; **F**, posterior fragment of a maxilla (UCMP 193272) in lateral, medial, and ventral views; **G**, dentary (UCMP V193413) in medial, ventral, lateral, dorsal, and symphyseal views; **H**, anterior basibranchial toothplate (UCMP V198894) in dorsal and ventral views; **I**, pharyngeal bone probably representing a posterior basibranchial toothplate (UCMP V193262) in lateral, medial, and ventral views. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

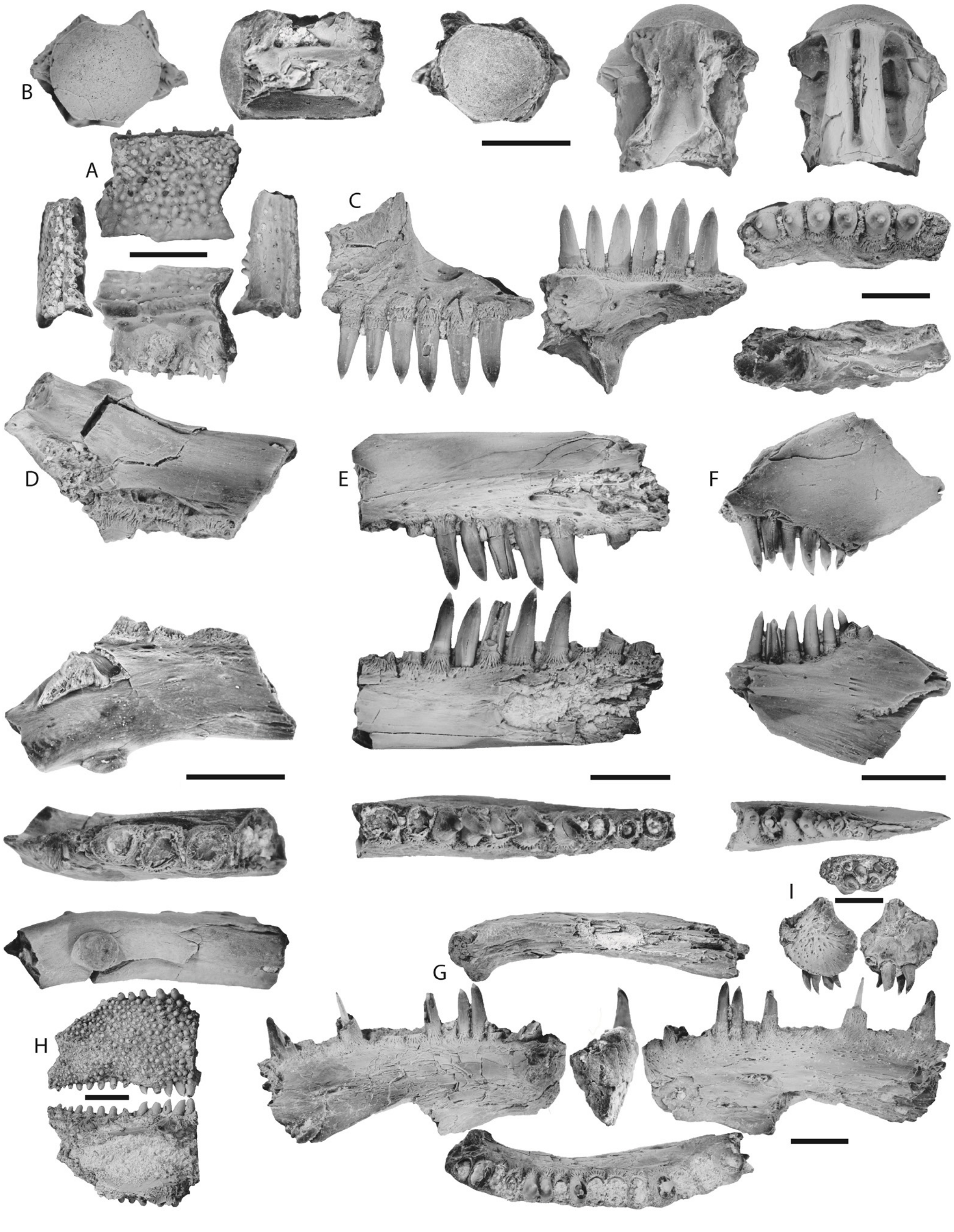
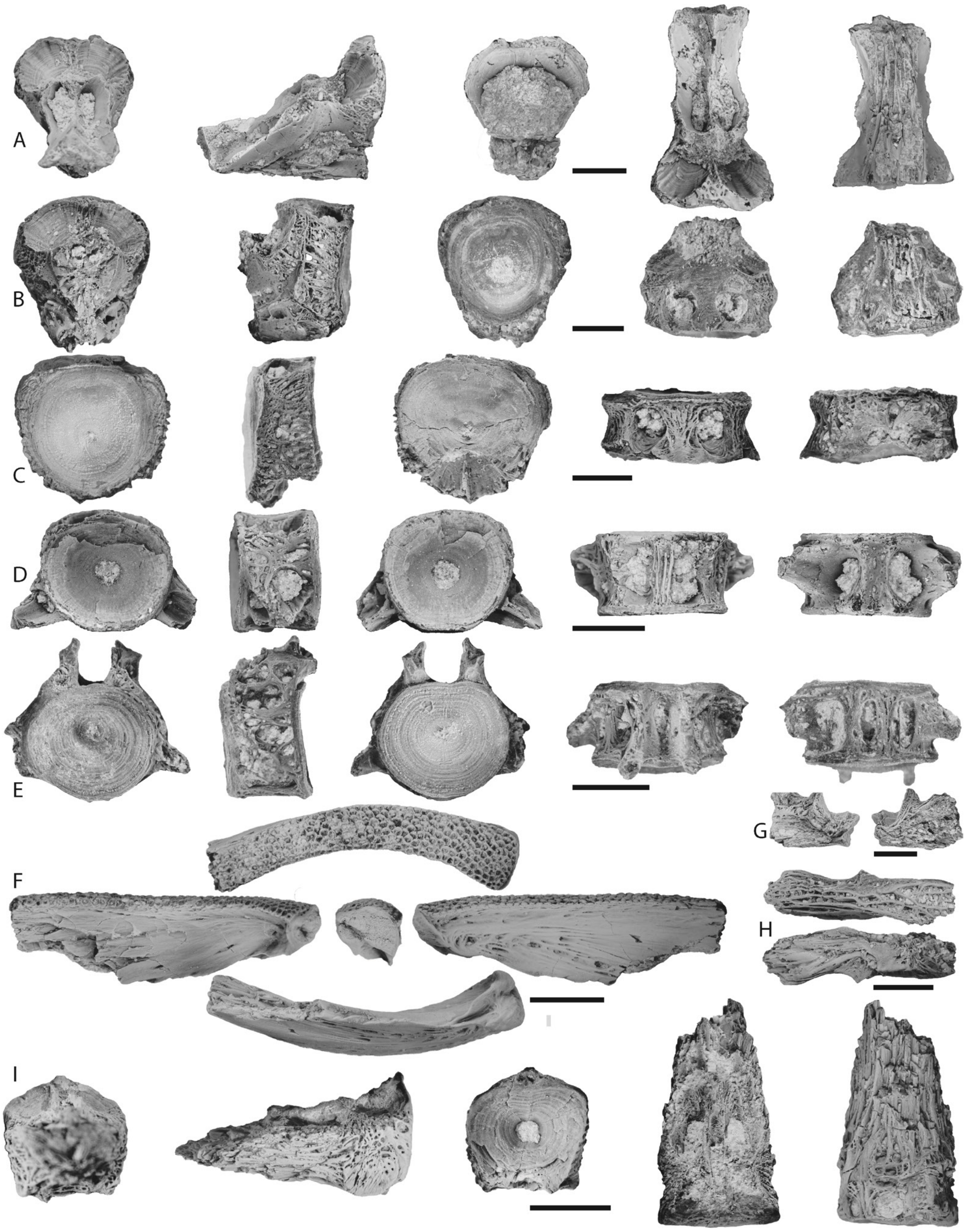

B
A
C
D
E
F
I
G
H

FIGURE 4.3. Bridger Formation fish material. **A**–**E**. *Phareodus* material: **A**, basioccipital (UCMP V198901); **B**, basioccipital and first centrum of the vertebral series preserved in articulation (UCMP V193336); **C**, first centrum of the vertebral series (UCMP V193339); **D**, anterior abdominal centrum (UCMP V198911); **E**, posterior abdominal centrum (UCMP V193602); **F**–**I**, Bridger Formation *Astephus* material: **F**, dentary (UCMP V198900) in medial, ventral, lateral, dorsal, and symphyseal views; **G**, articular (UCMP V193409) in lateral, medial, and dorsal views; **H**, post-temporal (UCMP 193297) in dorsal and ventral views; **I**, basioccipital (UCMP V198904). The basioccipitals and centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.


A
B
C
D
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F
G
H
I

FIGURE 4.4. Bridger Formation *Astephus* material. **A**, cleithrum fragment (UCMP V193283) in lateral and medial views; **B**, proximal fragment of a right pectoral fin spine (UCMP V193448) in anterior, lateral, and posterior views; **C**, distal fragment of a pectoral fin spine (UCMP V193451) in anterior, lateral, and posterior views; **D**, first Weberian centrum (UCMP V193552); **E**, first and complex centrum of the Weberian apparatus preserved in articulation (UCMP V193388); **F**, complex centrum of the Weberian apparatus with preserved neural arches (UCMP V193456); **G**, complex centrum of the Weberian apparatus and first post-Weberian centrum preserved in articulation (UCMP V193389); **H**, first post-Weberian centrum (UCMP V193558). The basioccipital, Weberian apparatus, and centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page or to the left in **E** and **G**. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

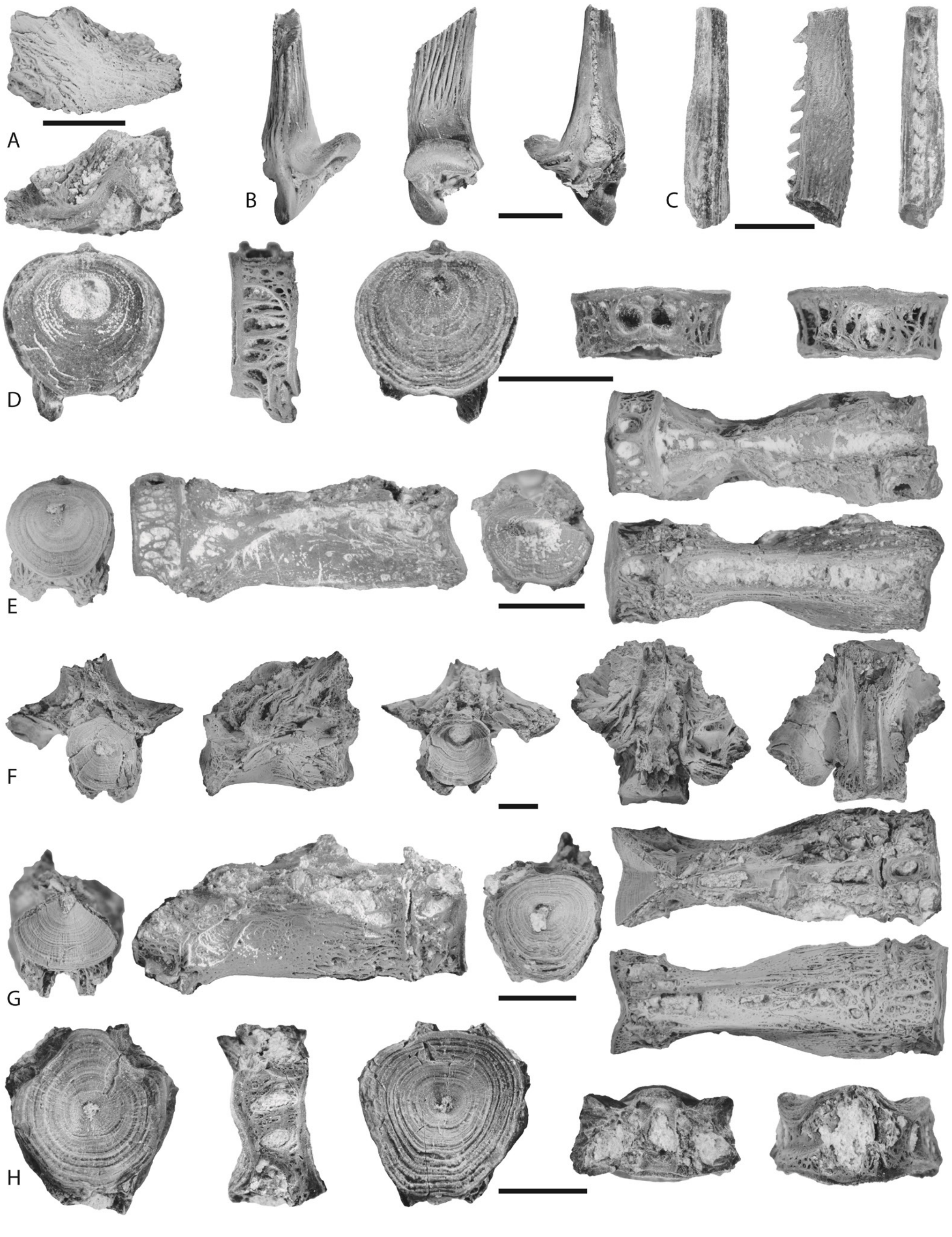
A
B
C
D
E
F
G
H

FIGURE 4.5. Bridger Formation *Astephus* centra. **A**, anterior abdominal centrum (UCMP V193479); **B**, posterior abdominal centrum (UCMP V193480). Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 5 mm.

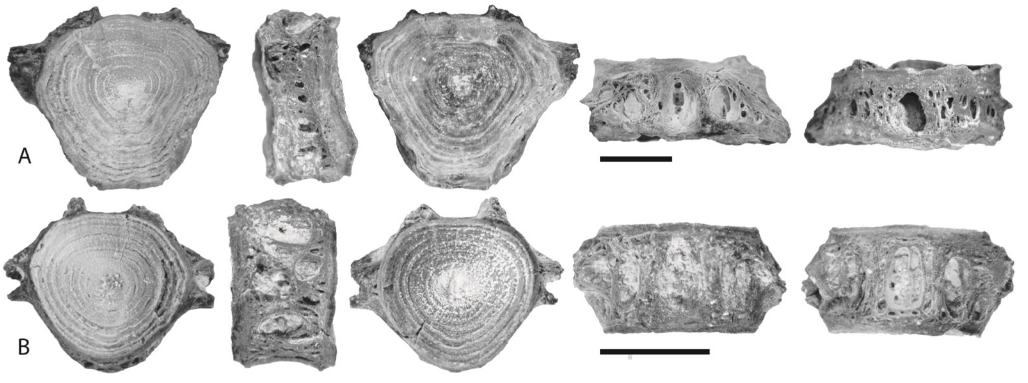
A
B

FIGURE 4.6. Comparison of longevities and growth rates determined from *Astephus* material from the Bridger (hollow symbols and white bars) and Cypress Hills (solid symbols and black bars) formations. **A**, total numbers of growth annuli observed in fossil centra (squares) were interpreted as representing the age of the individuals at time of death. Radial distances (RD) at annulus 5 (circles) are compared as a proxy for the rates of growth of these individuals. Total number of annuli and RD at annulus 5 are plotted for each individual centrum included in this study (N Bridger Formation = N Cypress Hills Formation = 20) to facilitate comparisons of both measurements between individual specimens. The first seven centra plotted from the Cypress Hills Formation are interpreted as representing Divay and Murray's (in press; Chapter 3) larger *Astephus* taxon A, while the remainder of the Cypress Hills sample is interpreted to correspond to the smaller *Astephus* taxon B. The Bridger Formation *Astephus* material has radial distances at annulus 5 that are within the range of values from the *Astephus* taxon B from the Cypress Hills Formation. **B**, comparison of the frequency distributions of longevities represented in Bridger (white bars) and Cypress Hills (black bars) assemblages. The longevity distributions of both assemblages overlap and have similar shapes. **C**, comparison of the frequency distributions of radial distances at annulus 5 represented in Bridger (white bars) and Cypress Hills (black bars) assemblages. The Bridger material and 13 centra from the Cypress Hills assemblage have similar radial distances (between two and four millimetres). The radial distances of the first seven Cypress Hills centra plotted in **A** form a second, distinct, peak in the distribution of radial distances from this assemblage (between five and seven millimetres).

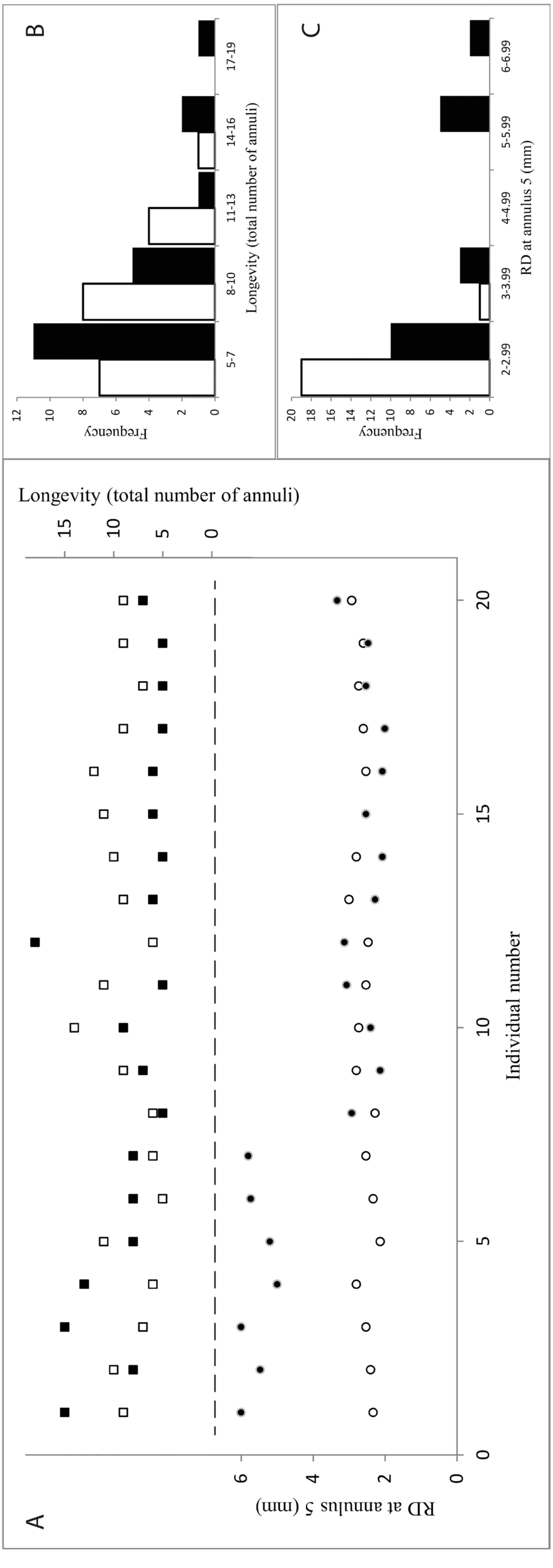
A
RD at annulus 5 (mm)
0
2
4
6
Individual number
0
5
10
15
20
Longevity (total number of annuli)
0
5
10
15
B
Frequency
0
2
4
6
8
10
12
5-7
8-10
11-13
14-16
17-19
Longevity (total number of annuli)
C
Frequency
0
2
4
6
8
10
12
14
16
18
20
2-2.99
3-3.99
4-4.99
5-5.99
6-6.99
RD at annulus 5 (mm)

TABLE 4.1. Descriptive statistics and statistical comparisons of Bridger Formation and Cypress Hills Formation *Astephus*. The Cypress Hills sample is partitioned into the hypothesized taxon A and B abdominal centra, based on differences in radial distances at annulus 5. The data partition hypothesized to represent *Astephus* taxon A includes the first seven centra plotted in Fig. 6A. The remainder of the Cypress Hills centra are hypothesized to represent *Astephus* taxon B. Samples were compared using unpaired two-tailed t-tests, assuming unequal variances, and post-hoc Bonferroni-corrected 0.05 α-level of statistical significance. Because the longevities and radial distances at annulus five were compared among samples four times, the 0.05 α-level of statistical significance is reduced to 0.0125 according to the Bonferroni correction (α / number of iterations). Abbreviations: N, sample size; x̄, mean; RD, radial distance (mm).

Sample	N	$\bar{x}$ longevity	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Bridger Fm	20	8.8	5–14	5.64	0.586	0.562	0.0125
Cypress Hills Fm	20	8.2	5–18	16.33			

Sample	N	$\bar{x}$ longevity	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Bridger Fm	20	8.8	5–14	5.64	1.36	0.211	0.0125
Cypress Hills Fm Taxon A	7	10.71	8–15	11.9			

Sample	N	$\bar{x}$ longevity	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Bridger Fm	20	8.8	5–14	5.64	1.74	0.097	0.0125
Cypress Hills Fm Taxon B	13	6.85	5–18	12.64			

Sample	N	$\bar{x}$ longevity	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Cypress Hills Fm Taxon A	7	10.71	8–15	11.9	2.37	0.034	0.0125
Cypress Hills Fm Taxon B	13	6.85	5–18	12.64			

Sample	N	$\bar{x}$ RD at annulus 5	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Cypress Hills Fm	20	3.61	2–6	2.43	2.92	0.004	0.0125
Bridger Fm	20	2.58	1.23–3	0.05			

Sample	N	$\bar{x}$ RD at annulus 5	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Cypress Hills Fm Taxon A	7	5.6	5–6	0.152	19.34	< 0.001	0.0125
Bridger Fm	20	2.579	2.13–3	0.051			

Sample	N	$\bar{x}$ RD at annulus 5	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Cypress Hills Fm Taxon A	7	5.6	5–6	0.152	15.91	< 0.001	0.0125
Cypress Hills Fm Taxon B	13	2.533	2–3.33	0.2			

Sample	N	$\bar{x}$ RD at annulus 5	Range	Sample variance	t	p-value	Bonferroni-corrected α-level
Bridger Fm	20	2.579	2.13–3	0.05	0.34	0.739	0.0125
Cypress Hills Fm Taxon B	13	2.533	2–3.33	0.2			

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APPENDIX 4.1. Comparative material examined. All of these specimens are dried skeletons, and each number represents an individual specimen.

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Family Catostomidae: *Carpiodes carpio* (Rafinesque, 1820a) – KU 12732; *Carpiodes cyprinus* (Lesueur, 1817b) – CMN 77-183; *Catostomus catostomus* (Forster, 1773) – UAMZ F8558, F8582; *Ictiobus cyprinellus* (Valenciennes in Cuvier and Valenciennes, 1844) – KU 15337; *Moxostoma macrolepidotum* (Lesueur, 1817b) – ROM R7377

Family Centrarchidae: *Lepomis gibbosus* (Linnaeus, 1758) – CMN 73-236C; *Lepomis macrochirus* Rafinesque, 1819 – ROM R6210; *Micropterus dolomieui* Lacepède, 1802 – CMN 73-258, ROM R6125 (juvenile); *Pomoxis nigromaculatus* (Lesueur in Cuvier and Valenciennes, 1829) – CMN 76-075

Family Chanidae: *Chanos chanos* (Forskål, 1775) – UAMZ F8550

Family Cottidae: *Cottus bairdi* Girard, 1850 – ROM R6589; *Cottus cognatus* Richardson, 1836 – CMN 80-185; *Myoxocephalus octodecemspinosus* (Mitchill, 1814) – ROM R2430

Family Cyprinidae: *Campostoma anomalum* (Rafinesque, 1820b) – ROM R7890; *Chrosomus eos* Cope, 1861 – ROM R7897; *Clinostomus elongatus* (Kirtland, 1840a) – ROM R7754; *Cyprinella spiloptera* (Cope, 1867) – ROM R6823; *Cyprinus carpio* Linnaeus, 1758 – UAMZ F8557; *Hybognathus hankinsoni* Hubbs in Jordan, 1929 – ROM R2569; *Luxilus cornutus* (Mitchill, 1817) – ROM R6425; *Macrhybopsis storeriana* (Kirtland, 1844) – ROM R6385; *Nocomis biguttatus* (Kirtland, 1840a) – ROM R5358; *Notemigonus crysoleucas* (Mitchill, 1814) – ROM R7664; *Notropis atherinoides* Rafinesque, 1818a – ROM R2561; *Pimephales notatus* (Rafinesque, 1820b) –

ROM R7750; *Ptychocheilus oregonensis* (Richardson, 1836) – ROM R6513; *Semotilus atromaculatus* (Mitchill, 1818) – ROM R5885; *Semotilus margarita* (Cope, 1867) – CMN Z-668

Family Esocidae: *Esox lucius* Linnaeus, 1758 – UAMZ F8551, F8552; *Esox masquinongy* Mitchill, 1824 – ROM R2243; *Esox niger* Lesueur, 1818 – CMN 87-385

Family Fundulidae: *Fundulus heteroclitus* (Linnaeus, 1766) – ROM R3852

Family Hiodontidae: *Hiodon alosoides* (Rafinesque, 1819) – UAMZ F8556

Family Ictaluridae: *Ameiurus natalis* (Lesueur, 1819) – ROM R7245; *A. nebulosus* (Lesueur, 1819) – CMN 77-254; *Ictalurus punctatus* (Rafinesque, 1818b) – UAMZ F8553; *Noturus flavus* Rafinesque, 1818c – CMN 77-182, UAMZ 7527

Family Lotidae: *Lota lota* (Linnaeus, 1758) – CMN 85-603, ROM R1850

Family Moronidae: *Morone americana* (Gmelin, 1789) – ROM R6327; *Morone chrysops* (Rafinesque, 1820c) – ROM R6377; *Morone saxatilis* (Walbaum, 1792) – UAMZ F8554

Family Osmeridae: *Osmerus mordax* (Mitchill, 1814) – CMN Z-4079

Family Percidae: *Perca flavescens* (Mitchill, 1814) – UAMZ 4821, UMMZ 171120, 175905 (8 of 9), 175905 (9 of 9), 179978, 194309; *Stizostedion vitreum* (syn. *Sander vitreus*) (Mitchill, 1818) – UAMZ F8420, F8421

Family Percopsidae: *Percopsis omiscomaycus* (Walbaum, 1792) – ROM R6493

Family Salmonidae: *Coregonus clupeaformis* (Mitchill, 1818) – CMN 73-259b.; *Stenodus leucichthys* (Güldenstädt, 1772) – CMN Z4206

Family Scianidae: *Aplodinotus grunniens* Rafinesque, 1819 – CMN Z-275; *Rhinichthys cataractae* (Valenciennes in Cuvier and Valenciennes, 1842) – ROM R6592

Family Umbridae: *Umbra limi* (Kirtland, 1840b) – ROM R7818

CHAPTER 5

An early Eocene fish fauna from the Bitter Creek area of the Wasatch Formation of southwestern Wyoming, U. S. A.[*]

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INTRODUCTION

The early Eocene Wasatch Formation was named and briefly described by Hayden (1873), soon after which, fossils collected from the area east of Bitter Creek Station in the Washakie basin of the greater Green River Basin, southwestern Wyoming, were sampled and described by Cope (1873) and Marsh (1876). Additional fossils from the Bitter Creek area were later described by Gazin (1962), who briefly mentioned fish material but focused on describing mammalian fossils, including some collected by Marsh in 1882. In the early 1970s, the University of California Museum of Paleontology sampled and screenwashed material from the main body of the Wasatch Formation, in stratigraphically-controlled localities of the northwestern Washakie Basin, including in the Bitter Creek area. This material represents mammalian taxa alongside reptile, amphibian and fish taxa, the latter three of which account for 50 to 100% of the material in some localities (Savage et al., 1972). Material from some of these localities formed the basis of a study on the Bitter Creek herpetological assemblages (Smith and Gauthier, 2013), but the fish material from these localities has not been reported until now. The teleosts from one of these Bitter Creek localities from the early Eocene of the Washakie Basin of southwestern Wyoming are here described.

The fishes previously found in the Wasatch Formation include the rhombodontid myliobatiform chondrichthyan *Washakiebatis kirklandi* Zeigler et al., 2005, from the Niland Tongue of the formation, which overlies the Luman Tongue of the Green River Formation, stratigraphically higher than the main body of the Wasatch (Roehler, 1992). Additionally, several isolated lepisosteid bones were reported by Cope (1873) from the Washakie Basin; however, the stratigraphic position of the localities from which these were recovered cannot be determined from the original report, and Grande (2010) in his comprehensive review did not list any lepisosteid material unambiguously found in the formation. Cope (1873) also described catfish material from the area, which Lundberg (1975) considered to represent an indeterminate species of *Astephus*.

Geological Setting

In the Greater Green River Basin, the main body of the Wasatch Formation is composed of fluvial deposits pre-dating the deposition of the lacustrine Green River Formation, which it underlies (Bradley, 1964; Roehler, 1993). The Wasatch Formation persisted on the outskirts of Lake Gosiute until the final infilling of the lake, and Wasatch deposits intertongue with lake deposits, both formations being overlain by the Bridger Formation (Bradley, 1964; Roehler, 1993). The main body of the Wasatch therefore represents the fluvial environment immediately pre-dating the formation of the great lakes system that is represented by the deposits of the Green River Formation, approximately 55–53Ma (Wilf, 2000), a time period corresponding to the early part of the earliest Eocene Wasatchian North American Land Mammal Age (NALMA). Although the biostratigraphy of the Bitter Creek area has not been studied in detail, the main body of the Wasatch Formation is generally regarded as corresponding to the Graybullian part of the Wasatchian, zones Wa1–Wa5 (Smith and Gauthier, 2013). This time period corresponds to the final part of the global warming trend that resulted in the warmest climates of the Cenozoic, during the Early Eocene Climatic Optimum (Smith and Gauthier, 2013; Wilf, 2000). The warming trend was not constant, however, and leaf-margin and leaf-area analysis in the Greater Green River Basin show that, after a thermal maximum in the latest Paleocene, temperatures dropped slightly until the late Graybullian, before rapidly increasing to reach their highest levels of the Cenozoic (Wilf, 2000). The assemblage described here was deposited at the onset of this final, rapid increase in temperatures (Smith and Gauthier, 2013). Therefore, when more Bitter Creek fish assemblages become available for comparisons, this assemblage could be integrated into a study of the response of local diversities to climatic change, similar to that proposed by Smith and Gauthier (2013) for the Bitter Creek herpetological assemblages.

The red variegated sequences that were mentioned by Hayden (1873) are characteristic of the Wasatch Formation along the outskirts of the Greater Green River Basin (Roehler, 1993). These sedimentological features were interpreted as indicating a well-drained depositional environment probably resulting from streams flowing to the center of the basin because of moderate topographic relief (Roehler, 1993). However, deposits at the center of the basin lack this reddish color but are brown and grey instead (Savage et al., 1972). Deposits of these colors correspond to poorly drained environments with little to no relief, and correspond to the depositional environment in the Bitter Creek area (Savage et al., 1972; Roehler, 1993; Smith and Gauthier, 2013).

The main body of the Wasatch Formation is approximately 515 meters thick (Roehler, 1992, reported as 1,691 feet). Deposits are mostly composed of channel and floodplain sandstones and mudstones, with some limestones, and lacustrine claystones and siltstones that are sometimes carbonaceous (Savage et al., 1972; Roehler, 1993). These deposits locally form repeated sedimentary cycles, which Savage et al. (1972) interpreted as evidence that the depositional environment was a well-vegetated area, with laterally shifting sand-bottomed streams running through a marshy expanse, dotted by repeatedly forming ephemeral lakes and ponds.

The sample studied here was recovered in zonule 3 of the Bitter Creek Promontory Section, a horizon composed of grey carbonaceous siltstone (Savage et al., 1972). According to the stratigraphic columns presented in Savage et al. (1972), Bitter Creek Promontory Section zonule 3 is stratigraphically close to Patrick Draw Southeast Section zonule M, from which was recovered the oldest sample included in Smith and Gauthier's (2013) study of the Bitter Creek herpetofauna. This suggests that the sample studied here was deposited in the later part of zone Wa4 (Smith and Gauthier, 2013).

MATERIALS AND METHODS

The sample described here represents the teleost material recovered from the University of California Museum of Paleontology (UCMP) locality V70220, "Barb's Saddle," by several UCMP field expeditions led by B. T. Waters and J. H. Hutchison between 1970 and 1972. These field expeditions formed part of an extensive sampling of localities in the northwest of the Washakie Basin (Fig. 5.1), in Tp. 17 R. 100 W (approximately latitude

41.4428552, longitude -108.6768341), Tp. 18 R. 99 W (approximately latitude 41.5296907, longitude -108.5614916), and Tp. 18 R. 100 W (approximately latitude 41.5298407, longitude -108.6769061). Fossils were collected through surface picking, quarrying, and screen-washing of dried matrix (Savage et al., 1972). Locality V70220 is one of the localities where screen-washing was conducted.

Material Examined

All of the fossil material from the Wasatch Formation included in this study is curated in the University of California Museum of Paleontology (UCMP), Berkeley, California, U. S. A. Extant comparative material (Appendix 5.1) is from the Canadian Museum of Nature (CMN), Ottawa, Ontario, Canada, the University of Kansas Natural History Museum (KU), Lawrence, Kansas, U. S. A., the Royal Ontario Museum (ROM), Toronto, Ontario, Canada, the University of Alberta Museum of Zoology (UAMZ), Edmonton, Alberta, Canada, and the University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Michigan, U. S. A. Comparative fossil material from the Green River Formation is curated in the Royal Tyrrell Museum of Palaeontology (RTMP) and the University of Alberta Laboratory of Vertebrate Palaeontology (UALVP). Comparative fossil material from the Wood Mountain Formation is curated in the CMN and the ROM (see Chapter 2; Divay and Murray, 2013). Comparative fossil material from the Cypress Hills Formation is from the collections of the ROM (see Chapter 3; Divay and Murray, in press).

Methods

The identification of the Wasatch material was based on comparisons with the modern taxa listed in Appendix 5.1, as well as with articulated fossils from the Green River Formation and isolated fossil elements from the Wood Mountain Formation (Chapter 2; Divay and Murray, 2013) and from the Cypress Hills Formation (Chapter 3; Divay and Murray, in press). Some of the Wasatch Formation fossils were identified based on comparisons with a Green River Formation *Diplomystus dentatus* specimen (TMP 1986.224.0135) from which abdominal centra were mechanically extracted and acid prepared to allow their observation in three dimensions. Nelson's (2006) classification was followed, except where more recent classifications have been published (e.g., Murray and Wilson, 2013, for ellimmichthyiforms). Wherever possible, attributions were based on structures interpreted as being apomorphies; however, general phenetic similarities also had to be used. The material was coated in ammonium chloride prior to photographing. A Nikon DXM 1200C digital camera mounted on a Zeiss Discovery.V8 stereo microscope was used to photograph the specimens.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII Cope, 1887

Division TELEOSTEI Müller, 1846

Subdivision OSTARIOCLUPEOMORPHA (= OTOCEPHALA) Arratia, 1997

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

Order ELLIMMICHTHYIFORMES Grande, 1982

Suborder ARMIGATOIDEI Murray and Wilson, 2013

Family ARMIGATIDAE Murray and Wilson, 2013

DIPLOMYSTUS Cope, 1877

(Fig. 5.2A, C, E, F)

Material—Two dentaries (UCMP V198887 IVa, b), Fig. 5.2A; seven fragments of basioccipitals representing the posterior articular surface and adjacent areas (UCMP V198888 VIa–d, UCMP V198889 IVa–c), Fig. 5.2C; 36 abdominal centra (UCMP V198888 IIa–c, UCMP V198888 Xa–j, UCMP V198889 Va–f, UCMP V198890 Ia,b, UCMP V198890 IIa–d, UCMP V198891 Ia–e, UCMP V198892 IIIa–d, UCMP V198892 IVa, b), Fig. 5.2E, F.

Description— The dentaries (Fig. 5.2A) are incomplete posteriorly and the tooth-bearing surface is heavily weathered. However, small, shallow, circular tooth bases are preserved along the lateral and anterior margins of the tooth-bearing surface, which is restricted to the anterior part of the dentary. The symphysis is teardrop-shaped, being wider dorsally than ventrally, and taller than wide. There is a sharp crest persisting for the full length of the ventral surface of the bone. Anteriorly, this crest forms a right angle with the symphysis. A slight trench is ventral to the tooth-bearing surface on both medial and lateral sides. The medial surface has a deep longitudinal trench at mid-height, which persists for the full length of the dentary. Laterally, there is a series of large foramina at approximately mid-height of the bone, and some superficial pitting in its anterior region. The rest of the bone surfaces are flat and essentially featureless.

The isolated basioccipitals from the Wasatch Formation (Fig. 5.2C) were identified based on comparisons with the basioccipital of a single articulated specimen of *Diplomystus dentatus* from the Green River Formation, which is preserved in lateral view (Fig. 5.2D). The posterior articular surface of the Wasatch basioccipitals (Fig. 5.2C) is shallow, higher than wide, with a central or slightly ventral notochordal foramen. The dorsal surface has widely flared facets for articulation with the exoccipitals adjacent to the posterior articular surface. A thin, median sheet of bone, anterior to these facets, extends for the full height and preserved length of the basioccipital. Lateral surfaces widen anteriorly and dorsally, forming a Y-shape in anterior view. Apart from some superficial pitting, these surfaces are smooth. The ventral surface is narrow and flat, with a very shallow median depression.

Anterior abdominal centra (Fig. 5.2E) are oval in end view, being wider than high, with distinctively flattened or concave mid-ventral margins and a dorsal notochordal foramen. Gradually, more posterior centra (Fig. 5.2F) become circular in end view, then oval, being higher than wide, in the posterior-most abdominal centra. The notochordal foramen is central in all but the anterior abdominal centra. In all cases, the articular surfaces at the anterior and posterior ends of the centrum are surrounded by a slightly projecting margin of smooth bone. Shallow neural arch articular pits are usually limited to the anterior half of the dorsal surface, although they are proportionately longer in smaller centra. The pits are characteristically triangular in all but the posterior-most abdominal centra, where they are more rounded. The medial margins of these articular pits project from the surface of the centrum and extend to the posterior end of the centrum. In anterior abdominal centra, the lateral edges of the neural arch pits project from the medio-lateral margin of the centrum, to form a shelf. In some larger centra, the neural arch pits are in contact medially, but in most cases, their medial margins are separated by a pit, which extends to the posterior end of the centrum. A low, thin mid-dorsal ridge extends for the full length of the centrum along its midline. There is a pair of deep dorso-lateral pits that is laterally delimited by a pair of ridges extending posteriorly from the lateral margin of the neural arch pits. Large parapophyses fuse to the centrum on the anterior part of the lateral surface, extending from the lateral margin of the neural arch pits to the ventro-lateral margin of the centrum in anterior centra. The parapophyses become more restricted to the ventral part of the lateral surface of the centrum in more posterior positions of the vertebral series. The parapophyses delimit the anterior and ventral margins of large, rectangular rib articular pits that extend to the posterior end of the centrum. The rest of the lateral surface has a variable number of longitudinal ridges delimiting elongate accessory pits, the number of which depends upon the placement of the centrum along the vertebral series. In the posterior-most abdominal centra, the parapophyses extend ventro-laterally from the surface of the centrum, and their base is limited to an area adjacent to the anterior end of the centrum. Paired longitudinal ridges extend for the full length of the centrum on its ventro-lateral margin, originating anteriorly on the bases of the parapophyses. In anterior centra, there is a single or paired median ventral ridge, bisecting a large pit extending to the ventro-lateral margin of the centrum. The ventro-lateral longitudinal ridges become closer to one another in more posterior centra, delimiting a single, wide, long mid-ventral pit between them.

Remarks—The morphology of the dentaries described here is most characteristic in the restriction of the tooth-bearing surface to the anterior part of the bone. This condition is also seen in articulated specimens of *Diplomystus* (Fig. 5.2B). The relatively small size of the tooth bases, the ventral curvature of the bone posterior to the tooth-bearing surface, and the ventral crest being at a right angle to the symphysis are also features consistent with the identification of these dentaries as belonging to *Diplomystus*. Similarly, the basioccipitals are most characteristic in their dorso-posterior facets for articulation with the exoccipitals, and the anteriorly and dorsally widening lateral surfaces with a median sheet of bone, which are features also seen in the basioccipital of an articulated specimen of *Diplomystus* (Fig. 5.2D). Both anterior and posterior abdominal centra have distinctively triangular and shallow articular pits for the autogenous neural arches, as are also seen in centra of *Diplomystus* from the Green River Formation (Fig. 5.2G). Other characteristics are consistent with this attribution, such as the fused parapophyses, the dorsal and ventral pits with median bony struts that are sometimes double on the ventral surface, and the convex ventral surface of the anterior abdominal centra.

Several characteristics of the disarticulated specimens from the Wasatch Formation differentiate these from the Green River articulated specimens, with which they were compared. The wide lateral foramina of the Bitter Creek dentaries are present but relatively much smaller in adult Green River specimens. Furthermore, the relatively large notochordal foramina of the abdominal centra of the Wasatch sample are absent in centra extracted from adult Green River specimens. However, based on the relatively much smaller total sizes of the fossils in the Wasatch sample, these features may be ontogenetic, and would provide evidence that none of the elements in the Wasatch sample represent adult specimens. Therefore, these characteristics are interpreted not to indicate that the Wasatch specimens represent a different taxon, but rather that the individuals these represent were probably young juveniles. There are fewer than two growth annuli on the articular surfaces at the anterior and posterior ends of these centra, and most specimens lack annuli altogether. These circular marks correspond to seasonal growth cessation in several fish taxa; the number of these annuli is therefore correlated to the age of the individual. *Diplomystus* specimens can be reliably aged from the presence of such annuli on their centra, as demonstrated by the growth analysis conducted on *Diplomystus* specimens by Newbrey et al. (2010). The absence of a succession of clearly discernible annuli in most of the Wasatch fossils is therefore consistent with the interpretation that these represent young juveniles.

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

Order GONORYNCHIFORMES Berg, 1940

Family GONORYNCHIDAE Bonaparte, 1850

NOTOGONEUS Cope, 1885

(Figs. 5.2H; 3B, C, F; 5.4A)

Material—Three basioccipitals (UCMP V198888 V, UCMP V198890 V, UCMP V198891 VII), Fig. 5.2H; 10 anterior abdominal centra, representing one of the first three vertebrae modified to form the Weberian apparatus (UCMP V198888 VIIa–c, UCMP V198889 IIIa, b, UCMP V198890 VIa, b, UCMP V198891 Va–c), Fig. 5.3B, C; 34 abdominal centra (UCMP V198888 IIIa–e, UCMP V198888 IX, UCMP V198888 XIIa–e, UCMP V198889 VIIa–i, UCMP V198890 IIIa–c, UCMP V198890 IV, UCMP V198891 IIIa–c, UCMP V198891 VIa–c, UCMP V198892 IIa, b, UCMP V198892 Va, b), Figs. 5.3F, 5.4A.

Description—The basioccipitals included here (Fig. 5.2H) have an oval posterior articular surface, being higher than wide, with a flattened ventral margin. The large notochordal foramen is centrally located on the posterior articular surface. A pair of thin ridges extends for the full length of the basioccipital along the midline of its dorsal surface. The median ridges extend between two pairs of dorsal pits, probably for articulation with the exoccipitals, of which the anterior pair is distinctly longer than the posterior pair. Adjacent to the posterior articular surface, the ventral half of the lateral surfaces has a triangular fossa that tapers anteriorly. There is a large circular mid-ventral pit, with slightly projecting margins. Bone fibres extend longitudinally anterior to this pit, and are more robust on the ventro-lateral margins than along the midline of the basioccipital.

The shape of the articular surfaces on the anterior and posterior ends of the centra that are modified to form the Weberian apparatus (Fig. 5.3B, C) range from being circular to rectangular, being higher than wide, with flattened margins. In all cases, the notochordal foramen is centrally located. The centra are narrower at mid-length than at either end, giving them an hourglass-shape in dorsal and ventral views, which is most noticeable in the longer centra. The dorso-lateral and ventro-lateral margins of the centrum form pointed projections at the anterior and posterior ends of the centrum. The dorsal surface is highly diagnostic, having a pair of neural arch articular pits with rounded margins, at mid-length of the centrum. These pits are circular in shorter centra, and more elongate in longer ones. The mid-dorsal ridge separating the dorsal pits narrows at mid-length, giving it an hourglass shape, but is otherwise flat and featureless. The lateral surface has low longitudinal ridges extending for the full length of the centrum; these are interconnected with transverse ridges. The number of longitudinal and transverse ridges varies between centra. There is a large, rectangular mid-ventral pit, the lateral margins of which are constituted by the same sheets of bone that form the lateral surface of the centrum. In several cases, this ventral pit has a low bony ridge subdividing it longitudinally, extending the full length of the centrum. This median ridge is absent in other centra.

The articular surfaces at the anterior and posterior ends of abdominal centra (Figs. 5.3F; 5.4A) have a central notochordal foramen, and are either circular or are slightly wider ventrally than dorsally, with rounded margins. The bases of the fused neural arch form the dorso-lateral margins of the centrum, extending for its full length, and delimit the lateral edges of a large mid-dorsal pit. This pit is bisected by a low, thin, longitudinal bony ridge that also extends for the full length of the centrum. Lateral surfaces typically have a longitudinal ridge extending for the full length of the centrum at approximately mid-height, although many of these centra have several ridges in this area. The larger centra (Fig. 5.3F) have relatively more robust lateral ridges than those of smaller centra (Fig. 5.4A). At approximately mid-length of the centrum, transverse bony ridges form connections between longitudinal ridges, and in some instances extend to the dorso- and ventro-lateral margins of the centrum. The parapophyseal articular pit is triangular and restricted to the ventral half of the lateral surface. It is adjacent to the anterior end of the centrum, and its margins project from the surrounding lateral and ventro-lateral surfaces. It is more ventral in placement in more posterior centra of the vertebral series. In most cases, the posterior-most edge of the parapophyseal articular pit is connected to the posterior end of the centrum by a longitudinal bony ridge, although the pit extends for the full length of the centrum in the smallest specimens. A pair of ventro-lateral ridges delimits the lateral edges of a deep mid-ventral pit that extends for the full length of the centrum.

Remarks—The basioccipitals are attributed to *Notogoneus* because they show the same two pairs of dorso-lateral pits and triangular ventro-lateral facets adjacent to the posterior articular surface as visible in articulated specimens of *Notogoneus* preserving the basioccipital in lateral view (Fig. 5.2I). Furthermore, articulated *Notogoneus* specimens preserving the basioccipital in ventral view (Fig. 5.3A) show the same round mid-ventral pit adjacent to the posterior articular surface as the Wasatch specimens. Abdominal centra are characteristic in their lateral surfaces having a triangular parapophyseal articular pit restricted to the ventral half of the surface and a longitudinal ridge extending for the full length of the centrum at mid-height; both are features also seen in articulated *Notogoneus* specimens (Fig. 5.4B–D). Additionally, large articulated *Notogoneus* specimens (Fig. 5.4B, C) have a relatively more robust lateral longitudinal ridge than smaller specimens (Fig. 5.4D), in which this ridge is narrower. This also corresponds to the condition seen in the disarticulated centra described above. Although none of the articulated *Notogoneus* specimens examined had anterior-most abdominal centra visible, the centra described above can be attributed to this genus on the basis of comparisons with the extant gonorynchiform, *Chanos chanos* (Fig. 5.3 D, E). In gonorynchiforms, the first three abdominal centra are modified to form a primitive Weberian apparatus (Grande and Arratia, 2010), and those of *Chanos chanos* are similar to the Wasatchian fossils in their characteristic rounded neural arch pits that are unique among the comparative material examined. Other similarities include the longitudinal bony struts on the lateral surface, and the ventral pit that is sometimes bisected by a median longitudinal bony ridge.

Subdivision ACANTHOMORPHA Rosen, 1973 (sensu Stiassny, 1986)
Order PERCOPSIFORMES Berg, 1940 (sensu Springer and Orrell, 2004)
Aff. AMBLYOPSIDAE Bonaparte, 1846
(Figs. 5.4E, F; 5.5A, C)

Material—14 first centra (UCMP V198888 VIIIa–e, UCMP V198889 II, UCMP V198890 VIII, UCMP V198891 VIIIa–g), Figs. 5.4E, F, 5.5A; eight abdominal centra (UCMP V198888 XIIIa–e, UCMP V198890 X, UCMP V198891 IXa, b), Fig. 5.5C.

Description—The first centra (Figs. 5.4E, F; 5.5A) are long, and have a tripartite anterior articular surface for articulation with the basioccipital and the exoccipitals. The anterior articular surface for articulation with the basioccipital and the articular surface at the posterior end of the centrum are deep, with a notochordal foramen located slightly dorsally. The anterior surface for articulation with the basioccipital is either circular or slightly taller than wide, while the posterior articular surface is oval, being clearly taller than wide, with lateral postzygapophyses. The facets for articulation with the exoccipitals are slightly wider than high, shallow, and widely separated medially. The bases of the fused neural arch originate anteriorly on the medial margin of these facets, and extend posteriorly for the full length of the centrum, diverging laterally in an area adjacent to the posterior end of the centrum to connect with the postzygapophyses. The dorsal surface between the neural arch bases is flat and fibrous. Fibres are arranged both longitudinally and transversely, and tend to be more tightly interconnected in more posterior parts of the dorsal surface of the specimens. Lateral surfaces are smooth, with a slight triangular depression in the area of the bases of the postzygapophyses. Ventral surfaces are much narrower than the dorsal surfaces. In most centra, the ventral surface forms a sharp, narrow keel that is pinched at approximately mid-length, or slightly anterior to that point (Fig. 5.4E). However some centra have a wider, gently rounded ventral surface (Fig 5.4F). In these centra, the facets for articulation with the exoccipitals project less markedly and the surface texture is deeply fibrous. Other first centra are intermediate in having a narrow but rounded ventral surface that lacks the pinching of the narrow keel (Fig. 5.5A).

Abdominal centra (Fig. 5.5C) are much longer than high, and are as high as they are wide. The articular surfaces at their anterior and posterior ends are approximately circular, deep, with a central notochordal foramen. The dorsal surface has a deep mid-dorsal pit, extending for the full length of the centrum.

This pit is delimited laterally by a pair of thin bony struts, at the anterior end of which the bases of the neural arches are fused. Lateral surfaces have an elongate bony strut extending for the full length of the centrum, at approximately mid-height, with deep accessory pits both dorsal and ventral to this strut. The parapophyses are fused to the centrum, projecting laterally from the anterior part of this lateral strut, and connect to the neural arch bases by struts of bone adjacent to the articular surface at the anterior end of the centrum. Shallow rib articular pits are immediately posterior to the parapophyses. The ventral surface has a deep rectangular mid-ventral pit extending for the full length of the centrum, on either side of which are two thin bony struts. These struts sometimes project enough from the surface of the centrum to be visible in anterior and posterior views.

Remarks—Among the acanthomorph comparative material examined, the general morphology of the first centra is uniquely characteristic of percopsiform fishes (Fig. 5.5B) in the large, rounded facets for articulation with the exoccipitals that are widely flared laterally, and in the fused neural arches. Within the Percopsiformes, that the facets for articulation with the exoccipitals project anteriorly from the dorso-lateral margins at the anterior end of the centrum is an uncommon feature. The first centrum of most percopsiform fishes is also much shorter than the fossils. These centra are very reminiscent of some of the fossils described by Divay and Murray (in press; Chapter 3) from the Eocene–Oligocene deposits of the Cypress Hills Formation of Saskatchewan, Canada. The Cypress Hills fossils were tentatively attributed to the Amblyopsidae on the basis of their characteristic length and because the articular plane of the facets for articulation with the exoccipitals is similar to that of the surface for articulation with the basioccipital (Chapter 3; Divay and Murray, in press). The Wasatch Formation centra share these characteristics, and therefore also likely represent amblyopsid fishes, extending the fossil record of the family to the early Eocene. The abdominal centra are characteristic of percopsiform abdominal centra (Fig. 5.5D) based on their long relative length, the parapophyses being characteristically restricted to the anterior end of the centrum, and on the longitudinal bony strut at mid-height of the lateral surface extending for the full length of the centrum.

The first centra show some variation in the morphology of the ventral surfaces and in the surface texture of the bone that may indicate the presence of up to three different closely related percopsiform taxa in the Wasatch Formation. However, because these differences may also be ontogenetic, preservational, or due to pathologies, and because the abdominal centra of the sample show no variation, these are not separated here.

Two percopsiform genera, *Amphiplaga* and *Erismatopterus*, are known from the lake deposits of the Green River Formation, but both were considered to belong in Percopsidae (Grande, 1984). None of the articulated specimens examined were preserved in such a way as to make their first centrum visible, therefore comparisons between disarticulated Wasatch fossils and articulated Green River fossils were uninformative. The Wasatch material may therefore represent previously unrecognised amblyopsid fishes in the area, or may represent one or both of the percopsiform genera previously reported from the Green River Formation. In the latter case, the amblyopsid-like characters of the first centra could either suggest that the Green River percopsiforms had affinities with the Amblyopsidae, or that these were plesiomorphic characters, shared between amblyopsid and primitive percopsid fishes. However, extant percopsids do not have a similar morphology of the first centrum.

Series PERCOMORPHA Rosen, 1973

Order PERCIFORMES Bleeker, 1859

Family CENTRARCHIDAE Gill, 1862b

(Figs. 5.5 E, G; 5.6A)

Material—Three fragmentary dentaries (UCMP V198887 Va–c), Fig. 5.5E; seven first centra (UCMP V198888 IVa–c, UCMP V198891 IVa–c, UCMP V198892 VI), Fig. 5.5G, 5.6A.

Description—The tooth-bearing surface of the dentary (Fig. 5.5E) is of constant width, bearing numerous relatively small tooth bases tightly packed together. On both lateral and medial surfaces, trenches extend for the full length of the dentary, immediately ventral to the tooth-bearing surface. The trench on the lateral surface becomes much deeper and wider in the posterior part of the dentary, which is dorso-ventrally wider posteriorly than it is anteriorly. There is a sharp antero-ventral crest on the entire ventral surface of the element, extending anteriorly to form the narrow ventral margin of the triangular symphysis. The medial surface has a relatively small mental foramen, while the lateral surface has a large oval foramen at approximately mid-height. More posteriorly, the foramina are adjacent to the ventral margin of the lateral surface.

First centra (Fig. 5.5G; 5.6A) are characterised by their tripartite articular surface at their anterior end, with one median surface for articulation with the basioccipital and lateral facets for articulation with the exoccipitals. The median articular surface is slightly higher than wide, widest at the dorso-lateral margin, with a dorsal notochordal foramen; the articular surface at the posterior end of the centrum is similar in shape, but has lateral postzygapophyses. The facets for articulation with the exoccipitals are widely flared, projecting from the dorso-lateral margin of the centrum, and are broadly joined medially. The posterior part of this area projects from the dorsal surface of the centrum as a tall, transverse ridge. Posterior to this, the dorsal surface has two large pits for articulation with the autogenous neural arch, separated by a mid-dorsal pit that is slightly anterior to the two lateral pits. The remainder of the dorsal surface, as well as the lateral and ventral surfaces, are covered in small, superficial pitting, giving the bone a spongy appearance. However, the area immediately ventral to the antero-lateral articular facets has more loosely arranged bony fibres than the rest of the surfaces. These centra are slightly longer dorsally than ventrally, appearing wedge-shaped in lateral view. The larger first centra included here (Fig. 5.5G) have relatively longer ventral surfaces than the smaller centra (Fig. 5.6A).

Remarks—The dentary is attributed to the Centrarchidae because of its resemblance to that of some members of the family, such as *Pomoxis* (Fig. 5.5F). The constant width of the tooth-bearing surface, the progressively deeper lateral trench beneath the tooth-bearing surface, the first lateral foramen being adjacent to the symphysis at mid-height of the bone, and the more posterior lateral foramina being adjacent to the ventral margin of the bone, in particular, are characters of the Wasatch fossils shared with these centrarchid dentaries.

The first centra are similar to those of centrarchid fishes in having a broad medial connection between the articular facets for articulation with the exoccipitals, the posterior margin of which forms a transverse ridge projecting from the dorsal surface of the centrum (Fig. 5.6B). In comparison, these articular facets are separated in the Percidae and in the Percopsiformes, which also differ from the fossils in having fused neural arches. That the ventral surface is relatively shorter in smaller centra could be due to ontogenetic change; alternately, this may indicate the presence of two closely related centrarchids in the sample.

Family CENTRARCHIDAE Gill, 1862b or "*PRISCACARA*" sensu Cope, 1877

(Figs. 5.6C, E, H; 5.7D; 5.8A, B)

Material— Three vomers (UCMP V198887 Ia–c), Fig. 5.6C; two fragmentary dentaries (UCMP V198887 VIa, b), Fig. 5.6E; one fifth ceratobranchial (UCMP V198887 II), Fig. 5.6H; four first centra (UCMP V198889 Ia–c. UCMP V198890 IX), Fig. 5.7D; 127 abdominal centra (UCMP V198888 Ia–x, UCMP V198888 XIa–s, UCMP V198889 VIa–s, UCMP V198890 VIIa–x, UCMP V198891 IIa–s, UCMP V198891 Xa–j, UCMP V198892 VIIa–l), Fig. 5.8A, B.

Description—The vomers (Fig. 5.6C) are arrow-shaped, with an arched anterior end and a posterior parasphenoid process, which is incomplete in all specimens. The single, continuous toothplate on the ventral side of the vomer extends across the arched anterior end to the lateral extents, is uninterrupted medially, and is of constant width along its full extent. There are numerous, small tooth bases. The dorso-ventral thickness and lateral width of the vomer are greatest anteriorly, at the dentigerous area, while the parasphenoid process is much thinner and narrower posteriorly. There is a distinctively flat and porous surface anteriorly, on the dorsal side of the vomer, where it would have articulated with the mesethmoid. More posteriorly, the dorsal surface is essentially flat and featureless. The ventral surface is more fibrous, with bone fibres oriented longitudinally.

The dentaries (Fig 5.6E) have a distinctively wide tooth-bearing surface anteriorly, which abruptly narrows for the more posterior part of the bone. Tooth bases are small and numerous. A shallow trench immediately ventral to the tooth-bearing surface extends for the full length of the dentary on its medial surface. A second trench originates at mid-height on the medial surface of the dentary, and extends for its full preserved length, progressively becoming deeper and wider. The wide anterior tooth-bearing surface projects from the lateral surface of the dentary, forming a shelf. Immediately posterior to this area, the lateral surface has a deep, elongate pit in its dorsal half, and a large foramen adjacent to its ventral margin. A longitudinal, low, rounded ridge extends for the full length of the dentary, between the oval pit and the large foramen. A sharp antero-ventral crest forms the narrow ventral margin of the triangular symphyseal surface. This crest extends posteriorly for the full length of the element, narrowing dorso-ventrally posterior to the symphysis, then gradually widening for the remainder of the preserved length of the dentary.

The fifth ceratobranchial (Fig. 5.6H) is triangular, plate like, and fibrous in texture. It is covered with relatively large, rounded teeth.

The first centra (Fig. 5.7D) have a characteristic tripartite anterior articular surface for articulation with the basioccipital and the exoccipitals, and are slightly wider dorsally than ventrally. The anterior surface for articulation with the basioccipital is higher than wide, and widest in an area corresponding to the antero-lateral margin of the facets for articulation with the exoccipitals. The notochordal foramen is located dorsally. The articular surface at the posterior end of the centrum is slightly less narrow than the anterior surface, but is also higher than wide. The facets for articulation with the exoccipitals project dorso-laterally from the surface of the centrum, and are broadly joined medially. The posterior margin of these facets projects dorsally from the surface of the centrum where they meet medially. Posterior to this, the dorsal surface has a small median pit, followed by a pair of larger pits for articulation with the neural arch. The rest of the dorsal surface is essentially flat. Widely flared postzygapophyses are placed laterally, projecting from the posterior surface of the centrum. Elongate accessory pits are present on the lateral surface of the centrum, approximately at mid-height. Ventral to these accessory pits is a pair of bony ridges on the ventro-lateral margin of the centrum, delimiting a large rectangular mid-ventral pit occupying the rest of the ventral surface. All lateral and ventral surfaces around these pits are covered in very small, superficial pitting, giving this bone a spongy appearance.

Anterior abdominal centra (Fig. 5.8A) are higher than wide, and wider than long. These centra are somewhat angular in end view, with a dorsal notochordal foramen. Neural arch bases are fused to the dorsal side of the centrum and are posteriorly connected to postzygapophyses, on the dorso-lateral margin of the centrum. The dorsal surface between the neural arch bases is covered in small pitting, giving the bone a spongy appearance. Lateral and ventral surfaces are fibrous, the bony fibres being mostly oriented longitudinally, with some interconnections. The ventral surface has a deep rectangular pit extending for its full length

More posterior abdominal centra (Fig. 5.8B) become wider and longer relative to their height, becoming less angular and more deeply amphicoelous. The notochordal foramen becomes progressively more centrally placed in these centra. Dorsal pre- and postzygapophyses are of gradually smaller sizes, and are absent from more posterior centra. In all positions along the vertebral series, the neural arch bases are fused to the dorsal surface, and extend for the full length of the centrum. The mid-dorsal surface is composed of longitudinal bony fibres, which become more loosely arranged in more posterior centra, eventually forming an elongate mid-dorsal pit along the midline of the centrum. Parapophyses are fused to the dorso-lateral margin of the centrum in the more anterior centra, gradually becoming more lateral and then more ventral in placement in more posterior positions along the vertebral series. The anterior and ventral margins of rib articular pits are delimited by the parapophyses. The ventral surface has a rectangular pit extending for the full length of the centrum. All surfaces are covered with longitudinal bony fibres; these are interconnected, giving the bone a spongy appearance.

Remarks—The vomer is similar to that of modern centrarchids (Fig. 5.6D) in its characteristic arrow shape, with a continuous tooth patch on the ventral surface of its anterior end, extending to the full lateral extent. Although Whitlock (2010) described the vomer of "*Priscacara*" as lacking teeth, the possibility that the Wasatch fossils represent this genus cannot be excluded because of Cope's (1883) report of teeth on the vomer of "*Priscacara*", and Haseman's (1912) description of small vomerine tooth bases in two specimens of "*Priscacara*" *serrata*, corresponding to the morphology of the Wasatch fossils. None of the articulated specimens of "*Priscacara*" observed preserve details of the ventral morphology of the vomer. The Wasatch specimens are therefore left as representing an indeterminate perciform, probably either a centrarchid of modern morphology or "*Priscacara*" possessing vomerine teeth.

The dentaries included here are similar to those of some centrarchids, such as *Lepomis* (Fig. 5.6F). Specifically, the tooth-bearing surface being wider anteriorly, the anterior constriction of the antero-ventral crest, which then widens posteriorly, the lateral foramina being adjacent to the ventral margin of the bone, and the characteristically deep and elongate lateral pit immediately ventral to the tooth-bearing surface, are all characters seen in both the Wasatch dentaries and those of *Lepomis*. However, the dentaries of articulated "*Priscacara*" specimens (Fig. 5.6G) also show all of these characters. Therefore, the Wasatch dentaries are here attributed either to a centrarchid fish or to "*Priscacara*".

Likewise, the fifth ceratobranchial is similar to those of some centrarchids, based on its fibrous bony texture and numerous rounded teeth, the crowns of which have a smooth surface. These are characters observed in *Lepomis* (Fig. 5.7A). However, "*Priscacara*" *serrata* also has a similar fifth ceratobranchial (Fig. 5.7B, C), and Brinkman et al. (2014:fig. 14D, E) attributed a similar element from the Late Cretaceous Hell Creek Formation to "*Priscacara*". Therefore, this element could either represent an indeterminate centrachid fish or "*Priscacara*".

The first centra included here possess the medially joined dorso-lateral facets for articulation with the exoccipitals forming a transverse ridge at their posterior margin, which is a centrarchid character. However, these centra differ from the centrarchid centra described above in the presence of accessory pits on the lateral and ventral surfaces, which are not seen in any of the comparative centrarchid material. Although the morphology of the anterior-most centra is difficult to distinguish in articulated specimens of "*Priscacara*" (Fig. 5.7E, F, G), the first centra of several species of that genus have such lateral pits and ventro-lateral bony ridges delimiting a median ventral pit. Therefore, the Wasatch specimens either represent a centrarchid morphology not seen in the comparative material, or centra of "*Priscacara*" very similar in morphology to those of modern centrarchids.

Abdominal centra correspond to those of several centrarchids, such as *Pomoxis* (Fig. 5.8C). In particular, the rib articular pit being surrounded by a margin of bone projecting from the lateral surface, formed by the parapophysis anteriorly and ventrally, and connected dorsally to the neural arch base, is a feature of the Centrarchidae. However, the abdominal centra of "*Priscacara*" (Fig. 5.7E, F, G) also appear to be very similar to these elements. Therefore, the centra included here probably either represent the abdominal centra of the centrarchid taxon decribed above, or abdominal centra of "*Priscacara*", with no characters permitting their differentiation. The abdominal centra of centrarchids have previously been noted to be difficult to recognise from those of percid fishes (Chapter 3; Divay and Murray, in press), unless the preservation of first centra from both families allowed their differentiation based on bone texture (Chapter 2; Divay and Murray, 2013). Therefore, this general morphology of the abdominal centra may be a primitive character, also shared by "*Priscacara*".

The monophyly of "*Priscacara*" has been called into question, and the taxon has been considered a 'form genus' uniting disparate fishes, rather than a natural group of related species (Grande, 2001). Furthermore, the phylogenetic relationships of "*Priscacara*" have been debated, and affinities with the Centropomidae (Cope, 1877), Cichlidae (Woodward, 1901; Haseman, 1912; Hesse, 1936), Percichthyidae (Cavender, 1986) and Moronidae (Whitlock, 2010) have all been suggested. The creation of a new family, Priscacaridae, was also proposed by Jordan (1923) and was since used by other authors (e.g., Wilson, 1977; Grande, 1984). Although the validity and affinities of "*Priscacara*" are beyond the scope of the present study, based on the numerous similarities between the disarticulated "*Priscacara*" fossils of the Wasatch and some modern centrarchid genera, it seems possible that at least some of the fishes included in "*Priscacara*" have affinities with the Centrarchidae.

DISCUSSION

The ichthyofauna of locality V70220 includes material representing a lepisosteiform and an amiine (Divay, pers. obs.) in addition to the teleosts described above. Therefore, this ichthyofauna comprises up to ten taxa in at least six different families. The uncertainty in the number of taxa represented is due to the variability of the percopsiform material, as well as the unresolved affinities of "*Priscacara*".

Most of the families identified here are present in the lake deposits of the Green River Formation (Grande, 1984). This indicates that the considerable diversity of the ichthyofauna represented in the Green River Formation was not limited to lake environments, but was also found in the rivers of the area. Similarities between the Wasatch and Green River ichthyofaunas also indicate that the rapid climatic warming occurring between the deposition of the main body of the Wasatch and that of the Green River Formation had a limited impact on the fishes of the area.

Because the Wasatch Formation underlies the Green River Formation, the sample documented here also indicates that a considerable diversity of fishes was locally present prior to the formation of the Green River lake system. Furthermore, the Wasatch assemblage is notably similar to those of Mesozoic fluvial deposits; apart from the Centrarchidae and the Amblyopsidae, all taxa recognised here were also found in Late Cretaceous microvertebrate material (Brinkman et al., 2013; Brinkman et al., 2014). Because these Paleogene fishes were already present in North America prior to to the K-Pg event, the assemblage suggests that the end-Mesozoic extinction had a relatively limited influence on North American freshwater ichthyofaunas.

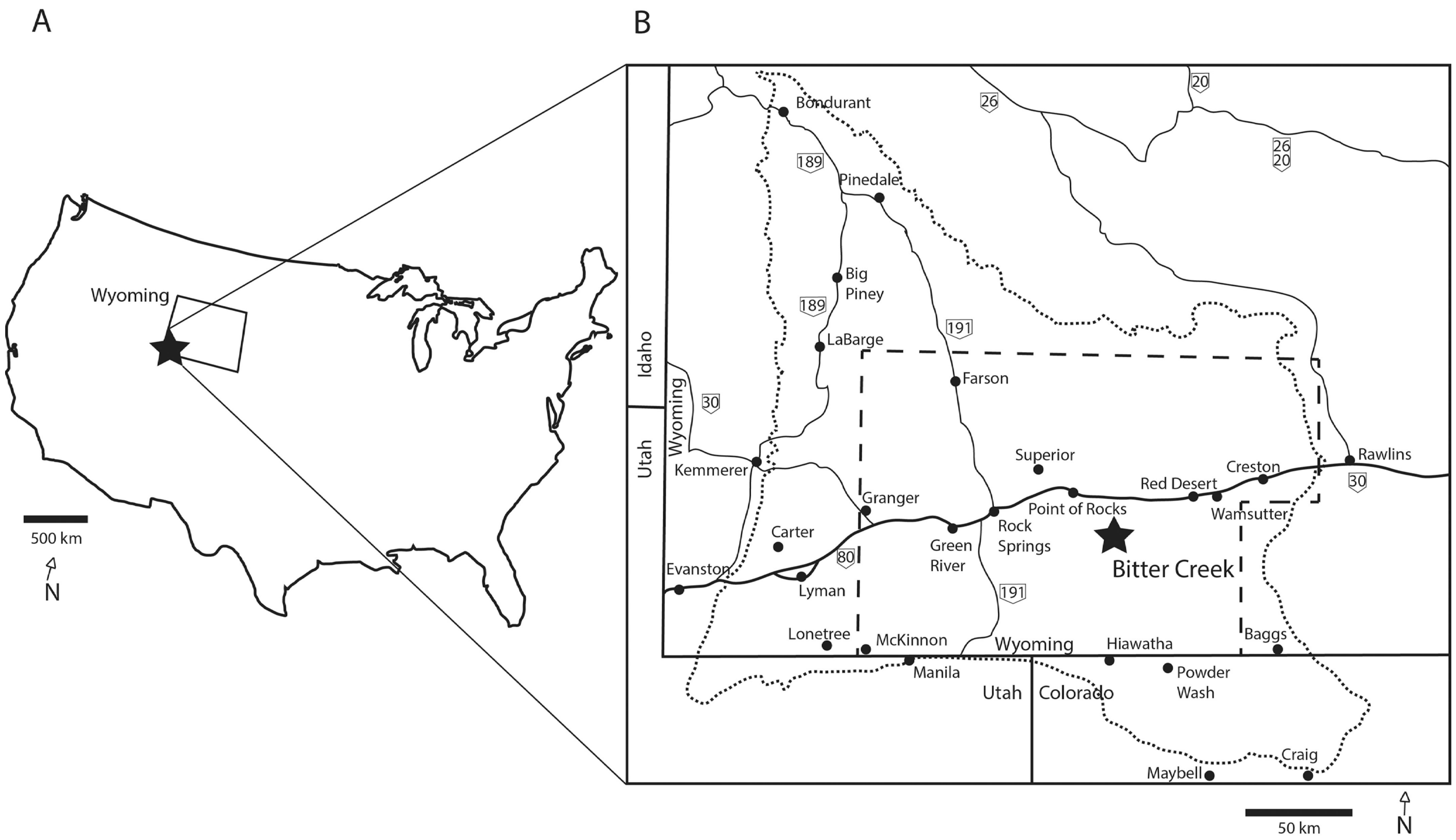
Therefore, many of the fishes of the Green River Formation ichthyofauna were opportunistic taxa that were already present long before the appearance of the lakes, prior to the end-Mesozoic event, rather than having evolved after these lake environments had become available to them. This correspondence of the Wasatch fauna to assemblages of both underlying and overlying formations extends to the generic level, with *Diplomystus*, “*Priscacara*”, and *Notogoneus* all being present in North America as early as the Late Cretaceous, and persisting at least until the Eocene Green River Formation (Grande, 1984). *Diplomystus* were reported from Late Cretaceous deposits of Utah, where they occur in both the Cenomanian Dakota Formation and the early Santonian part of the John Henry Member in the Straight Cliffs Formation (Brinkman et al., 2013) , as well as from the Campanian Dinosaur Park Formation of Alberta, Canada (Brinkman and Neuman, 2002:fig. 7). The Maastrichtian Hell Creek Formation of Montana preserves “*Priscacara*” (Brinkman et al., 2014). Furthermore, the characteristic centra recognised here as representing the modified centra of the primitive Weberian apparatus of *Notogoneus* were also described as teleost centrum morphotype HvB by Brinkman et al. (2013:fig. 10.26A) from the Turonian Smoky Hollow Member of the Straight Cliffs Formation of Utah and by Brinkman et al. (2014:fig. 10C) from the Hell Creek Formation of Montana. These centra were also reported as occurring in the Late Cretaceous Dinosaur Park Formation of Alberta by Brinkman et al. (2013:fig. 10.26B). This indicates that, like *Diplomystus* and “*Priscacara*”, *Notogoneus* were already part of the fluvial ichthyofauna of North America prior to the K-Pg event, and were widely distributed latitudinally.

Palaeoenvironmental Reconstruction

The considerable differences between the ichthyofauna of the early Eocene locality described here and that of the overlying Bridger Formation (Chapter 4), in which only three taxa tolerant of anoxic conditions were represented (Lepisosteidae, *Phareodus*, and *Astephus*), suggest that ichthyofaunal compositions can be used to reconstruct local palaeoenvironments as early as the early Paleogene. These two localities only share a single fish taxon, a lepisosteiform, and have widely different fish diversities.

The Wasatch sample described here is consistent with the previous local palaeoenvironmental reconstructions based on the sedimentology of the area (Savage et al., 1972; Roehler, 1993; Smith and Gauthier, 2013). The very small sizes of all of the fossils in the sample are consistent with a very shallow depositional environment, such as found in the small pools and ponds of a marshy area. The abundant vegetation of the area suggested by Savage et al. (1972) is supported by the presence of a lepisosteiform, an amiid and centrarchids (Scott and Crossman, 1973). Furthermore, along with the small size of the elements, the relatively large lateral foramina of the dentaries and large notochordal foramina of the centra from the Wasatch sample indicate that most of the elements represent juvenile individuals. Because the sample preserves no indication that larger fishes were present, these waters were likely only accessible to individuals of very small sizes, where they may have preferentially lived in order to evade predation from larger fishes. Therefore, the sample described here preserves no indication of the presence of deeper waters in the immediate vicinity. In additon, the preservation of such small elements in a microvertebrate assemblage suggests water flow sufficient to disarticulate remains, but slow enough to allow them to settle and be buried in the area. That the waters of the depositional environment were not stagnant is further indicated by the presence of percopsiforms and centrarchids, which are indicative of well-oxygenated environments (Scott and Crossman, 1973). Therefore, although flow strengths were low and all evidence suggests that all water bodies of the vicinity were shallow, the system of marshy ponds where these deposits were probably deposited most likely remained connected to an active river channel, which maintained a high oxygen content in the waters of the area.

FIGURE 5.1. Locality map for the Bitter Creek locality, UCMP V70220, Wasatch Formation, Wyoming. **A**. Location of the Washakie Basin (marked with a star) relative to Wyoming and the contiguous United States. **B**. Enlarged locality map showing the greater Green River Basin (dotted line), Sweetwater county (dashed line), and the Bitter Creek locality (star) relative to the borders of Wyoming, Idaho, Utah, and Colorado.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McKinnon
Manila
Green River
Rock Springs
Farson
Superior
Point of Rocks
Bitter Creek
Red Desert
Wamsutter
Creston
Rawlins
Baggs
Hiawatha
Powder Wash
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FIGURE 5.2. Wasatch Formation (**A**, **C**, **E**, **F**, **H**) and comparative material (**B**, **D**, **G**, **I**). **A,** Wasatch Formation *Diplomystus* dentary (UCMP V198887 IVa) in lateral, ventral, medial, dorsal and symphyseal views; **B**, left dentary of an articulated Green River Formation *Diplomystus dentatus* (TMP 1986.224.0135) in left lateral view; **C**, Wasatch Formation *Diplomystus* basioccipital (UCMP V198889 IVa); **D**, articulated Green River Formation *Diplomystus dentatus* (UALVP 17731) basioccipital in right lateral view; **E**, **F**, Wasatch Formation *Diplomystus* abdominal centra: **E**, anterior abdominal centrum (UCMP V198890 IIa); **F**, posterior abdominal centrum (UCMP V198888 IIa); **G**, extracted abdominal centrum from an articulated Green River Formation *Diplomystus dentatus* (TMP 1986.224.0135); **H**, Wasatch Formation *Notogoneus* basioccipital (UCMP V198890 V); **I**, right lateral view of the basioccipital of an articulated Green River Formation *Notogoneus osculus* (UALVP 17660). The disarticulated or extracted centra and basioccipital are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

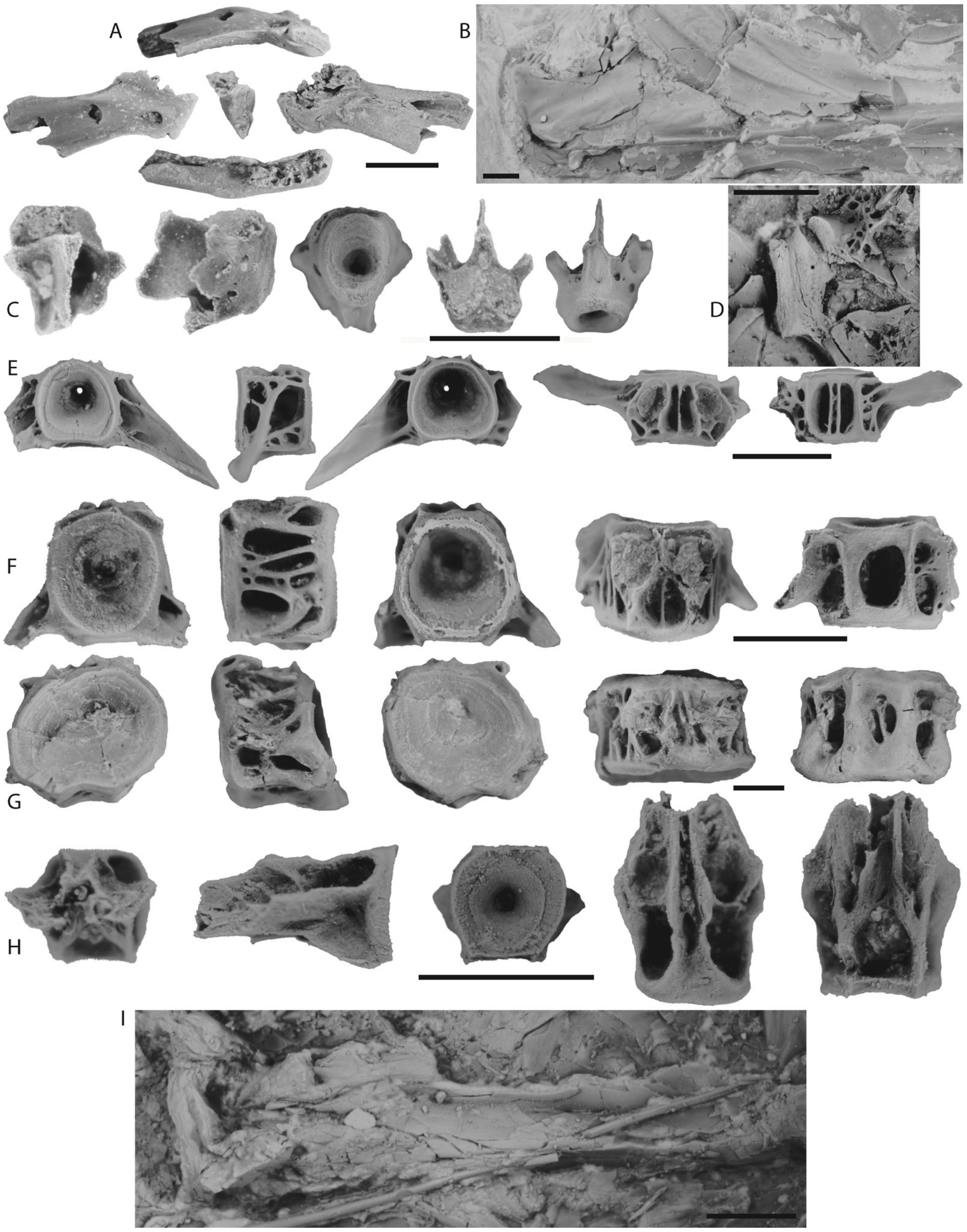
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FIGURE 5.3. Wasatch Formation (**B**, **C**, **F**) and comparative gonorynchiform material (**A**, **D**, **E**). **A**, ventral view of the basioccipital of an articulated Green River Formation *Notogoneus osculus* (UALVP 15084); **B**, long anterior-most abdominal centrum (UCMP V198889 IIIa) of the Wasatch Formation *Notogoneus*; **C**, Wasatch Formation *Notogoneus* short anterior-most abdominal centrum (UCMP V198888 VIIa); **D**, *Chanos chanos* (UAMZ F8550) first centrum; **E**, second centrum of *Chanos chanos* (UAMZ F8550); **F**, large abdominal centrum (UCMP V198890 IIIa) of the Wasatch Formation *Notogoneus*. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

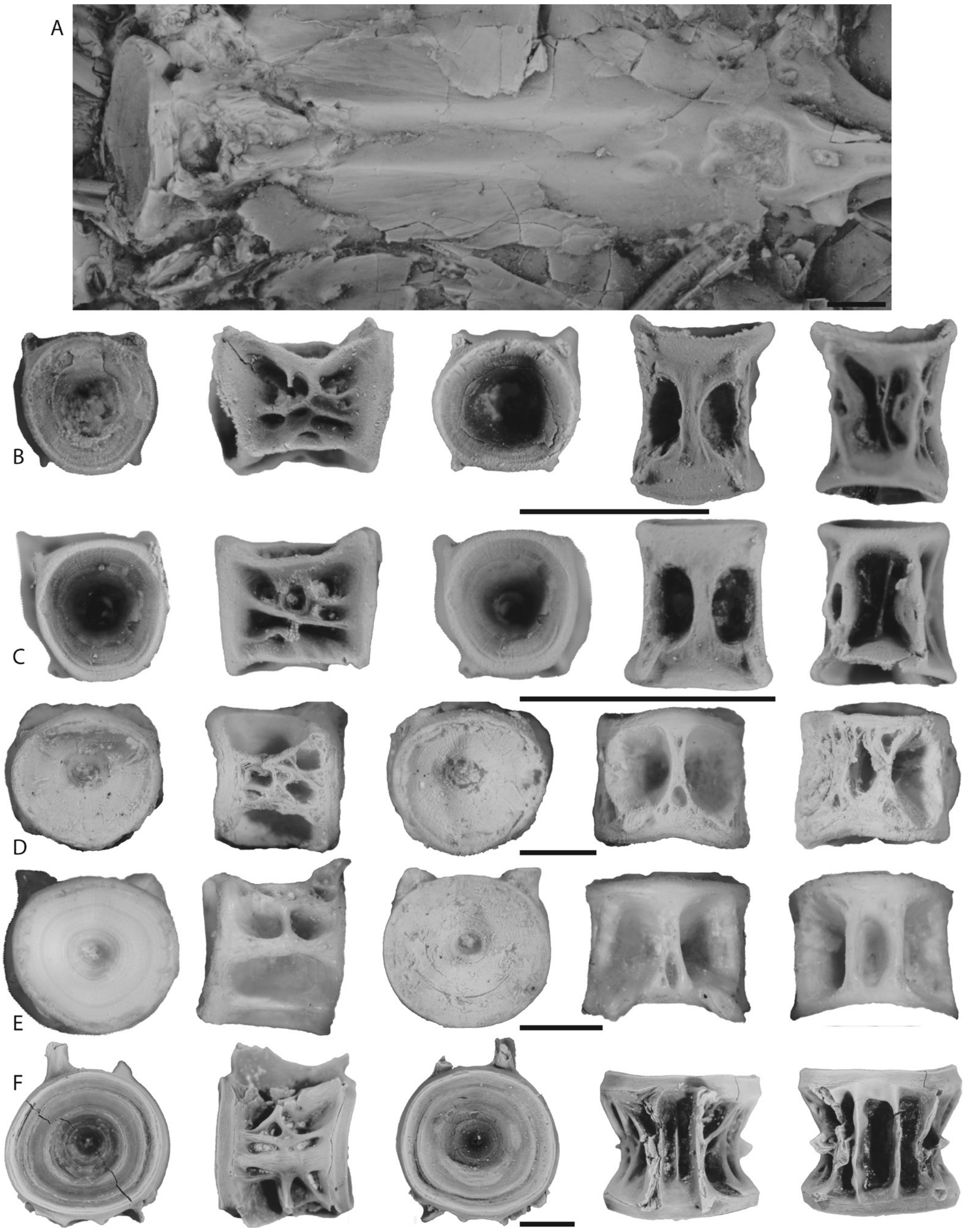
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FIGURE 5.4. Wasatch Formation (**A**, **E**, **F**) and comparative material (**B**–**D**). **A**, small abdominal centrum (UCMP V198892 Va) of the Wasatch Formation *Notogoneus*; **B**, right lateral view of the anterior part of the vertebral series of a large articulated Green River Formation *Notogoneus osculus* specimen (UALVP 15084); **C**, right lateral view of the posterior abdominal vertebral series of the same Green River Formation *Notogoneus osculus* specimen (UALVP 15084); **D**, right lateral view of the mid-abdominal vertebral series of a smaller articulated Green River Formation *Notogoneus osculus* specimen (UALVP 17660); **E**, first centrum (UCMP V198891 VIIIa) of an amblyopsid-like Wasatch Formation percopsiform, showing a thin, laterally pinched ventral surface; **F**, first centrum (UCMP V198889 II) of a Wasatch Formation amblyopsid-like percopsiform, showing a thick and rounded ventral surface and short anterior facets for articulation with the exoccipitals. Disarticulated centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

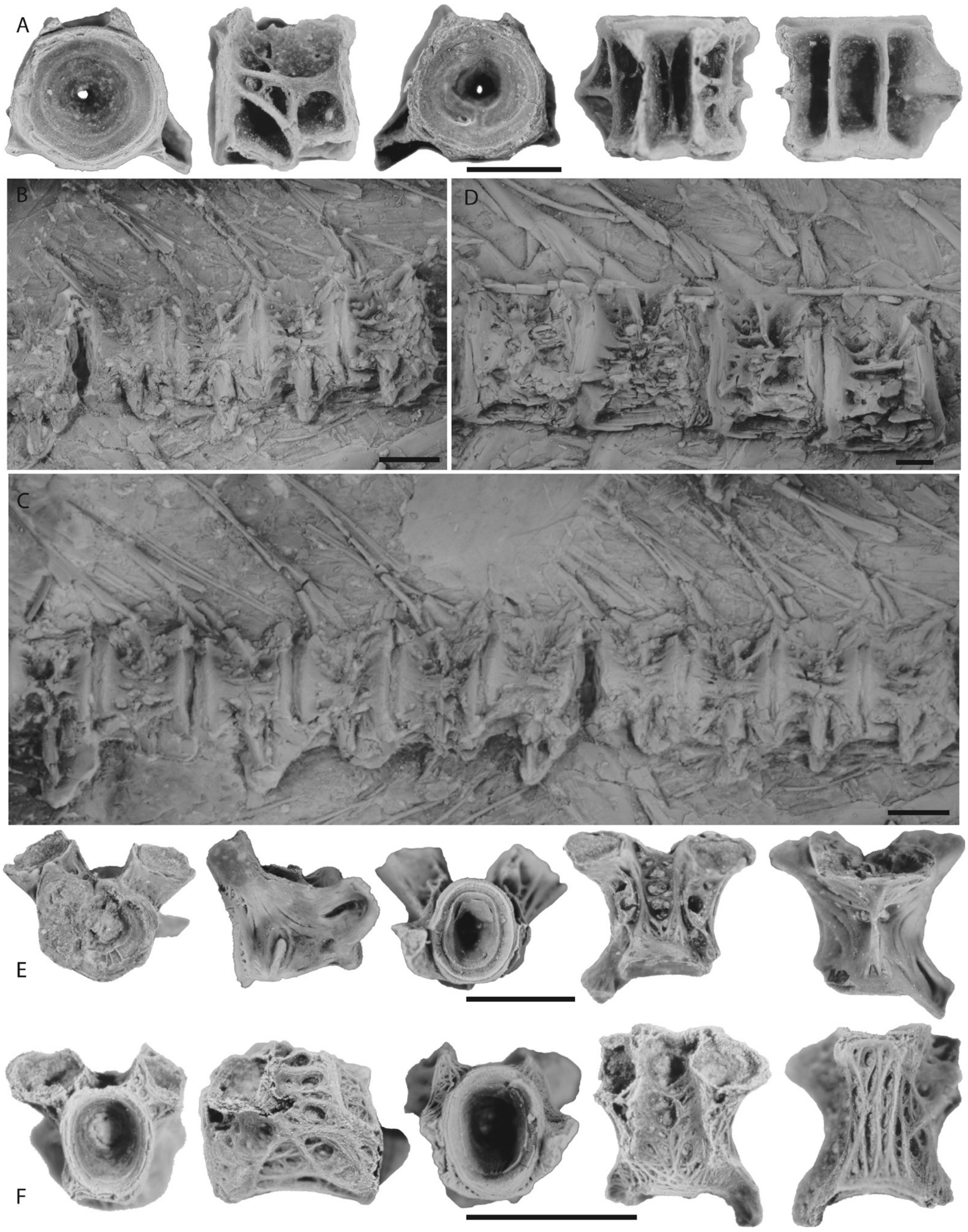
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FIGURE 5.5. Wasatch Formation (**A**, **C**, **E**, **G**) and comparative acanthomorph material (**B**, **D**, **F**). **A**, first centrum of a Wasatch Formation amblyopsid-like percopsiform (UCMP V198888 VIIIa), showing a thin, rounded ventral surface and fibrous surface texture; **B**, *Percopsis omiscomaycus* (ROM R6493) first centrum; **C**, Wasatch Formation percopsiform abdominal centrum (UCMP V198888 XIIIa); **D**, *Percopsis omiscomaycus* (ROM R6493) abdominal centrum; **E**, dentary (UCMP V198887 Va) of a Wasatch Formation centrarchid; **F**, *Pomoxis nigromaculatus* (CMN 76-075) dentary; **G**, large first centrum (UCMP V198892 VI) of a Wasatch Formation centrarchid. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Dentaries are presented in lateral, ventral, medial, dorsal and symphyseal views. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

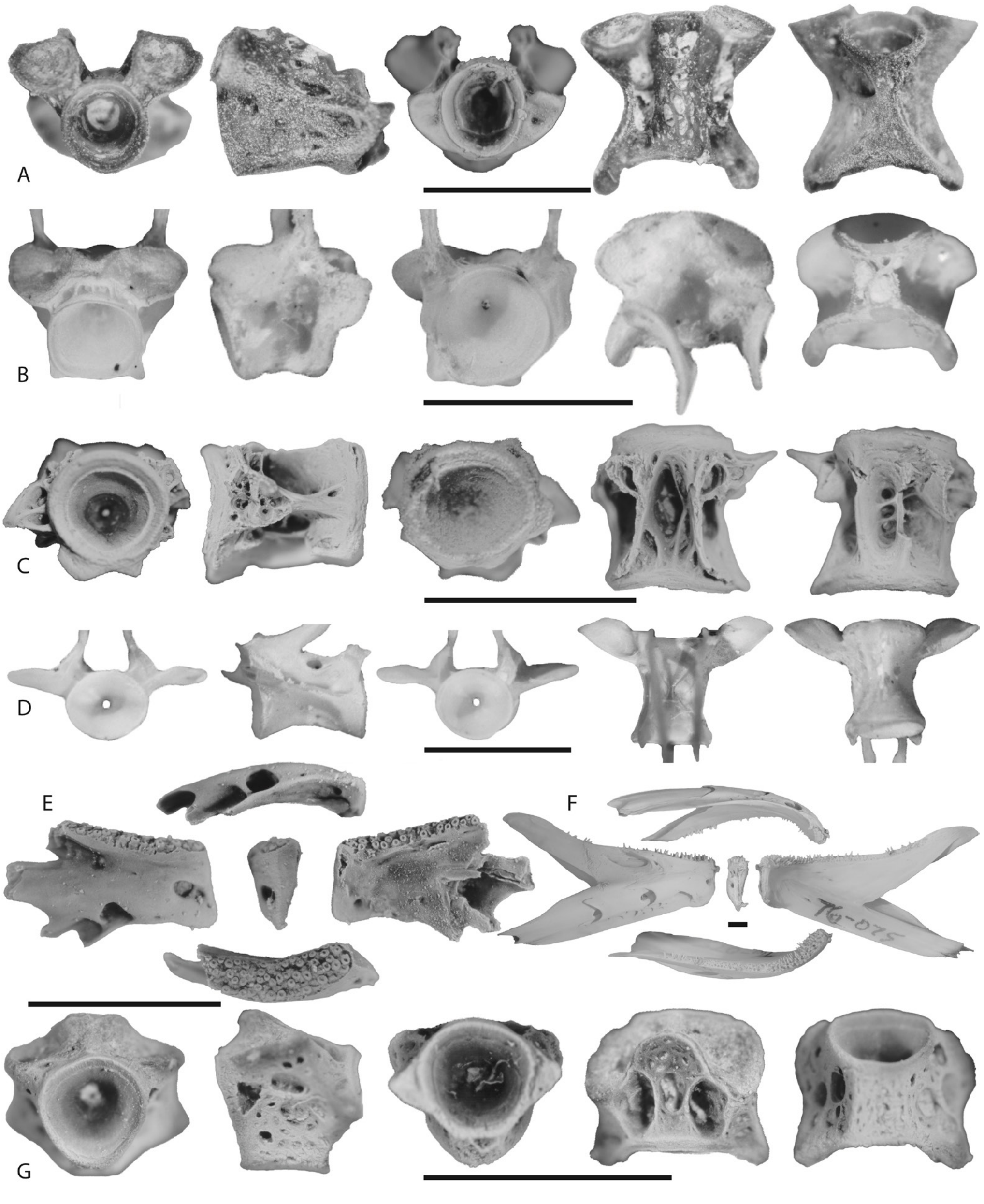
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FIGURE 5.6. Wasatch Formation (**A**, **C**, **E**, **H**) and comparative perciform material (**B**, **D**, **F**, **G**). **A**, small first centrum (UCMP V198891 IVa) of a Wasatch Formation centrarchid; **B**, *Pomoxis nigromaculatus* (CMN 76-075) first centrum; **C**, vomer (UCMP V198887 Ia) of a Wasatch Formation centrarchid or "*Priscacara*" in dorsal, lateral and ventral views; **D**, *Pomoxis nigromaculatus* (CMN 76-075) vomer in ventral view; **E**, dentary (UCMP V198887 VIa) of a Wasatch Formation centrarchid or "*Priscacara*"; **F**, *Lepomis gibbosus* (CMN 73-236C) dentary; **G**, dentaries of an articulated Green River Formation *"Priscacara" liops* (UALVP 17726) in left lateral view; **H**, fifth ceratobranchial (UCMP V198887 II) of a Wasatch Formation centrarchid or "*Priscacara*" in dorsal and ventral views. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

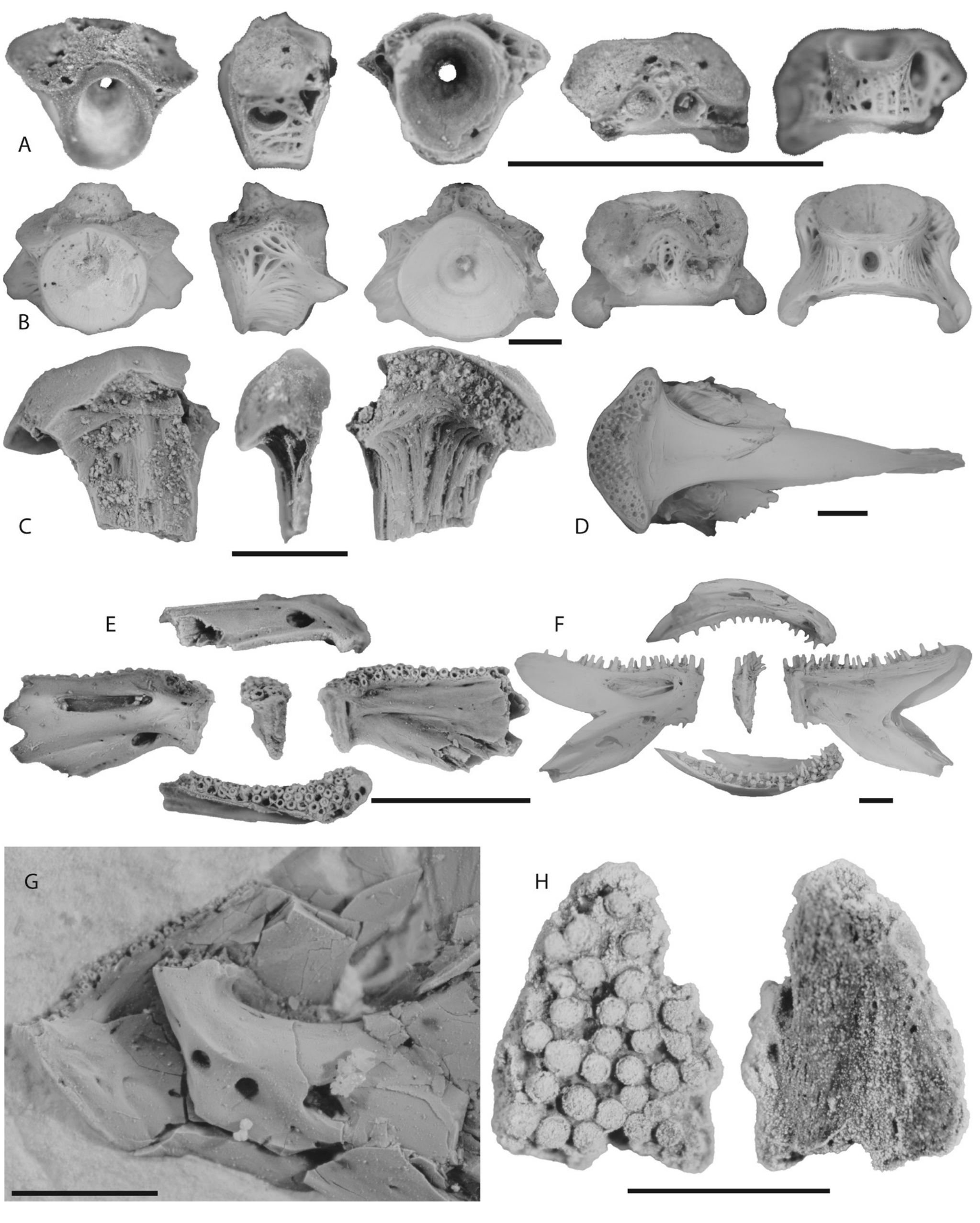
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FIGURE 5.7. Wasatch Formation centrarchid or “*Priscacara*” (**D**) and comparative perciform material (**A**, **B**, **C**, **E**, **F**, **G**). **A**, *Lepomis gibbosus* (CMN 73-236C) fifth ceratobranchial in dorsal and ventral views; **B**, skull of an articulated Green River Formation “*Priscacara*” *serrata* (UALVP 20578) in left lateral view, preserving the fifth ceratobranchial; **C**, close up view of the fifth ceratobranchial of “*Priscacara*” *serrata* (UALVP 20578); **D**, first centrum (UCMP V198889 Ia) of a Wasatch Formation centrarchid or “*Priscacara*”; **E**, anterior abdominal vertebral series of an articulated Green River Formation *“Priscacara” liops* (UALVP 20357) in left lateral view; **F**, anterior abdominal vertebral series of an articulated Green River Formation *“Priscacara” liops* (UALVP 17725) in right lateral view; **G**, anterior abdominal vertebral series of an articulated Green River Formation *“Priscacara” peali* (UALVP 1874) in right lateral view. The Wasatch Formation centrum is presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.

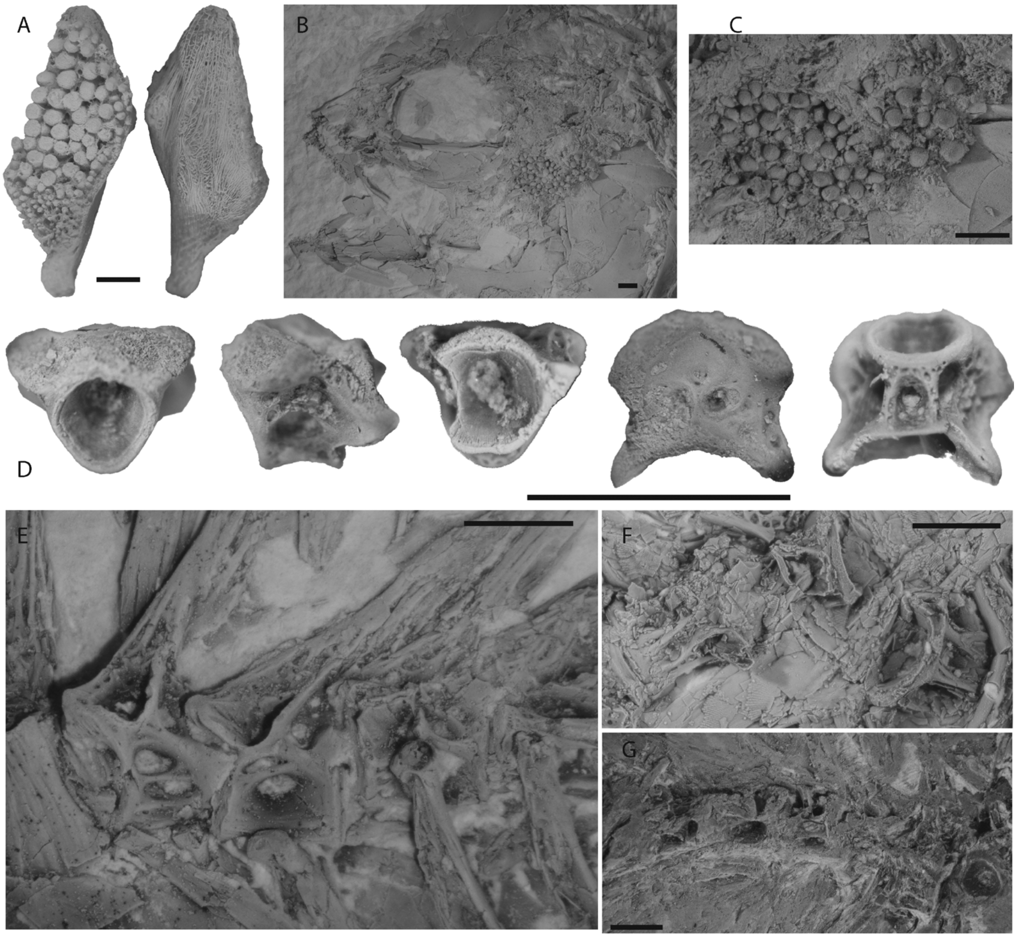
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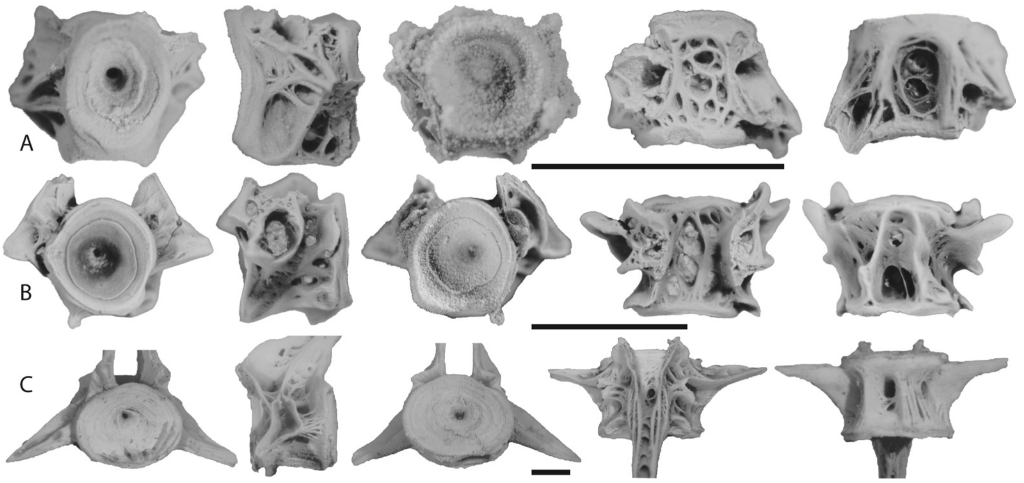
FIGURE 5.8. Wasatch Formation centrarchid or “*Priscacara*” (**A**, **B**) and comparative perciform material (**C**). **A**, Wasatch Formation anterior-most abdominal centrum (UCMP V198889 VIa) of a centrarchid or “*Priscacara*”; **B**, more posterior abdominal centrum (UCMP V198888 Ia) of a Wasatch Formation centrarchid or “*Priscacara*”; **C**, *Pomoxis nigromaculatus* (CMN 76-075) abdominal centrum. Centra are presented, from left to right, in anterior, lateral, posterior, dorsal and ventral views; for lateral view, anterior is towards the left; for dorsal and ventral views, anterior is to the top of the page. Specimens were coated in ammonium chloride prior to photographing. All scale bars equal 2 mm.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APPENDIX 5.1. Comparative material examined. All of these specimens are dried skeletons, and each number represents an individual specimen.

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Family Catostomidae: *Carpiodes carpio* (Rafinesque, 1820a) – KU 12732; *Carpiodes cyprinus* (Lesueur, 1817b) – CMN 77-183; *Catostomus catostomus* (Forster, 1773) – UAMZ F8558, F8582; *Ictiobus cyprinellus* (Valenciennes in Cuvier and Valenciennes, 1844) – KU 15337; *Moxostoma macrolepidotum* (Lesueur, 1817b) – ROM R7377

Family Centrarchidae: *Lepomis gibbosus* (Linnaeus, 1758) – CMN 73-236C; *Lepomis macrochirus* Rafinesque, 1819 – ROM R6210; *Micropterus dolomieui* Lacepède, 1802 – CMN 73-258, ROM R6125 (juvenile); *Pomoxis nigromaculatus* (Lesueur in Cuvier and Valenciennes, 1829) – CMN 76-075

Family Chanidae: *Chanos chanos* (Forskål, 1775) – UAMZ F8550

Family Cottidae: *Cottus bairdi* Girard, 1850 – ROM R6589; *Cottus cognatus* Richardson, 1836 – CMN 80-185; *Myoxocephalus octodecemspinosus* (Mitchill, 1814) – ROM R2430

Family Cyprinidae: *Campostoma anomalum* (Rafinesque, 1820b) – ROM R7890; *Chrosomus eos* Cope, 1861 – ROM R7897; *Clinostomus elongatus* (Kirtland, 1840a) – ROM R7754; *Cyprinella spiloptera* (Cope, 1867) – ROM R6823; *Cyprinus carpio* Linnaeus, 1758 – UAMZ F8557; *Hybognathus hankinsoni* Hubbs in Jordan, 1929 – ROM R2569; *Luxilus cornutus* (Mitchill, 1817) – ROM R6425; *Macrhybopsis storeriana* (Kirtland, 1844) – ROM R6385; *Nocomis biguttatus* (Kirtland, 1840a) – ROM R5358; *Notemigonus crysoleucas* (Mitchill, 1814) – ROM R7664; *Notropis atherinoides* Rafinesque, 1818a – ROM R2561; *Pimephales notatus* (Rafinesque, 1820b) –

ROM R7750; *Ptychocheilus oregonensis* (Richardson, 1836) – ROM R6513; *Semotilus atromaculatus* (Mitchill, 1818) – ROM R5885; *Semotilus margarita* (Cope, 1867) – CMN Z-668

Family Esocidae: *Esox lucius* Linnaeus, 1758 – UAMZ F8551, F8552; *Esox masquinongy* Mitchill, 1824 – ROM R2243; *Esox niger* Lesueur, 1818b – CMN 87-385

Family Fundulidae: *Fundulus heteroclitus* (Linnaeus, 1766) – ROM R3852

Family Hiodontidae: *Hiodon alosoides* (Rafinesque, 1819) – UAMZ F8556

Family Ictaluridae: *Ameiurus natalis* (Lesueur, 1819) – ROM R7245; *A. nebulosus* (Lesueur, 1819) – CMN 77-254; *Ictalurus punctatus* (Rafinesque, 1818b) – UAMZ F8553; *Noturus flavus* Rafinesque, 1818c – CMN 77-182, UAMZ 7527

Family Lotidae: *Lota lota* (Linnaeus, 1758) – CMN 85-603, ROM R1850

Family Moronidae: *Morone americana* (Gmelin, 1789) – ROM R6327; *Morone chrysops* (Rafinesque, 1820c) – ROM R6377; *Morone saxatilis* (Walbaum, 1792) – UAMZ F8554

Family Osmeridae: *Osmerus mordax* (Mitchill, 1814) – CMN Z-4079

Family Percidae: *Perca flavescens* (Mitchill, 1814) – UAMZ 4821, UMMZ 171120, 175905 (8 of 9), 175905 (9 of 9), 179978, 194309; *Stizostedion vitreum* (syn. *Sander vitreus*) (Mitchill, 1818) – UAMZ F8420, F8421

Family Percopsidae: *Percopsis omiscomaycus* (Walbaum, 1792) – ROM R6493

Family Salmonidae: *Coregonus clupeaformis* (Mitchill, 1818) – CMN 73-259b.; *Stenodus leucichthys* (Güldenstädt, 1772) – CMN Z4206

Family Scianidae: *Aplodinotus grunniens* Rafinesque, 1819 – CMN Z-275; *Rhinichthys cataractae* (Valenciennes in Cuvier and Valenciennes, 1842) – ROM R6592

Family Umbridae: *Umbra limi* (Kirtland, 1840b) – ROM R7818

CHAPTER 6—GENERAL DISCUSSION AND CONCLUSIONS

FORMATION OF THE MODERN NORTH AMERICAN FRESHWATER FISH FAUNA

The assemblages described in this thesis can be compared with one another and other described assemblages to reconstruct the evolution of the North American freshwater fish fauna from the Mesozoic (e.g., Brinkman and Neuman, 2002; Brinkman et al., 2013; Brinkman et al., 2014) and through the Cenozoic (Chapters 2–5) to the present. The latitudinal influences on this fauna during this period can also be addressed, despite the variety of environmental conditions and depositional environments represented by these assemblages. Based on these comparisons, the North American ichthyofauna seems to have undergone gradual changes since the Late Cretaceous, with many early Cenozoic fishes already present prior to the Cretaceous-Paleogene transition. This suggests that the K-Pg extinction event had relatively little impact on the evolution of the early Cenozoic ichthyofauna, although a number of taxa (e.g., elasmobranchs, elopomorphs) were more diverse in the Cretaceous (Brinkman and Neuman, 2002; Brinkman et al., 2013; Brinkman et al., 2014). However, the reconstruction of this gradual faunal turnover (Fig. 6.1) allows the recognition of periods during which changes were more frequent, and therefore allows the suggestion of possible causes for these turnovers leading to the formation of the modern fish fauna. These suggestions can serve as hypotheses for future studies focusing on the main periods of faunal turnover recognised here.

The turnovers that led to the formation of the modern fauna appear to have occurred since the end-Cretaceous event and to have mostly taken place in two phases, one in the mid-Paleogene and the other in the late Neogene. These coincide with the increase of seasonality in North America between the middle and late Eocene (Storer, 1996), and the gradual cooling of climates eventually leading to the Plio-Pleistocene glaciations (Zachos et al., 2008), respectively. The increase in seasonality during the Eocene is concurrent with the disappearance or decrease in diversity of some of the major groups that were present prior to the K-Pg transition and abundant in the early Cenozoic (e.g., Osteoglossidae, Clupeomorpha, Gonorynchidae, "*Priscacara*"). By the late Paleogene, the North American ichthyofauna was essentially modern in composition, but seems to have been more geographically homogeneous than in modern times, with taxa typical of the southern coastal U.S.A. ranging north and west at least as far as southern Saskatchewan. The strong modern latitudinal gradient in faunal composition was absent as recently as the middle Neogene (c.f., the mid-Miocene Wood Mountain ichthyofauna; Chapter 2; Divay and Murray, 2013); it may therefore be the result of the late Neogene climatic cooling trend and the Plio-Pleistocene glaciations.

Several taxa typical of modern North American ichthyofaunas were already present and widely established by the Late Cretaceous. The Lepisosteidae may have inhabited the continent as early as the Early Cretaceous (Grande, 2010), although reports prior to the Turonian are based on non-diagnostic material and may therefore be unreliable (Brinkman et al., 2013). The first reliable occurrence of the extant genus *Lepisosteus* is in the Turonian localities of the Smoky Hollow Member of the Straight Cliffs Formation (Brinkman et al., 2013). By the Campanian, both extant genera *Lepisosteus* and *Atractosteus* were established (Brinkman et al., 2013; Grande, 2010). In the Cretaceous, lepisosteids ranged as far as Western and Arctic North America, in addition to eastern Canada and the eastern and southern parts of the U. S. A., where they are still currently present (Grande, 2010). Likewise, the Amiidae were established in North America as early as the Cretaceous, with the first representative of the Amiinae, the only extant subfamily of the group, appearing in the late Maastrichtian of Alberta, Canada (Grande and Bemis, 1998).

Several modern teleost families were also established as early as the Cretaceous, including both the Hiodontidae and the Esocidae. Late Cretaceous hiodontids have been documented from Utah, where they occur from the Cenomanian Dakota Formation to the late Campanian Kaiparowits Formation (Brinkman et al., 2013), in the Campanian Dinosaur Park Formation of Alberta, Canada (Brinkman and Neuman, 2002), and in the Maastrichtian Hell Creek Formation of Montana (Brinkman et al., 2014). Furthermore, growth characteristics of both the Canadian (Newbrey et al., 2007) and Hell Creek (Brinkman et al., 2014) material indicate a greater taxonomic diversity than could be determined from discrete morphological features alone, with at least two species in each of these two formations. North American esocids have also been reported from the Late Cretaceous, with the oldest representatives occurring in the Santonian Milk River Formation and in the Campanian Belly River Group of Alberta, as well as in the Maastrichtian Hell Creek and Lance formations of Montana and Wyoming, respectively (Wilson et al., 1992; Brinkman et al., 2013; Brinkman et al., 2014), and in the Campanian Kaiparowits Formation of Utah (Brinkman et al., 2013).

In addition to these, the Late Cretaceous ichthyofauna of North America contained taxa which would persist into the early Paleogene, becoming extinct later in the Cenozoic. These include ellimmichthyiform, osteoglossid and gonorynchid taxa, as well as the indeterminate perciform "*Priscacara*", all of which are well known from the late Paleocene to late Eocene Green River Formation (Grande, 1984). The ellimmichthyiform *Diplomystus* is one of the most common Green River taxa (Grande, 1984), but was also recently reported from the Cenomanian Dakota Formation and the early Santonian part of the John Henry Member in the Straight Cliffs Formation, both of which are located in Utah (Brinkman et al., 2013). Centra similar to this Late Cretaceous material had also previously been described from the Campanian Dinosaur Park Formation of Alberta (Brinkman and Neuman, 2002:fig. 7), indicating that the genus was already present and widely distributed in North America prior to the K-Pg transition. Likewise, although North American representatives of *Phareodus* are only represented in the early to middle Eocene Green River and Bridger formations (Grande, 1984; Li et al., 1997a; Chapter 3), another closely related osteoglossine osteoglossid was already present in the Campanian Oldman Formation of Alberta (Li, 1996). Two other osteoglossids are known from the Paleocene of North America, in the Paskapoo Formation of Alberta (Li and Wilson, 1996) and the Sentinel Butte Formation of North Dakota (Newbrey and Bozek, 2000), although these represent a different subfamily, being heterotidines. The earliest report of the Gonorynchidae is in the Campanian Two Medicine Formation of Montana (Grande and Grande, 1999), representing *Notogoneus*, a genus that would persist into the Eocene. However, centra similar to the *Notogoneus* Weberian centra from the Wasatch assemblage described in this thesis (Chapter 5) predate this occurrence, having been described from the Turonian Smoky Hollow Member of the Straight Cliffs Formation of Utah (Brinkman et al., 2013,fig. 10.26A). Similar centra were also recovered from the Campanian Dinosaur Park Formation of Alberta (Brinkman et al., 2013:fig. 10.26B), and the Maastrichtian Hell Creek Formation of Montana (Brinkman et al., 2014:fig. 10C). Lastly, "*Priscacara*" was also recently shown to predate the K-Pg transition, having been recovered from the Maastrichtian Hell Creek Formation of Montana (Brinkman et al., 2014). The next appearance of this taxon in the fossil record is in the Eocene lake deposits of the Green River Formation (Grande, 1984) and of the Horsefly beds close to Horsefly, British Columbia (Wilson, 1977). The presence of "*Priscacara*" in the fluvial Hell Creek deposits studied by Brinkman et al. (2014) and in the Wasatch assemblage studied in this thesis (Chapter 5) further demonstrates that this taxon was not limited to lake environments. "*Priscacara*" may therefore have been continuously present in the relatively poorly known North American fluvial environments between the Maastrichtian and the Eocene.

According to the descriptions included in this thesis (Chapters 2–5), and the suggested synapomorphies summarised in Appendix 6.1, Cretaceous ostariophysan material that had not previously been attributed to specific taxonomic orders may indicate that catostomid- or cyprinid-like cypriniforms would also have already been present in North America prior to the K-Pg transition. Several first centra of the Weberian apparatus were documented from Turonian to late Campanian localities of the Grand Staircase region of Utah (Brinkman et al., 2013:fig. 10.20A–C) and in the Maastrichtian Hell

Creek Formation of Montana (Brinkman et al., 2014:fig. 7A, B), and were attributed to an indeterminate ostariophysan. These are characteristic in being disc-shaped, with a pair of circular articular pits for the scaphium on their dorsal surface. Furthermore, based on figures of Brinkman et al. (2013:fig. 10.20A–C; 2014:fig. 7A, B), the centra lack the pair of ventral processes for articulation with the complex vertebra of the Weberian apparatus that is characteristic of the first Weberian centrum of ictalurids. Instead, they have lateral or ventro-lateral transverse processes, as are seen in catostomids and cyprinids. However, these centra have an accessory ventral pit that is absent from Cenozoic and extant cypriniforms, but is present in siluriforms. The presence of this ventral pit was the basis of the suggestion that these centra represent a taxon with affinities to the Siluriformes (Brinkman et al., 2013; Brinkman et al., 2014). If these centra represent a stem catfish or sister group, as suggested by Brinkman et al. (2013) and Brinkman et al. (2014), they would be expected to indicate the presence of a catfish of distinctive morphology, unlike any ictalurid examined (Chapters 2–4). Alternatively, if the synapomorphies suggested in this thesis (Appendix 6.1) are correct, these centra would be more cypriniform-like in morphology, and may indicate that the order has been present in North America since the Late Cretaceous.

The documentation of these taxa in the Cretaceous and Cenozoic suggests that the Cretaceous-Paleogene transition did not result in a large scale turnover of the freshwater fish fauna of North America; instead, the faunal turnovers were likely more progressive. The identification of several of these same taxa in the Wasatch (Chapter 5) and Bridger assemblages (Chapter 4) further supports this similarity between Late Cretaceous and Early Cenozoic fish faunas, and demonstrates that several fishes of the Green River lakes were present in the area prior to the appearance of lacustrine environments. Many of the fishes associated with the lakes of the Green River Formation were capable of inhabiting fluvial environments for considerable periods of time and may have been more widespread than previously thought, colonising the lakes as opportunistic taxa rather than evolving within them in the Eocene. This is also indicated by the presence of a lepisosteid, *Phareodus* and *Astephus* in the Bridger assemblage (Chapter 4), demonstrating that these taxa were not limited to lacustrine environments, and persisted in the fluvial environments that replaced the Green River lakes after those lakes disappeared.

Furthermore, several modern genera appeared in North America in the first half of the Paleogene, shortly after the K-Pg transition. The first appearance of *Amia*, for instance, is in the late Paleocene Paskapoo Formation of Alberta, which also represents the northernmost and westernmost occurrence of the genus in North America (Grande et al., 2000). The Paleocene also marks the earliest occurrence of *Esox*, in the Paskapoo and Ravenscrag formations, from Alberta and Saskatchewan respectively (Wilson, 1980). The first evidence of *Hiodon* is also in the Paleogene, in the Eo-Oligocene Kishenehn Formation of Montana (Li and Wilson, 1994). [If, however, one follows Hilton and Grande (2008), who regarded *Eohiodon* as a junior synonym of *Hiodon*, then the earliest occurrence of the genus *Hiodon* is in the late early Eocene Green River Formation, Wyoming (Li et al., 1997b).] In addition to these first occurrences of modern genera, the first half of the Paleogene marks the appearance of the Catostomidae, represented by the Eocene to Oligocene genus *Amyzon*, found in Osino, Nevada (Cope, 1872), in the Green River Formation (Grande, 1984), and in the middle Eocene Princeton and Horsefly beds of British Columbia (Wilson, 1977), as well as in the Eo–Oligocene Florissant Formation of Colorado (Cope, 1875). The early Paleogene also marks the first occurrence of the Ictaluridae, represented by *Astephus* in the Polecat Bench Formation of Wyoming (Lundberg, 1975), as well as the first occurrence of the Percopsidae in the Paskapoo Formation of Alberta (Murray and Wilson, 1996; Murray, 1996), dating to the early and middle Paleocene, respectively. Additionally, the early Eocene Wasatch assemblage (Chapter 5) includes centrarchid material slightly older than the previously documented oldest occurrence of the family, in the later Eocene of northern Montana (Cavender, 1998). This same Wasatch assemblage also marks the first appearance of the Amblyopsidae, a group which previously lacked a fossil representative altogether (Chapter 5).

The late Eocene–early Oligocene Cypress Hills assemblage (Chapter 3) is significantly different from earlier ichthyofaunas. Although most of the taxa it includes were already present in Late Cretaceous or early Paleogene deposits, this assemblage lacks osteoglossids, paraclupeids, clupeids, gonorynchids, and "*Priscacara*", all of which had been present and sometimes abundant in earlier Cenozoic deposits, such as those of the Green River Formation (Grande, 1984). However, several archaic groups persisted at least until the Eo–Oligocene boundary, including a previously unknown probable salmoniform of unique morphology and the indeterminate perciform *Mioplosus*. Alongside these, the assemblage also includes leuciscine material, the first occurrence of which is from the similarly aged Eo–Oligocene John Day Formation of

Oregon (Cavender, 1998), as well as the oldest evidence of North American moronids.

This transition from the fauna typical of early Paleogene times, which remained similar to that of the Late Cretaceous, to an essentially modern ichthyofauna, which nevertheless included a few archaic groups, represents the largest faunal turnover documented in this thesis. Although it could indicate that taxa typical of early Cenozoic formations are absent from the Cypress Hills assemblage (Chapter 3) because the local environment was unsuitable for them, or because these taxa were latitudinally restricted to the south of southern Saskatchewan, it could also indicate that these archaic groups had disappeared from the North American ichthyofauna between the middle and the late Eocene. In this latter case, the transition from an early Paleogene fauna to an almost modern ichthyofauna coincides with the onset of increased seasonality between the middle and late Eocene, to which has been attributed major mammalian faunal turnovers (Storer, 1996). Therefore, although it had remained relatively unchanged during the K-Pg transition and major climatic events such as the Early Eocene Climatic Optimum (Zachos et al., 2008), the North American ichthyofauna may have been deeply influenced by the increased seasonality first occurring in the Eocene.

By the middle Neogene (Chapter 2), the faunal composition of the continent had become modern. The archaic groups that were still present at the Eo–Oligocene boundary, represented in the Cypress Hills assemblage (Chapter 3) by *Mioplosus* and the indeterminate salmoniform, are no longer found in southern Saskatchewan by the mid-Miocene. Conversely, modern taxa that had previously been absent, such as percids, are represented in the fossil record by the Miocene (Murray and Divay, 2011), and most Neogene material can be attributed to extant genera (Chapter 2; Divay and Murray, 2013). The mid-Miocene North American ichthyofauna is still markedly different from that of modern times, however, in that the Miocene fauna found in Saskatchewan is currently typical of the southern U.S.A., and unlike the salmoniform-rich ichthyofauna that would now be found at such latitudes (Chapter 2; Divay and Murray, 2013). This probably indicates that the modern latitudinal gradient in faunal composition was formed more recently, concurrent with—and therefore possibly caused by—the late Neogene climatic cooling trend, which culminated in the Plio-Pleistocene glaciations (Zachos et al., 2008).

GENERAL CONCLUSIONS

The Cenozoic freshwater fish assemblages studied here (Chapters 2–5) have been used to reconstruct the palaeoenvironments and palaeoclimates of the geological formations or specific fossil localities in which they were found. These assemblages have also extended the geographic and stratigraphic ranges of several lineages, including several first fossil occurrences (e.g., *Stizostedion*, Chapter 2), which are palaeobiogeographically significant and indicate that the ranges of several fishes were significantly different from what was previously thought.

Palaeoenvironmental Reconstructions Based on Ichthyofaunas

The rationale for all of the palaeoenvironmental reconstructions presented based on the studied fluvial assemblages (Chapters 2–5) is that the environmental tolerances and preferences of the taxa present should correspond to the environments of the floodplain at time of deposition (Fig. 6.2). However, the palaeoenvironmental reconstructions differ depending on whether the material was recovered from several localities within a formation or from a single locality. Material recovered from a single locality is most likely to represent a single, local environment, as in the case of the Wasatch (Chapter 4) and Bridger assemblages (Chapter 5), although these assemblages may have undergone some degree of lateral or vertical mixing. Conversely, material recovered from several localities in a formation is more likely to be more diverse, representing a lateral mix of several different environments within the floodplain, as for the Cypress Hills (Chapter 3) and Wood Mountain assemblages (Chapter 2).

As expected, the single locality assemblages included here represent fewer taxa than mixed assemblages, with up to ten taxa in the Wasatch sample and only three taxa in the Bridger sample, while the Cypress Hills and the Wood Mountain samples represent at least fourteen and over sixteen different taxa, respectively. In spite of having lower diversities, assemblages from single localities are sufficient to propose palaeoenvironmental reconstructions. Furthermore, the low taxonomic diversity of the Bridger assemblage is the main environmental indicator of hypoxic conditions, since the only three fishes present are resistant to this type of environment (Fig. 6.3). Likewise, that the Wasatch assemblage is exclusively composed of very small-sized fossils strengthens the previous suggestion (Savage et al., 1972) that the depositional environment was composed of very shallow—but normoxic—waters (Fig. 6.4), and may represent evidence that these small fishes were evading predation by remaining in waters too shallow for potential predators.

Because combining material from several localities in a single formation results in lateral mixing, palaeoenvironmental reconstructions from these mixed assemblages represent an overview of the environmental diversity of the floodplain, rather than a single local environment. This makes the recognition of precise local conditions more difficult, and may not support the suggestion of specific behaviours, such as predator evasion. However, mixed faunas allow the reconstruction of the environment of the surrounding areas, which cannot be determined otherwise. Mixed faunas are also more representative of the total taxonomic diversity present in a floodplain, as opposed to basing diversity estimates on more restricted local assemblages. Therefore, assemblages composed of material recovered from several discrete localities, like the Cypress Hills assemblage, combine the advantages of single and mixed assemblages. In this case, multiple localities only possessing hypoxia-tolerant taxa, such as the ictalurid *Astephus*, probably represent environments similar to that represented by the Bridger assemblage, but the combination of these with other localities represents a better estimate of the full diversity of the floodplain (Fig. 6.5). Likewise, the Wood Mountain assemblage probably represents the combination of several localities distributed among varied sub-environments in a diverse floodplain (Fig. 6.6).

Palaeoclimatic Reconstructions Based on Ichthyofaunas

The reconstruction of palaeoclimates from fish assemblages rests on a rationale similar to that of the reconstruction of palaeoenvironments from the same material: the intersection of the geographic ranges of the taxa recovered should correspond to an area with a climate similar to that of the fossil locality at time of deposition, assuming that the temperature preferences of the fauna at the time were similar to those of their extant relatives. Therefore, the precision of climatic reconstructions depends on the recovery of a group of taxa corresponding to a precise area, as well as the faunal composition of the fossil assemblage being well-enough understood for the ranges of these taxa to be known.

This explains why the only quantified—and therefore most precise—palaeoclimatic reconstruction proposed in this thesis corresponds to the Wood Mountain Formation ichthyofauna (Chapter 2), which is both the most diverse and the youngest assemblage included. Mixed assemblages, being more diverse than assemblages representing single localities, are more likely to include a group of taxa indicative of more precise climatic conditions than the more taxonomically-restricted assemblages derived from a single locality. Furthermore, as illustrated in this thesis by the Wood Mountain assemblage, the North American Neogene ichthyofauna is modern enough in composition to derive precise and quantified climatic information relating to the time of deposition. Although Paleogene fish ranges are not currently as well known, the precision of the palaeoclimatic indications derived from fish assemblages can be expected to progressively extend further back through time, as the ranges of more archaic fish groups become better understood.

Palaeobiogeographically Significant Range Extensions

The assemblages described here have several important implications for the palaeobiogeography of specific taxa, representing the first occurrence of these fishes outside of the range they were previously thought to occupy, or their first appearance in North America. These occurrences and their significance are summarised here.

The lepisosteid and amiid material recovered in the Miocene Wood Mountain Formation (16.4 to 14.6 Ma) represents the latest occurrence of these fishes in the western interior of Canada (Divay and Murray, 2013; Chapter 2). Both taxa had previously been unknown from the area since the Oligocene (Grande and Bemis, 1998; Grande, 2010). Their presence in the western interior during the Miocene demonstrates that their range became more restricted later than previously thought, in the late Neogene. This time period is one of gradually cooling climates (Zachos et al., 2008), which may therefore have caused the restriction of the ranges of these fishes.

The presence of probable amblyopsids in both the Wasatch and Cypress Hills assemblages (Chapters 5 and 3) indicates that the family was widespread both longitudinally and latitudinally in the Paleogene. Currently, amblyopsids are limited to restricted areas in the central United States (Murray, 1994), which Niemiller et al. (2012) hypothesized to represent relict ranges in Pleistocene periglacial refugia. Therefore, this evidence that amblyopsids were more widespread in the Paleogene provides important support to Niemiller et al.'s (2012) hypothesis, although the absence of this taxon in the Miocene Wood Mountain Formation may indicate that its range had become more restricted prior to the Pleistocene glaciations, in the early Neogene.

The late Eocene to early Oligocene Cypress Hills Formation also contains the first occurrence of *Mioplosus* outside of the Green River Formation (Chapter 3). Although this does not represent a large extension of the stratigraphic range of the genus, as *Mioplosus* has been found in Green River Formation deposits spanning from the late Paleocene to the late middle Eocene (Grande, 2001), this does indicate that *Mioplosus* had a wider geographic range than previously thought. The Cypress Hills Formation is much further north than the Green River Formation, indicating that *Mioplosus* was not latitudinally restricted to the southern United States, which may also indicate that the climate was more favourable at the time.

Lastly, the Wood Mountain Formation *Stizostedion* material (Chapter 2) is biogeographically significant, representing the oldest unambiguous percid material in North America (Murray and Divay, 2011). Previously, the oldest evidence of the family was from the Pliocene (5 or 4 Ma) of Ellesmere Island, Canada (Murray et al., 2009), and was also attributed to *Stizostedion* (as *Sander*). The Wood Mountain material (16.4 to 14.6 Ma) further demonstrates that percids had dispersed to North America prior to the Pliocene, in the mid Miocene or earlier (Murray and Divay, 2011).

Stratigraphic Range Extension and Molecular Clock Calibration

In addition to their palaeobiogeographical significance, several first occurrences extend the stratigraphic ranges of specific taxa. Such occurrences may also have implications for molecular clock estimates for the timing of divergence events between modern taxa.

The presence of probable amblyopsid remains in both the Wasatch and Cypress Hills assemblages represent the first and only fossil remains of the family (Chapters 5 and 3), suggesting that it had diverged from the rest of the Percopsiformes in the early Eocene at the latest. Dillman et al. (2011) obtained molecular clock estimates that also place the origin of the family in the Eocene. However, the estimated divergence time for the family obtained using molecular evidence is in the late Eocene, at approximately 33.9 Ma, consistent with the depositional period of the Eastend area of the Cypress Hills Formation (37–30 Ma), but younger than the early Eocene Wasatch assemblage (55–53 Ma). If this molecular-derived timing is correct, it may indicate that the morphological features of the fossils that led to their identification as probable amblyopsids are plesiomorphic features, found in other members of the order and not indicative of the family. Nevertheless, these features are unique to amblyopsids among the material examined, and no other percopsiform was observed to have a similar morphology. Alternately, the molecular clock estimate proposed by Dillman et al. (2011) may be an underestimate of the age of the Amblyopsidae, as was the case with previous molecular clock estimates for the age of North American percids (Murray and Divay, 2011).

The first evidence of North American percids is represented by the approximately 15 million year old remains of *Stizostedion* in the Wood Mountain assemblage (Murray and Divay, 2011). Previously, molecular clock estimates had placed the divergence between North American and Eurasian *Stizostedion* species at approximately 10 Ma (Billington et al., 1990; 1991), or as recently as 4 Ma (Faber and Stepien, 1998). The Wood Mountain fossils demonstrated that all of these were underestimates of the colonisation of North America by *Stizostedion*. A more recent molecular clock study, not calibrated with the North American *Stizostedion* fossils, has found results more congruent with the fossil evidence, estimating the divergence event at approximately 15.4 Ma (Haponski and Stepien, 2013), corresponding to the estimated depositional period of the Wood Mountain Formation, between 16.3 and 13.6 Ma.

The probable moronid centra described from the Cypress Hills Formation (Chapter 3) may represent the earliest North American occurrence of this family. This depends on the affinities of "*Priscacara*", which has been suggested to represent a moronid (Whitlock, 2010), and has been recovered in much older deposits, in the Maastrichtian Hell Creek Formation of Montana (Brinkman et al., 2014). Nevertheless, the oldest reliable occurrence of the Moronidae in North America is in the Piacenzian (3 Ma) Sand Draw local fauna of Nebraska (Böhme and Ilg, 2003). The Wood Mountain and Cypress Hills material is morphologically much more similar to *Morone* than to "*Priscacara*", and therefore this material probably represents the first occurrence of relatives of modern North American moronids, predating the Piacenzian material by approximately 30 Ma.

FIGURE 6.1. Occurrence of fish taxa in North America since the Mesozoic, and formation of the modern ichthyofauna. Star symbols indicate the presence of a fish taxon in the assemblages studied (Chapters 2–5): in the Wasatch assemblage (black circled star), in the Bridger assemblage (white circled star), in the Cypress Hills assemblage (solid black star), and in the Wood Mountain assemblage (hollow star). Shaded bar segments indicate the extension of known stratigraphic ranges based on the findings of this thesis; dashed lines indicate hypothetical stratigraphic range extensions based on newly proposed identifications of previously published fossils.

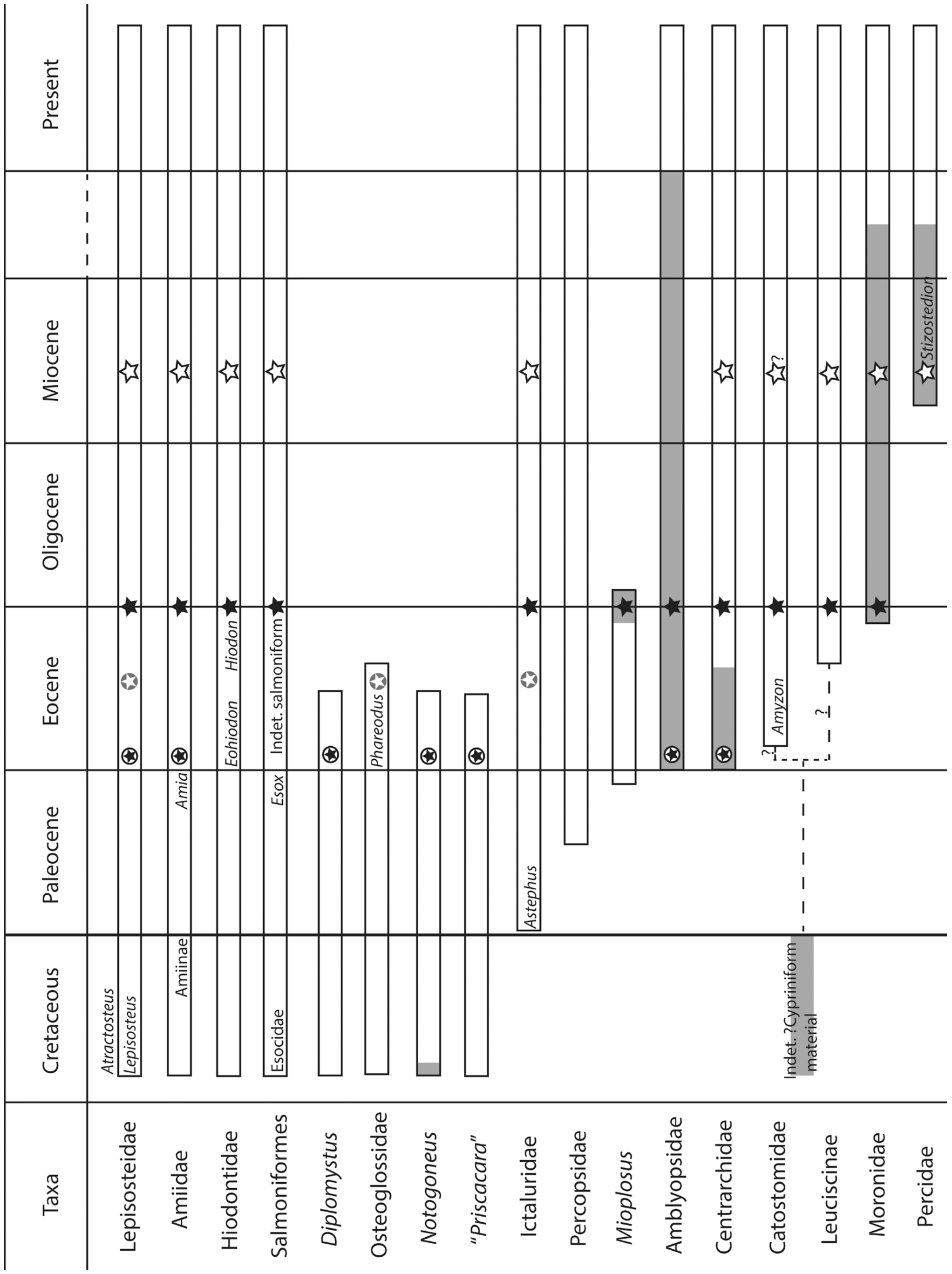

Taxa
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Present
Lepisosteidae
Amiidae
Hiodontidae
Salmoniformes
Diplomystus
Osteoglossidae
Notogoneus
"Priscacara"
Ictaluridae
Percopsidae
Mioplosus
Amblyopsidae
Centrarchidae
Catostomidae
Leuciscinae
Moronidae
Percidae
Atractosteus
Lepisosteus
Amiinae
Amia
Eohiodon
Hiodon
Esocidae
Esox
Indet. salmoniform
Phareodus
Astephus
Amyzon
Indet. ?Cypriniform material
Stizostedion
?

FIGURE 6.2. Cross-section of a generalised floodplain, showing the various sub-environments typically represented. The lateral floodplain is represented by shallow backwaters that may be isolated from active river channels. As a result, these environments may be hypoxic, and are susceptible to dry up if they remain isolated over long periods of time. The remainder of the lateral floodplain is represented by secondary channels that are seasonally connected to active primary channels. Such environments are typically shallow, vegetated, normoxic, slowly flowing waters. Main channels are permanent, and typically represent the deepest environments in a floodplain.

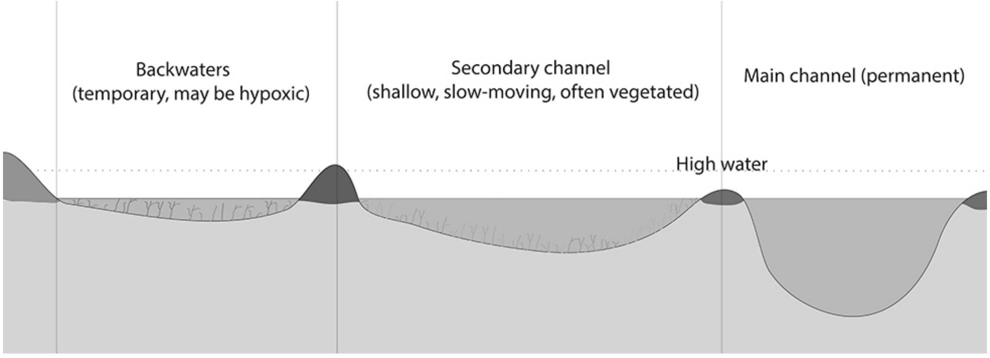

Backwaters
(temporary, may be hypoxic)
Secondary channel
(shallow, slow-moving, often vegetated)
Main channel (permanent)
High water

FIGURE 6.3. Palaeoenvironmental indications of the fishes indentified in the Eocene Farson Cutoff Fishbed assemblage, Bridger Formation of Wyoming. All of the taxa represented in this locality are tolerant to hypoxia, the locality was therefore probably deposited in shallow isolated backwaters on the lateral floodplain.

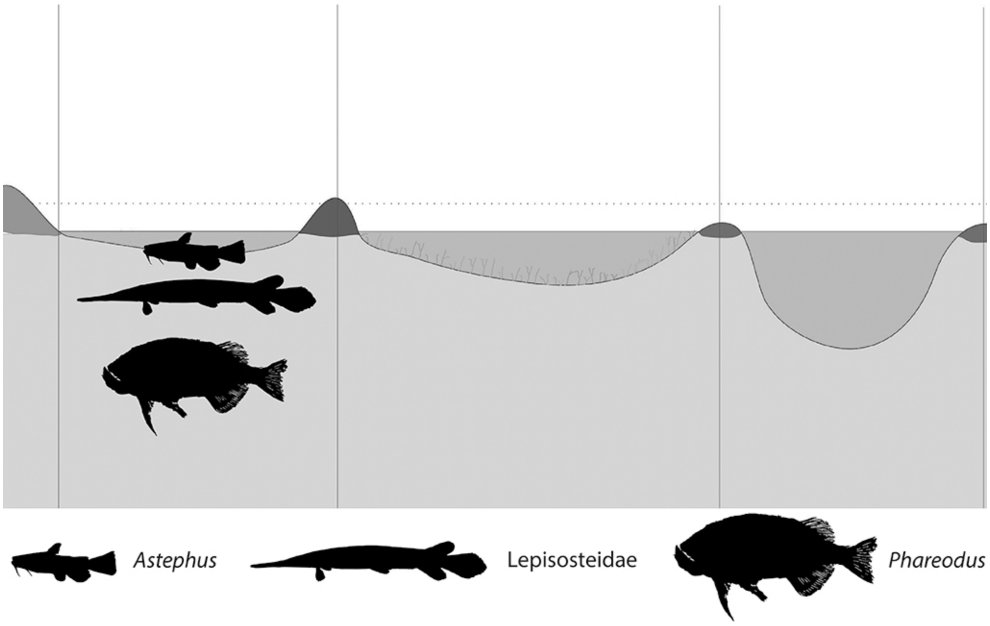

Astephus
Lepisosteidae
Phareodus

FIGURE 6.4. Palaeoenvironmental indications of the fishes identified in the early Eocene Wasatch Formation assemblage recovered from Barb’s Saddle locality, Wyoming. The presence of amblyopsids and centrarchids indicates that the environment was predominantly normoxic, and the small sizes of the individuals represented indicate a shallow depositional environment. The locality was therefore probably deposited in shallow, slow-moving waters that remained connected to active river channels.

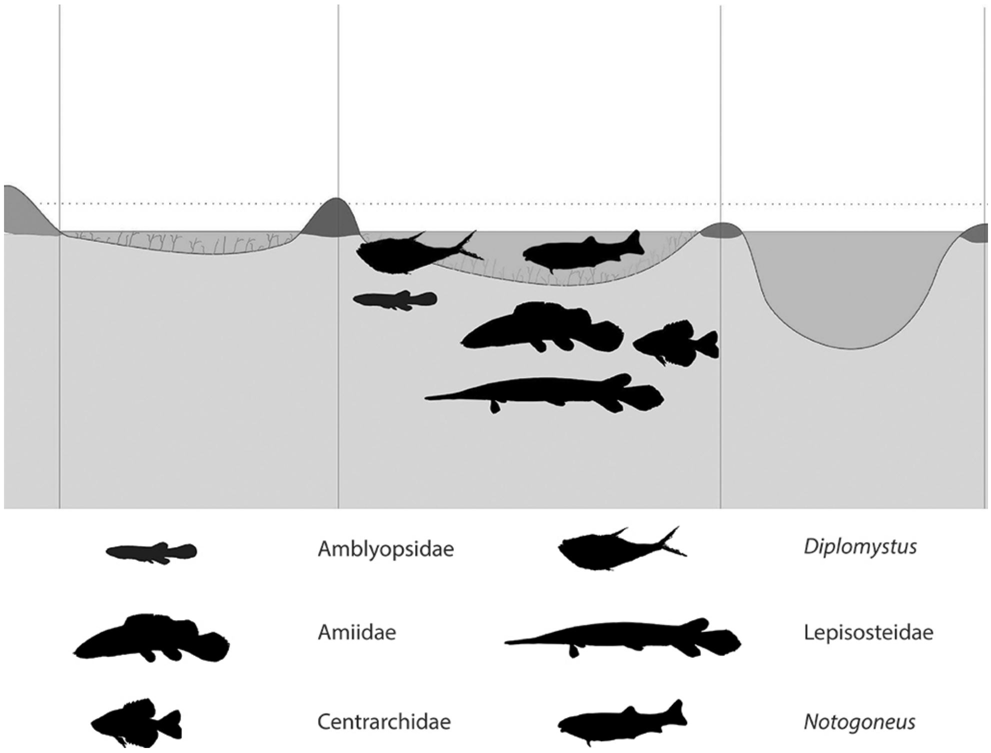

Amblyopsidae
Diplomystus
Amiidae
Lepisosteidae
Centrarchidae
Notogoneus

FIGURE 6.5. Palaeoenvironmental indications of the fish diversity recovered from the Eo-Oligocene Cypress Hills Formation assemblage of Saskatchewan. The high taxonomic diversity of this assemblage indicates the presence of several sub-environments in the floodplain. Several taxa recovered are tolerant to hypoxic conditions (lepisosteids, amiids, ictalurids), and probably indicate the presence of shallow isolated backwaters on the lateral floodplain. The large size of some taxa (*Astephus* taxon A and *Mioplosus*) indicates the availability of deep environments, such as may be found in primary channels. Taxa typical of shallow, normoxic, vegetated, slow-moving waters (cypriniforms, amblyopsids, centrarchids) probably indicate the presence of secondary channel-type environments.

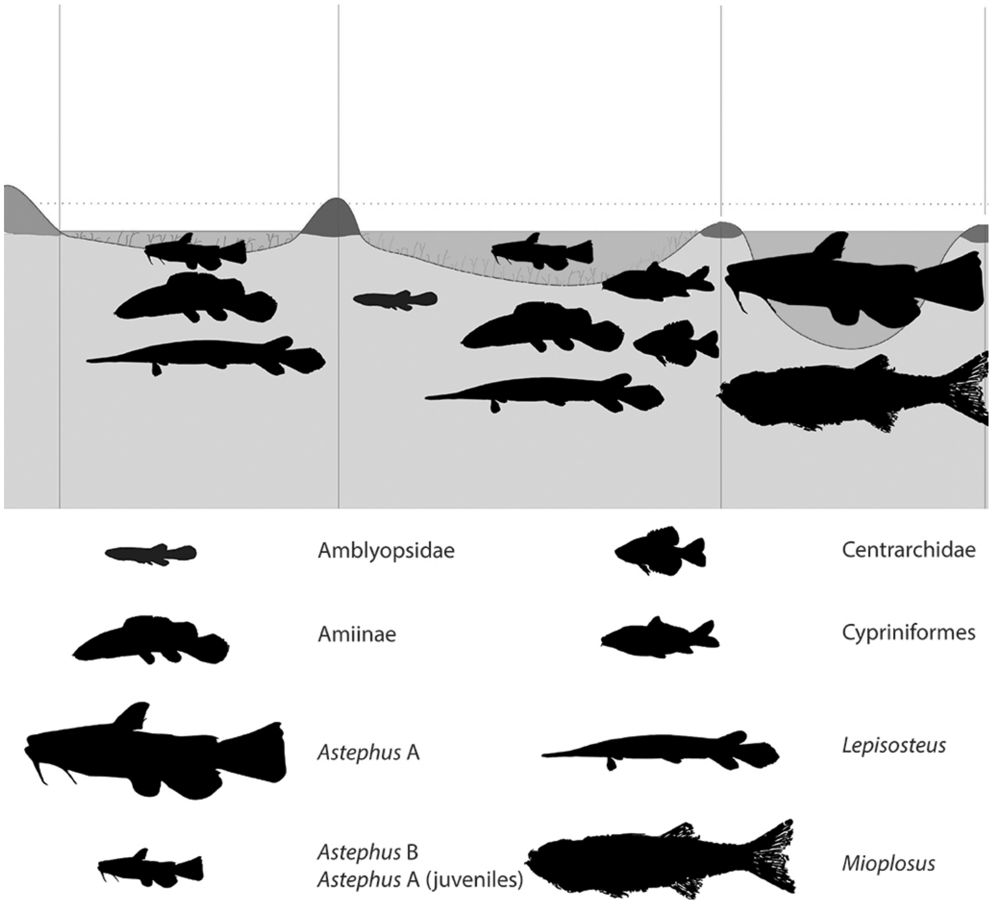
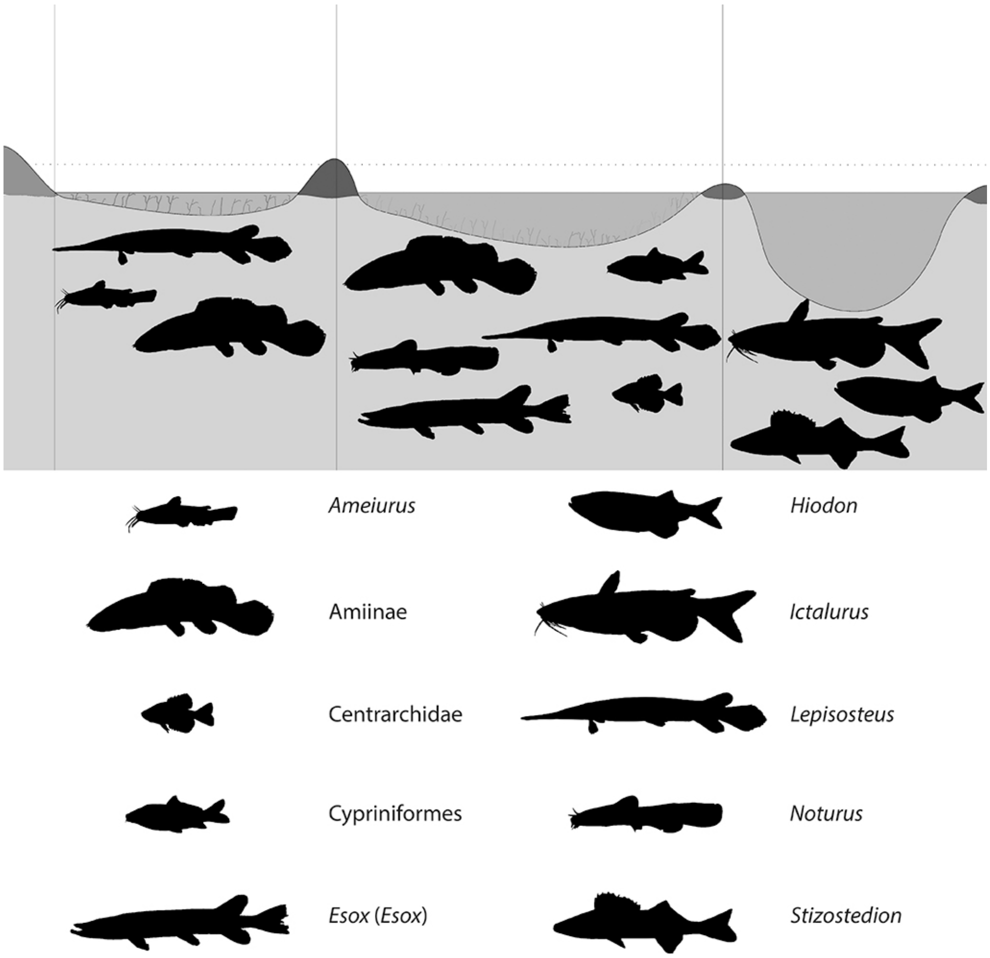

Amblyopsidae
Centrarchidae
Amiinae
Cypriniformes
Astephus A
Lepisosteus
Astephus B
Astephus A (juveniles)
Mioplosus

FIGURE 6.6. Palaeoenvironmental indications of the fish diversity recovered in the mid-Miocene Wood Mountain Formation assemblage of Saskatchewan. Deep, primary channel-type environments are indicated by the presence of *Hiodon*, *Ictalurus* and *Stizostedion*. Shallow and normoxic environments are indicated by cypriniforms, *Noturus*, *Esox* (*Esox*), and centrarchids. *Lepisosteus*, amiines and *Ameiurus* probably indicate the presence of shallow—possibly hypoxic—backwaters.


Ameiurus
Amiinae
Centrarchidae
Cypriniformes
Esox (*Esox*)
Hiodon
Ictalurus
Lepisosteus
Noturus
Stizostedion

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APPENDIX 6.1. Proposed synapomorphies of the fish elements preserved in the microvertebrate localities studied in this thesis. Based on comparisons between the microvertebrate material included in this thesis and a combination of fossil and recent comparative material, several morphological features were identified that may be characteristic of certain clades of fishes, and are interpreted here as possible synapomorphies. The fish taxa identified in all four assemblages studied are listed here, with a summary of the material recovered representing them, and any phylogenetically informative features that were identified.

Lepisosteiformes

Lepisosteiform material was recovered from all four assemblages included here, although the Wasatch lepisosteiform material was not described. All of the material is referable to the Lepisosteidae, representing either *Lepisosteus* or *Atractosteus*, when it could be ascribed to a particular genus. This taxon is represented by a lacrimomaxillary bone (sensu Grande, 2010), scales, and abdominal centra; several isolated teeth probably represent lepisosteids as well. The material included did not allow the recognition of phylogenetically informative features other than those given by Grande (2010).

Amiiformes

Amiiform material was found in assemblages from the Wood Mountain, Cypress Hills and Wasatch formations, although the Wasatch amiiform material was not included in this thesis. All of this material represents the

Amiidae, and, where the material allowed a more precise attribution, all of it could be referred to the Amiinae. Amiiforms are represented by a maxilla, a dentary, a coronoid toothplate (sensu Grande and Bemis, 1998), and both abdominal and caudal centra. None of the features recognised in this material refined the descriptions of Grande and Bemis (1998).

Osteoglossiformes

The only osteoglossiform material included in this thesis was recovered from the Bridger Formation. All of the material was referred to *Phareodus*, but did not allow specific attributions according to the criteria of Li (1994) and Li et al. (1997a). Premaxillae, maxillae, dentaries, anterior and posterior basibranchial toothplates, basioccipitals, first centra of the vertebral series and more posterior abdominal centra were described.

The characteristic features of osteoglossomorph centra described by Brinkman and Neuman (2002) are supported by comparisons of this osteoglossiform material with the only other osteoglossomorph taxon included in this thesis, the Hiodontiformes. These features are fused parapophyses and autogenous neural arches in most abdominal centra. However, this general morphology is not unique to the Osteoglossomorpha, as noted in Brinkman et al. (2013), and is not observed in all osteoglossomorph abdominal centra. The first centrum is of different—and unique— morphology, and the posterior-most abdominal centra may have fused neural arches, at least in the Osteoglossiformes.

Furthermore, several vertebral features appear to differentiate osteoglossiform fishes from the Hiodontiformes. As described by Brinkman and Neuman (2002), the neural arch pits of osteoglossiforms are deeper and characteristically rectangular. These pits also extend for the full length of the centrum, instead of being shallow, circular and restricted to the anterior part of the centrum, as in hiodontiforms. The first centrum is of distinctive morphology in the osteoglossiformes, and the articulation of the first centrum with the basioccipital is characteristic in this taxon. The first centrum is distinctive from other abdominal centra in its circular neural arch pits, in lacking parapophyses, and in possessing a pair of deep articular pits on its ventral surface. These ventral pits accommodate a posterior projection of the basioccipital, which is a condition unique to these fishes among all of the material examined. Therefore, this condition is probably synapomorphic of osteoglossiforms within the Osteoglossomorpha.

Hiodontiformes

Hiodontiform material was recovered from the Wood Mountain and Cypress Hills formations. Material representing or having affinities with *Hiodon* was recovered from both of these formations, while a different and unidentified probable hiodontiform was also recovered from the Wood Mountain Formation. *Hiodon* is represented by first and more posterior abdominal centra, while the unidentified hiodontiform is represented by a single abdominal centrum.

Comparisons with osteoglossiform material support Brinkman and Neuman's (2002) proposal that hiodontiforms are different from other osteoglossomorphs in their relatively shallow neural arch pits. These pits are also characteristically circular, and relatively small, being restricted to the anterior part of the centrum. The first centrum of *Hiodon* is also unique among all of the material examined in its possession of two pairs of anterior articular facets for articulation with the exoccipitals and basioccipital.

Within the Hiodontiformes, the length of the parapophyses seems to be diagnostic, since the Wood Mountain indeterminate hiodontiform possesses much shorter parapophyses than *Hiodon*, although this characteristic may vary along the vertebral series. Furthermore, the Cretaceous hiodontid material described by Brinkman and Neuman (2002) lacks the accessory pits observed above the parapophyses on the lateral surface of the *Hiodon* material described in this thesis. Because this pit is also seen in the modern comparative material, this feature may be diagnostic of the genus. However, the presence or absence of these pits in *Eohiodon* could not be determined, therefore it is currently unknown whether this feature is synapomorphic of *Hiodon* or whether it is present in a wider clade of related taxa that excludes Mesozoic hiodontids.

Ellimmichthyiformes

Ellimmichthyiform material was only recovered from the Wasatch Formation. All of this material was referred to *Diplomystus*. Dentaries, basioccipitals and abdominal centra were recovered in the assemblage.

The restriction of the tooth-bearing surface to the anterior end of the dentary is a characteristic feature of this taxon, and is unique among the comparative material examined. Likewise, the basioccipitals differ from those of all other taxa examined in their dorso-posterior facets for articulation of the exoccipitals and in the dorsally and anteriorly widening lateral sheets of bone. The centra support Brinkman et al.'s (2013) description of a general centrum morphology similar to that of osteoglossomorphs, with fused parapophyses and autogenous neural arches. However, the neural arches articulate within shallow articular pits that are unique among the material examined in their distinctively triangular shape.

All of these features may be synapomorphies of *Diplomystus* and related taxa, but none appear to be features found throughout the Ellimmichthyiformes, although the basioccipital of most of these fishes is of unknown morphology. Furthermore, that the centra of some ellimmichthyiforms, such as *Horseshoeichthys*, have circular neural arch articular pits (Newbrey et al., 2010) implies that the general morphologies of ellimmichthyiform and hiodontiform centra is similar in some taxa of both orders. The differentiation of these taxa therefore requires detailed comparisons, and cannot rely on the presence of discrete morphological features.

Gonorynchiformes

The Wasatch Formation assemblage was the only one found to include gonorynchiform elements, all of which are similar to *Notogoneus*. This material includes basioccipitals, anterior abdominal centra modified to form the primitive Weberian apparatus characteristic of this order of fishes, and more posterior abdominal centra.

The basioccipital and post-Weberian abdominal centra could be identified based on morphological details, but do not possess discrete anatomical features that could be proposed to be synapomorphic for the order. The basioccipital is superficially similar to that of certain siluriforms, and the post-

Weberian abdominal centra have a general morphology that resembles that of leuciscine cypriniforms, with fused neural arches and triangular articular pits on their ventro-lateral margins. Furthermore, the morphology of post-Weberian centra of *Notogoneus* appears to vary depending on the size of the individual, making it difficult to recognise discrete morphological features allowing their identification.

In contrast, centra modified to form the Weberian apparatus are highly distinctive. The dorsal surface bearing nearly circular articular pits for the autogenous neural arch at mid-length of the centrum is particularly characteristic of this centrum morphology. Because centra of similar morphology to the Wasatch specimens are found in Mesozoic assemblages (e.g., Brinkman et al., 2013:fig. 10.26; Brinkman et al., 2014:fig. 10C) and in modern gonorynchiforms such as *Chanos*, this centrum morphology appears to have been retained throughout the evolution of Gonorynchiformes. Therefore, this morphology may be a synapomorphy of the order.

Cypriniformes

Cypriniforms are absent from both the Bridger and Wasatch assemblages studied here, but are abundantly represented in the Wood Mountain and Cypress Hills formations. This material is relatively non-diagnostic at low taxonomic levels, however, and most of it could only be attributed to family and sub-family levels. Both formations preserve material that either represents a cryprinine cyprinid or a catostomid of cyprinine-like morphology. In addition to this material, the Cypress Hills assemblage preserves material that can be more reliably attributed to the Catostomidae. Both formations also have leuciscine cyprinid material, with the Cypress Hills fossils representing a taxon with affinities to *Ptychocheilus*, while the Wood Mountain material cannot be attributed to a particular genus. All of the cypriniform material recovered corresponds to abdominal centra, including the first and second Weberian centra, and post-Weberian abdominal centra.

The first Weberian centra of cypriniforms have a highly diagnostic disc shape, although it is less pronounced in leuciscines, where the centrum is slightly longer than in cyprinines or catostomids. The transverse processes may be indistinct, or project either dorso-laterally or ventro-laterally. The dorsal surface of these centra bears circular pits for articulation with the scaphium, while the ventral surface lacks processes. This general morphology appears to be unique, and may represent a synapomorphic character for this order. The second Weberian centrum is also highly diagnostic, having an anterior articular surface that is larger than the posterior articular surface, and very large articular pits that occupy the entire dorsal surface of the centrum, for articulation with the autogenous neural arch. This centrum morphology also seems to be unique to the Cypriniformes. Post-Weberian abdominal centra have a general morphology that is similar to that of gonorynchiform abdominal centra. The neural arch is fused to the centrum, and the autogenous parapophyses articulate within pits on the ventral half of the lateral surface. This general similarity with gonorynchiforms and the variability of morphological details among cyprinid subfamilies precludes the identification of characters synapomorphic to the Cypriniformes in these centra. That the post-Weberian centra of catostomids and cyprinine cyprinids are morphologically identical and different from those of leuciscine cyprinids probably indicates that this is a primitive condition. If this is the case, the derived morphology of leuciscines was acquired after they diverged from cyprinines, while catostomids and cyprinines retained the symplesiomorphic morphology.

Catostomidae—The only reliably identified catostomid material was recovered from the Cypress Hills Formation, and consists of first and second Weberian centra. The first Weberian centrum of catostomids is of unique morphology, and can be differentiated from that of cyprinids. In catostomids, the centrum is different from that of leuciscines in being shorter and more disc-like. The transverse processes of catostomids are either indistinct, or project laterally from the dorso-lateral margins of the centrum, whereas those of cyprinines project from the ventro-lateral margins of the centrum. These morphological differences may therefore allow the differentiation of these families and sub-families. However, Weberian centra of cyprinine morphology in the Wood Mountain and Cypress Hills formations, at a time when no other evidence for the North American presence of cyprinines is known, may indicate that some extinct catostomids may have had a more cyprinine-like morphology. If this were the case, the cyprinine-like morphology of the first Weberian centrum may represent a primitive character in catostomids.

The second Weberian centrum of cypriniforms retains the same general morphology throughout the order, and catostomids cannot be differentiated based on discrete morphological characters of this centrum. In cases where catostomid first centra are recovered, however, similarities between the shapes of the articular surfaces at the posterior end of the first centrum and at the anterior end of the second centrum may allow the identification of catostomid second centra. An example of such a case is the material recovered from the Cypress Hills assemblage studied in this thesis.

Post-Weberian abdominal centra have a highly characteristic morphology, with fused neural arches and autogenous parapophyses articulating in large pits that occupy the entire ventral half of the lateral surface of the centrum. The rest of the lateral surface has a single accessory pit bisected by a low bony strut connecting the parapophysis with the base of the neural arch. However, this morphology is also observed in cyprinines, therefore it cannot be reliably used to determine catostomid presence in the absence of more diagnostic material.

Leuciscinae—Leuciscines were recovered in both Wood Mountain and Cypress Hills assemblages, where these fishes are represented by post-Weberian abdominal centra. These post-Weberian centra are of similar general morphology to those of gonorynchiforms, with fused neural arches and triangular articular pits on the anterior part of the ventral lateral surface, for articulation with the parapophyses. Therefore, although detailed comparisons allow the identification of leuciscine centra, this material has no discrete synapomorphy allowing its identification.

Siluriformes

The Wood Mountain, Cypress Hills and Bridger assemblages all contain siluriform material. Although all of this material can be attributed to a single family, the Ictaluridae, it is diverse at the generic level, representing a probable species of *Noturus* as well as *Ictalurus* and *Ameiurus* in the Wood Mountain Formation, while the Cypress Hills and Bridger assemblages preserve at least three different species of *Astephus*. The material includes a parasphenoid, dentaries, articulars, basioccipitals, a fragmentary cleithrum, pectoral fin spines, dorsal fin spines, Weberian centra and post-Weberian abdominal centra.

Although all ictalurid elements share the same general morphologies, detailed comparisons are highly diagnostic at the generic level. Cranial bones, elements of the appendicular skeleton and fin spines can be identified based on the characters described by Lundberg (1975) and Cumbaa (1978). Vertebrae are also generally similar among the genera found in these assemblages, being holospondylous and therefore lacking articular pits. The first centrum is the only exception, articulating with the scaphium in a pair of dorsal pits. Although this first centrum is superficially similar to that of cypriniforms in being disc-shaped, it possesses a characteristic pair of ventral processes for articulation with the complex vertebra of the Weberian apparatus, which allows its differentiation from cypriniform material. All genera are also similar in that the parapophyses and neural arches fuse in the anterior post-Weberian abdominal centra, which is a characteristic unique to siluriforms among the comparative material examined. However, genera can be differentiated based on their shape in end view and on the shape of accessory pits, where present. Growth marks were also shown to be effective in differentiating congeneric species in centra that could not be differentiated in any other way.

Salmoniformes

Salmoniform material was recovered in both the Wood Mountain and Cypress Hills assemblages. All of the Wood Mountain material was attributed to *Esox* (*Esox*), while all of the Cypress Hills material represents an unidentified probable salmoniform taxon. The Wood Mountain *Esox* material includes isolated teeth, a basioccipital, first centra, as well as abdominal and caudal centra. The unidentified Cypress Hills salmoniform is only represented by abdominal centra.

The salmoniform characteristics of the centra recovered in these assemblages are similar to those identified by Brinkman and Neuman (2002). Both neural arches and parapophyses are autogenous and articulate in pits of equal sizes and similar morphologies in all abdominal positions apart from the first centrum, which lacks parapophyseal articular pits. Salmoniform centra also have characteristic ridges extending along the inside of the neural arch and parapophyseal articular pits at mid length, towards the core of the centrum. This feature is unique among the material examined, and is visible in extant and Cenozoic specimens, as well as in Cretaceous material (e.g., Brinkman and Neuman, 2002:fig. 2; Brinkman et al., 2013:fig.10.25; Brinkman et al., 2014:fig.7). It may therefore represent a synapomorphy of the Salmoniformes. In addition to these ridges, the articular pits on the abdominal centra of the indeterminate salmoniform from the Cypress Hills are subdivided by longitudinal ridges of bone. This morphology is unique and may represent a diagnostic characteristic of a primitive group of salmoniforms. The caudal centra of the Cypress Hills salmoniform are unknown, but those of the Wood Mountain *Esox* and of extant salmoniforms are holospondylous, with fused neural and haemal arches, therefore this may be a characteristic of the order.

Esocidae—Detailed morphological comparisons are required to distinguish esocids and salmonids based on centra, because both have similar general morphologies. No discrete morphological feature was found to be unique to esocids within the Salmoniformes among the material studied. However, several characteristics were found to differentiate the basioccipital and centra of the two esocid subgenera recognised by Grande et al. (2004), *Esox* (*Esox*) and *Esox* (*Kenoza*). The basioccipital of *Esox* (*Esox*) is laterally tapering and the pits on the dorsal surface are rectangular, whereas wide facets form the lateral surfaces of the basioccipital in *Esox* (*Kenoza*), and the dorsal pits are laterally constricted and hourglass-shaped. The parapophyseal articular pits on the abdominal centra of *Esox* (*Kenoza*) are transverse and hourglass shaped, while these pits are longitudinal and rectangular in *Esox* (*Esox*), allowing their differentiation. Likewise, the caudal centra of *Esox* (*Kenoza*) are recognisable in being laterally restricted at mid-length, while those of *Esox* (*Esox*) remain of similar width throughout their full length.

Percopsiformes

Percopsiforms were found in both the Cypress Hills and Wasatch assemblages. All were attributed to amblyopsids, representing a single taxon in the Cypress Hills Formation, and up to three different taxa in the Wasatch Formation. The material represents abdominal centra, including first centra.

First centra are most diagnostic, possessing the tripartite anterior surface for articulation with the exoccipitals and the basioccipital that is characteristic of acanthomorphs (sensu Stiassny, 1986), and having fused neural arches. Among all of the fossils described here, this combination of characters was only observed in percopsiforms, although it is also present in other taxa included in the Paracanthopterygii (sensu Greenwood et al., 1966). In addition to this, percopsiforms have larger facets for articulation with the exoccipitals than the other acanthomorphs described, and these facets are more widely flared and project anteriorly more markedly from the rest of the centrum in percopsiforms. Most abdominal centra can be recognised based on a suite of characters; however, these bones lack a single discrete morphological feature differentiating them from those of other acanthomorphs. Percopsiform centra are holospondylous, which is a typical acanthomorph general morphology, but percopsiform centra are characteristically longer than those of most other acanthomorphs. Additionally, the parapophyses of percopsiforms are restricted to the anterior end of the centrum, where they project laterally. A longitudinal bony strut extends from the base of the parapophysis to the posterior end of the centrum. Although this morphology seems to be unique to percopsiforms, anterior-most abdominal centra may be shorter than more posterior centra, and those of percopsiforms may be indistinguishable from those of other acanthomorphs.

The lack of synapomorphies clearly identified for percopsiforms may be due to the restricted diversity of the comparative material used. The only specimens that could be accessed were percopsids, and the only modern genus available for comparisons was *Percopsis*; all other taxa could only be observed through previously published illustrations (e.g., Murray, 1994). The relative rarity and small size of percopsiform fossils precluded the use of the mechanical extraction and acid preparation technique employed on *Diplomystus dentatus* specimen TMP 1986.224.0135. Further observations of more diverse percopsiforms may allow the recognition of diagnostic morphological features for the order in the future.

Amblyopsidae—The percopsiform material recovered in both Cypress Hills and Wasatch formations can be differentiated from percopsid material based on comparisons with *Percopsis* and illustrations of the first centra of other percopsiform families (Murray, 1994:figs. V-8–V-10). Amblyopsid first centra are unique among the Percopsiformes in that the articular plane of the facets for articulation with the exoccipitals is similar to that of the surface for articulation with the basioccipital. Amblyopsid first centra are also much longer, with near-circular facets for articulation with the exoccipitals that project further anteriorly in amblyopsids than in other percopsiforms.

Abdominal centra were identified based on percopsiform characters. The lack of amblyopsid comparative material precluded the identification of uniquely amblyopsid characters.

Perciformes

Diverse perciform material was found in the Wood Mountain, Cypress Hills and Wasatch assemblages. This material represents moronid, centrarchid and percid fishes, some of which could be identified at the generic level. In the Wood Mountain Formation, some of the centrarchid material could be identified as having affinities with *Pomoxis*, while some of the percid material was identified as the first North American occurrence of *Stizostedion*. In the Cypress Hills material, the only perciform identifiable to genus was *Mioplosus*. None of the material from the Wasatch Formation could be unequivocally attributed to a particular genus, although it is probable that some of it represents "*Priscacara*".

Perciforms are represented by a variety of bones, including premaxillae, vomers, dentaries, one fifth ceratobranchial, and abdominal centra, including first centra of the vertebral series. Perciform cranial material was identified through detailed comparisons, being too diverse to be identified based on a discrete morphological feature. First centra are characteristic among the fossils recovered in having the characteristic acanthomorph (sensu Stiassny, 1986) tripartite anterior articular surface for articulation with the exoccipitals and the basioccipital as well as autogenous neural arches. Posterior to the first centrum, the holospondylous abdominal centra have a suite of characteristics allowing their identification, but have a general morphology similar to that of other acanthomorphs. Anterior-most abdominal centra have dorso-lateral rib articular pits, hook-like dorsal prezygapophyses and widely flared dorso-lateral postzygapophyses. More posterior abdominal centra have fused parapophyses forming the anterior margin of the rib articular pit which gradually become lateral, then ventro-lateral in position. The size and shape of the parapophyses, the presence or absence of accessory pits, and the surface texture of the bone surfaces allow the attribution of these abdominal centra to lower taxonomic levels, but this general morphology is retained within the perciform fossil material recovered.

Mioplosus—The Cypress Hills assemblage is the only one included here that was found to contain *Mioplosus*. All of these elements were abdominal centra, including some characteristic anterior-most centra.

The anterior-most abdominal centra are highly distinctive, being the only non-Weberian centra among the material examined to have a distinctly larger articular surface at the anterior end than at the posterior end of the centrum.

This larger anterior articular surface is formed by the articular surface projecting ventrally from the ventral side of the centrum, which is also a unique feature of this centrum type among all of the material examined. More posterior abdominal centra are characterised by much shorter parapophyses than any other perciform centra examined, as well as very shallow and triangular rib articular pits that are not seen in any other perciform centra.

This morphology is unique to *Mioplosus* and markedly unlike that of any percid examined. This may undermine the placement of *Mioplosus* within the Percidae, as was suggested by several authors (e.g., Cope, 1877; Woodward, 1901; Grande, 1984). However, these centra are different from all of the comparative material examined, therefore *Mioplosus* may be a particularly derived member of a family represented in the comparative material used in this study, or may represent a relative of a family that was not included in the comparative material used, as was suggested by other authors, such as latids (Whitlock, 2010), or percichthyids (Cavender, 1986).

Moronidae—Moronid material was recovered in the Wood Mountain and Cypress Hills formations, and represents abdominal centra. These are distinctive and can be differentiated from other perciforms by having neural arches that are more robustly attached at the ends of the centrum, and parapophyses of unique morphology, being broad and wing-like.

Centrarchidae—Centrarchid material represents the majority of the perciform material identified. Premaxillae, vomers, dentaries, a fifth ceratobranchial, and abdominal centra, including first centra of the vertebral series, were identified. Centra are very similar to percid material, but first centra can be recognised by the facets for articulation with the exoccipitals being broadly joined medially. The posterior margin of these facets also projects from the surface of the centrum, forming a transverse ridge that is not as developed in percid material. More posterior abdominal centra have no feature allowing their differentiation from percid centra, and can only be identified if they can be associated with the more diagnostic first centra, through similarities of the bone surface texture, for instance. Accessory pits, where present, allow the differentiation of centrarchid genera.

This centrum morphology precisely corresponds to that of "*Priscacara*", which were also found to be centrarchid-like in the morphology of several cranial elements, including the vomer, dentaries and fifth ceratobranchials. However, the phylogenetic placement of "*Priscacara*" has been problematic, with Grande (2001) further questioning the monophyly of the genus. Most recently, affinities with the Moronidae were suggested by Whitlock (2010), forming a clade united on the basis of characters that cannot be observed in the material included in this thesis. This is either because the characters relate to elements which were not recovered in the assemblage (e.g., scales) or to the loss of features (e.g., supramaxillary bones). Based on the morphology of the bones that were recovered in the assemblage, however, "*Priscacara*" material lacks the characters that were used to identify moronid material, and is indistinguishable from centrarchids. This may indicate that "*Priscacara*" grouped with moronids on the basis of homoplastic characters in Whitlock's (2010) phylogeny, or that centrarchids have retained a centrum morphology that is primitive for several perciform families, including the Moronidae and Percidae.

Percidae—The Wood Mountain Formation was the only one found to have material that could be attributed to the Percidae with certainty, including premaxillae and abdominal centra. First centra can be differentiated from centrarchid material in their possession of a medial separation between the facets for articulation with the exoccipitals. More posterior abdominal centra do not possess discrete features allowing their differentiation from centrarchid centra, and can only be identified if they can be associated with first centra. This may indicate that this centrum morphology is primitive for these families, and was retained from their last common ancestor.

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GENERAL APPENDICES

APPENDIX I—OCCURRENCE OF TAXA IN ALL FOUR STUDIED FORMATIONS

Comparison of the taxonomic composition of assemblages recovered from all four formations studied in this thesis. Material from several localities was combined to form the Wood Mountain (cf. General Appendix II) and Cypress Hills (cf. General Appendix III) assemblages. The Bridger Formation assemblage was recovered from a single locality, UCMP V96246 (cf. General Appendix IV). The Wasatch Formation assemblage also represents material recovered from a single locality, UCMP V70220 (cf. General Appendix V).

	Wyoming, U. S .A.		Saskatchewan, Canada	
	Wasatch Formation	Bridger Formation	Cypress Hills Formation	Wood Mountain Formation
Lepisosteidae	X	X	X	X
Lepisosteus			X	X
Amiinae	X		X	X
?Hiodontiformes				X
Hiodontidae			X	X
Phareodus		X		
Diplomystus	X			
Notogoneus	X			
Cypriniformes			X	X
Catostomidae			X	
Leuciscinae			X	X

	Wyoming, U. S .A.		Saskatchewan, Canada	
	Wasatch Formation	Bridger Formation	Cypress Hills Formation	Wood Mountain Formation
Ictaluridae		X	X	X
Astephus		X	X	
Ameiurus				X
Ictalurus				X
Cf. *Noturus*				X
Salmoniformes			X	X
Esox (*Esox*)				X
Aff. Amblyopsidae	X		X	
Mioplosus			X	
?Moronidae			X	X
?*Priscacara*	X			
Centrarchidae	X		X	X
Cf. *Pomoxis*				X
?Percidae				X
Stizostedion				X

APPENDIX II—WOOD MOUNTAIN FORMATION SPECIMENS

Royal Ontario Museum Specimens (N = 386)

#	Specimen number	Identification	Description	Comments
	Lsd. 16, Sec. 31, Tp. 2, Rge. 30, W. 2nd Meridian, Kleinfelder Farm, Rockglen, Saskatchewan			
1	ROM 63444	Family Amiidae	Fragmentary tooth plate	
2	ROM 64812	Subfamily Amiinae	Abdominal centrum	
3	ROM 64813	Subfamily Amiinae	Abdominal centrum	
4	ROM 64814	Subfamily Amiinae	Caudal centrum	
5	ROM 64815	Division Teleostei	Unidentified centrum	
6	ROM 64816	Division Teleostei	Unidentified caudal centrum	
7	ROM 64817	Division Teleostei	Unidentified caudal centrum	
8	ROM 64818	Division Teleostei	Unidentified caudal centrum	
9	ROM 64819	Division Teleostei	Unidentified caudal centrum	
10	ROM 64820	Division Teleostei	Unidentified caudal centrum	
11	ROM 64821	Division Teleostei	Unidentified caudal centrum	
12	ROM 64822	Division Teleostei	Unidentified caudal centrum	
13	ROM 64823	Division Teleostei	Unidentified caudal centrum	
14	ROM 64824	Division Teleostei	Unidentified caudal centrum	
15	ROM 64825	Division Teleostei	Unidentified caudal centrum	
16	ROM 64826	Division Teleostei	Unidentified caudal centrum	
17	ROM 64827	Division Teleostei	Unidentified caudal centrum	
18	ROM 64828	Division Teleostei	Unidentified caudal centrum	
19	ROM 64829	Division Teleostei	Unidentified caudal centrum	
20	ROM 64830	Division Teleostei	Unidentified caudal centrum	

21	ROM 64831	Division Teleostei	Unidentified caudal centrum
22	ROM 64832	Division Teleostei	Unidentified caudal centrum
23	ROM 64833	Division Teleostei	Unidentified caudal centrum
24	ROM 64834	Division Teleostei	Unidentified caudal centrum
25	ROM 64835	Division Teleostei	Unidentified caudal centrum
26	ROM 64836	Division Teleostei	Unidentified caudal centrum
27	ROM 64837	Division Teleostei	Unidentified caudal centrum
28	ROM 64838	Division Teleostei	Unidentified caudal centrum
29	ROM 64839	Division Teleostei	Unidentified caudal centrum
30	ROM 64840	Division Teleostei	Unidentified caudal centrum
31	ROM 64841	Division Teleostei	Unidentified caudal centrum
32	ROM 64842	Division Teleostei	Unidentified caudal centrum
33	ROM 64843	Division Teleostei	Unidentified caudal centrum
34	ROM 64844	Division Teleostei	Unidentified caudal centrum
35	ROM 64845	Division Teleostei	Unidentified caudal centrum
36	ROM 64846	Division Teleostei	Unidentified caudal centrum
37	ROM 64847	Division Teleostei	Unidentified caudal centrum
38	ROM 64848	Subdivision Osteoglossomorpha	Abdominal centrum
39	ROM 64849	Family Hiodontidae : cf. *Hiodon*	Anterior abdominal centrum
40	ROM 64850	Family Hiodontidae : cf. *Hiodon*	Anterior abdominal centrum
41	ROM 64851	Family Hiodontidae : cf. *Hiodon*	Anterior abdominal centrum

42	ROM 64852	Family Hiodontidae : cf. *Hiodon*	Abdominal centrum
43	ROM 64853	Order Cypriniformes	First centrum
44	ROM 64854	Order Cypriniformes	First centrum
45	ROM 64855	Order Cypriniformes	First centrum
46	ROM 64856	Order Cypriniformes	First centrum
47	ROM 64857	Order Cypriniformes	First centrum
48	ROM 64858	Order Cypriniformes	Abdominal centrum
49	ROM 64859	Order Cypriniformes	Abdominal centrum
50	ROM 64860	Order Cypriniformes	Abdominal centrum
51	ROM 64861	Order Cypriniformes	Abdominal centrum
52	ROM 64862	Order Cypriniformes	Abdominal centrum
53	ROM 64863	Order Cypriniformes	Abdominal centrum
54	ROM 64864	Order Cypriniformes	Abdominal centrum
55	ROM 64865	Order Cypriniformes	Abdominal centrum
56	ROM 64866	Order Cypriniformes	Abdominal centrum
57	ROM 64867	Order Cypriniformes	Abdominal centrum
58	ROM 64868	Order Cypriniformes	Abdominal centrum
59	ROM 64869	Order Cypriniformes	Abdominal centrum
60	ROM 64870	Order Cypriniformes	Abdominal centrum
61	ROM 64871	Order Cypriniformes	Abdominal centrum
62	ROM 64872	Order Cypriniformes (type II)	Abdominal centrum
63	ROM 64873	Order Cypriniformes (type II)	Abdominal centrum

64	ROM 64874	Order Cypriniformes (type II)	Abdominal centrum
65	ROM 64875	Subfamily Leuciscinae	Abdominal centrum
66	ROM 64876	Subfamily Leuciscinae	Abdominal centrum
67	ROM 64877	Family Ictaluridae : *Ameiurus*	First centrum
68	ROM 64878	Family Ictaluridae : *Ameiurus*	Anterior abdominal centrum
69	ROM 64879	Family Ictaluridae : *Ictalurus*	Anterior abdominal centrum
70	ROM 30620	Family Ictaluridae : *Noturus*	Very fragmentary pectoral fin spine
71	ROM 64880	Family Esocidae : *Esox* (*Esox*) sp.	First centrum
72	ROM 64881	Family Esocidae : *Esox* (*Esox*) sp.	First centrum
73	ROM 64882	Family Esocidae : *Esox* (*Esox*) sp.	First centrum
74	ROM 64883	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
75	ROM 64884	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum

76	ROM 64885	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
77	ROM 64886	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
78	ROM 64887	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
79	ROM 64888	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
80	ROM 64889	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
81	ROM 64890	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
82	ROM 64891	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
83	ROM 64892	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
84	ROM 64893	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
85	ROM 64894	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
86	ROM 64895	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
87	ROM 64896	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum

88	ROM 64897	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
89	ROM 64898	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
90	ROM 64899	Family Esocidae : *Esox* (*Esox*) sp.	Fragmentary centrum
91	ROM 64900	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
92	ROM 64901	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
93	ROM 64902	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
94	ROM 64903	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
95	ROM 64904	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
96	ROM 64905	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
97	ROM 64906	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
98	ROM 64907	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
99	ROM 64908	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum

100	ROM 64909	Order Perciformes	Fragmentary basioccipital
101	ROM 64910	Order Perciformes	Fragmentary basioccipital
102	ROM 64911	Order Perciformes	Caudal centrum
103	ROM 64912	Order Perciformes	Caudal centrum
104	ROM 64913	Order Perciformes	Caudal centrum
105	ROM 64914	Order Perciformes	Caudal centrum
106	ROM 64915	Order Perciformes	Caudal centrum
107	ROM 64916	Order Perciformes	Caudal centrum
108	ROM 64917	Order Perciformes	Caudal centrum
109	ROM 64918	Order Perciformes	Caudal centrum
110	ROM 64919	Order Perciformes	Caudal centrum
111	ROM 64920	Order Perciformes	Caudal centrum
112	ROM 64921	Order Perciformes	Caudal centrum
113	ROM 64922	Order Perciformes	Caudal centrum
114	ROM 64923	Order Perciformes	Caudal centrum
115	ROM 64924	Order Perciformes	Caudal centrum
116	ROM 64925	Order Perciformes	Caudal centrum
117	ROM 64926	Order Perciformes	Caudal centrum
118	ROM 64927	Order Perciformes	Caudal centrum
119	ROM 64928	Order Perciformes	Caudal centrum
120	ROM 64929	Order Perciformes	Caudal centrum
121	ROM 64930	Order Perciformes	Caudal centrum
122	ROM 64931	Order Perciformes	Caudal centrum
123	ROM 64932	Order Perciformes	Caudal centrum
124	ROM 64933	Order Perciformes	Caudal centrum

125	ROM 64934	Order Perciformes	Caudal centrum
126	ROM 64935	Order Perciformes	Caudal centrum
127	ROM 64936	Order Perciformes	Caudal centrum
128	ROM 64937	Order Perciformes	Caudal centrum
129	ROM 64938	Order Perciformes	Caudal centrum
130	ROM 64939	Order Perciformes	Caudal centrum
131	ROM 64940	Order Perciformes	Caudal centrum
132	ROM 64941	Order Perciformes	Caudal centrum
133	ROM 64942	Order Perciformes	Caudal centrum
134	ROM 64943	Family ?Moronidae	Abdominal centrum
135	ROM 64944	Family ?Moronidae	Abdominal centrum
136	ROM 64945	Family ?Moronidae	Abdominal centrum
137	ROM 64946	Family ?Moronidae	Abdominal centrum
138	ROM 64947	Family ?Moronidae	Abdominal centrum
139	ROM 64948	Family ?Moronidae	Abdominal centrum
140	ROM 64949	Family ?Moronidae	Abdominal centrum
141	ROM 64950	Family ?Moronidae	Abdominal centrum
142	ROM 64951	Family ?Moronidae	Abdominal centrum
143	ROM 64952	Family ?Moronidae	Abdominal centrum
144	ROM 64953	Family ?Moronidae	Abdominal centrum
145	ROM 64954	Family ?Centrarchidae	First centrum
146	ROM 63445	Family Centrarchidae : cf. *Pomoxis*	Partial left premaxilla
147	ROM 63556	Family Centrarchidae : cf. *Pomoxis*	Mostly complete right premaxilla

148	ROM 64955	Family Centrarchidae : cf. *Pomoxis*	First centrum
149	ROM 64956	Family Centrarchidae : cf. *Pomoxis*	First centrum
150	ROM 64957	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
151	ROM 64958	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
152	ROM 64959	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
153	ROM 64960	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
154	ROM 64961	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
155	ROM 64962	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
156	ROM 64963	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
157	ROM 64964	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
158	ROM 64965	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
159	ROM 64966	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum

160	ROM 64967	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
161	ROM 64968	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
162	ROM 64969	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
163	ROM 64970	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
164	ROM 64971	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
165	ROM 64972	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
166	ROM 64973	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
167	ROM 64974	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
168	ROM 64975	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
169	ROM 64976	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
170	ROM 64977	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
171	ROM 64978	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum

172	ROM 64979	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
173	ROM 64980	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
174	ROM 64981	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
175	ROM 64982	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
176	ROM 64983	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
177	ROM 64984	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
178	ROM 64985	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
179	ROM 64986	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
180	ROM 64987	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
181	ROM 64988	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
182	ROM 64989	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
183	ROM 64990	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum

184	ROM 64991	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
185	ROM 64992	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
186	ROM 64993	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
187	ROM 64994	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
188	ROM 64995	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
189	ROM 64996	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
190	ROM 64997	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
191	ROM 64998	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
192	ROM 64999	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
193	ROM 65000	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
194	ROM 65001	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
195	ROM 65002	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum

196	ROM 65003	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
197	ROM 65004	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
198	ROM 65005	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
199	ROM 65006	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
200	ROM 65007	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
201	ROM 65008	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
202	ROM 65009	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
203	ROM 65010	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
204	ROM 65011	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
205	ROM 65012	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
206	ROM 65013	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
207	ROM 65014	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum

208	ROM 65015	Family ?Percidae	First centrum
209	ROM 65016	Family ?Percidae	First centrum
210	ROM 65017	Family ?Percidae	First centrum
211	ROM 65018	Family ?Percidae	Anterior abdominal centrum
212	ROM 65019	Family ?Percidae	Anterior abdominal centrum
213	ROM 65020	Family ?Percidae	Anterior abdominal centrum
214	ROM 65021	Family ?Percidae	Anterior abdominal centrum
215	ROM 65022	Family ?Percidae	Anterior abdominal centrum
216	ROM 65023	Family ?Percidae	Anterior abdominal centrum
217	ROM 65024	Family ?Percidae	Anterior abdominal centrum
218	ROM 65025	Family ?Percidae	Anterior abdominal centrum
219	ROM 65026	Family ?Percidae	Anterior abdominal centrum
220	ROM 65027	Family ?Percidae	Anterior abdominal centrum
221	ROM 65028	Family ?Percidae	Anterior abdominal centrum
222	ROM 65029	Family ?Percidae	Anterior abdominal centrum
223	ROM 53651	Family Percidae : *Stizostedion*	Anterior abdominal centrum
224	ROM 53652	Family Percidae : *Stizostedion*	Anterior abdominal centrum
225	ROM 53653	Family Percidae : *Stizostedion*	Anterior abdominal centrum
226	ROM 65030	Family Percidae : *Stizostedion*	Anterior abdominal centrum
227	ROM 65147	Family Lepisosteidae: *Lepisosteus*	Scale

228	ROM 65148	Family Lepisosteidae: *Lepisosteus*	Scale
229	ROM 65149	Family Lepisosteidae: *Lepisosteus*	Scale
230	ROM 65150	Division Teleostei	Caudal centrum
231	ROM 65151	Division Teleostei	Caudal centrum
232	ROM 65152	Division Teleostei	Caudal centrum
233	ROM 65153	Family Hiodontidae : cf. *Hiodon*	First centrum
234	ROM 65154	Order Cypriniformes	First centrum
235	ROM 65155	Family Ictaluridae : *Ameiurus*	Pectoral fin spine
236	ROM 65156	Family ?Esocidae	Isolated tooth
237	ROM 65157	Family ?Esocidae	Isolated tooth
238	ROM 65158	Family ?Esocidae	Isolated tooth
239	ROM 65159	Family ?Esocidae	Isolated tooth
240	ROM 65160	Family ?Esocidae	Isolated tooth
241	ROM 65161	Order Perciformes	Median fin spine
242	ROM 65162	Order Perciformes	Median fin spine
243	ROM 65163	Order Perciformes	Median fin spine
244	ROM 65164	Order Perciformes	Median fin spine
245	ROM 65165	Order Perciformes	Median fin spine
246	ROM 65166	Order Perciformes	Median fin spine
247	ROM 65167	Order Perciformes	Median fin spine
248	ROM 65168	Order Perciformes	Median fin spine

249	ROM 65169	Order Perciformes	Median fin spine
250	ROM 65170	Order Perciformes	Median fin spine
251	ROM 65171	Order Perciformes	Median fin spine
252	ROM 65172	Order Perciformes	Median fin spine
253	ROM 65173	Order Perciformes	Median fin spine
254	ROM 65174	Order Perciformes	Median fin spine
255	ROM 65175	Order Perciformes	Median fin spine
256	ROM 65176	Order Perciformes	Median fin spine
257	ROM 65177	Order Perciformes	Median fin spine
258	ROM 65178	Order Perciformes	Median fin spine
259	ROM 65179	Order Perciformes	Median fin spine
260	ROM 65180	Order Perciformes	Median fin spine
261	ROM 65181	Order Perciformes	Median fin spine
262	ROM 65182	Order Perciformes	Median fin spine
263	ROM 65183	Order Perciformes	Median fin spine
264	ROM 65184	Order Perciformes	Median fin spine
265	ROM 65185	Order Perciformes	Median fin spine
266	ROM 65186	Order Perciformes	Median fin spine
267	ROM 65187	Order Perciformes	Right paired fin spine
268	ROM 65188	Order Perciformes	Left paired fin spine
269	ROM 65189	Order Perciformes	Left paired fin spine
270	ROM 65190	Order Perciformes	Caudal centrum
271	ROM 65191	Order Perciformes	Caudal centrum
272	ROM 65192	Order Perciformes	Caudal centrum
273	ROM 65193	Family ?Moronidae	Abdominal centrum

274	ROM 65194	Family ?Moronidae	Abdominal centrum
275	ROM 65195	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum
276	ROM 65196	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum
277	ROM 65197	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum
278	ROM 65198	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum
279	ROM 65199	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum
280	ROM 65200	Family Centrarchidae: cf. *Pomoxis*	Anterior abdominal centrum
281	ROM 65201	Family Centrarchidae: cf. *Pomoxis*	Anterior abdominal centrum
282	ROM 65202	Family Centrarchidae: cf. *Pomoxis*	Anterior abdominal centrum
283	ROM 65203	Family Centrarchidae: cf. *Pomoxis*	Anterior abdominal centrum
284	ROM 65204	Family Centrarchidae: cf. *Pomoxis*	Posterior abdominal centrum
285	ROM 65205	Family ?Percidae	Anterior abdominal centrum

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286	ROM 65143	Order Cypriniformes	Weberian apparatus (centrum 2)	Same taxon as the cypriniform first centra
287	ROM 65144	Family Ictaluridae	Fragmentary parasphenoid	Either *Ictalurus* or *Ameiurus*
288	ROM 65145	Family Ictaluridae : *Ameiurus*	Pectoral fin spine	
289	ROM 65146	Family Esocidae : *Esox* (*Esox*) sp.	Basioccipital	

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290	ROM 65206	Division Teleostei	Caudal centrum	Probably Cypriniformes or Ictaluridae
291	ROM 65207	Family Hiodontidae : cf. *Hiodon*	Anterior abdominal centrum	
292	ROM 65208	Family Hiodontidae : cf. *Hiodon*	Posterior abdominal centrum	
293	ROM 65209	Order Cypriniformes	Fragmentary autopalatine	

294	ROM 65210	Order Cypriniformes: Taxon I	Fragmentary abdominal centrum
295	ROM 65211	Family Ictaluridae	Fragmentary pectoral fin spine
296	ROM 65212	Family Ictaluridae: cf. *Noturus*	Fragmentary dorsal fin spine
297	ROM 65213	Family Ictaluridae: cf. *Noturus*	Fragmentary pectoral fin spine
298	ROM 65214	Family Ictaluridae: cf. *Noturus*	Fragmentary pectoral fin spine
299	ROM 65215	Family ?Esocidae	Isolated tooth
300	ROM 65216	Family ?Esocidae	Isolated tooth
301	ROM 65217	Family ?Esocidae	Isolated tooth
302	ROM 65218	Family ?Esocidae	Isolated tooth
303	ROM 65219	Family ?Esocidae	Isolated tooth

304	ROM 65220	Family ?Esocidae	Isolated tooth
305	ROM 65221	Family ?Esocidae	Isolated tooth
306	ROM 65222	Family ?Esocidae	Isolated tooth
307	ROM 65223	Family ?Esocidae	Isolated tooth
308	ROM 65224	Family ?Esocidae	Isolated tooth
309	ROM 65225	Family ?Esocidae	Isolated tooth
310	ROM 65226	Family ?Esocidae	Isolated tooth
311	ROM 65227	Family ?Esocidae	Isolated tooth
312	ROM 65228	Order Perciformes	Median fin spine
313	ROM 65229	Order Perciformes	Median fin spine
314	ROM 65230	Order Perciformes	Median fin spine
315	ROM 65231	Order Perciformes	Median fin spine

316	ROM 65232	Order Perciformes	Median fin spine
317	ROM 65233	Order Perciformes	Median fin spine
318	ROM 65234	Order Perciformes	Median fin spine
319	ROM 65235	Order Perciformes	Median fin spine
320	ROM 65236	Order Perciformes	Median fin spine
321	ROM 65237	Order Perciformes	Median fin spine
322	ROM 65238	Order Perciformes	Median fin spine
323	ROM 65239	Order Perciformes	Median fin spine
324	ROM 65240	Order Perciformes	Median fin spine
325	ROM 65241	Order Perciformes	Median fin spine
326	ROM 65242	Order Perciformes	Median fin spine
327	ROM 65243	Order Perciformes	Median fin spine

328	ROM 65244	Order Perciformes	Median fin spine
329	ROM 65245	Order Perciformes	Median fin spine
330	ROM 65246	Order Perciformes	Median fin spine
331	ROM 65247	Order Perciformes	Median fin spine
332	ROM 65248	Order Perciformes	Median fin spine
333	ROM 65249	Order Perciformes	Median fin spine
334	ROM 65250	Order Perciformes	Median fin spine
335	ROM 65251	Order Perciformes	Median fin spine
336	ROM 65252	Order Perciformes	Median fin spine
337	ROM 65253	Order Perciformes	Median fin spine
338	ROM 65254	Order Perciformes	Median fin spine
339	ROM 65255	Order Perciformes	Median fin spine

340	ROM 65256	Order Perciformes	Left paired fin spine	
341	ROM 65257	Order Perciformes	Fragmentary basioccipital	
342	ROM 65258	Order Perciformes	Caudal centrum	
343	ROM 65259	Order Perciformes	Caudal centrum	
344	ROM 65260	Family ?Percidae	First centrum	NB: anterior articular facets in medial contact

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345	ROM 65261	Subfamily Amiinae	Fragmentary caudal centrum	
346	ROM 65262	Division Teleostei	Caudal centrum	Probably Cypriniformes or Ictaluridae
347	ROM 65263	Order Cypriniformes: Taxon I	Fragmentary abdominal centrum	
348	ROM 65264	Family Ictaluridae: cf. *Noturus*	Fragmentary pectoral fin spine	

349	ROM 65265	Family ?Esocidae	Isolated tooth	
350	ROM 65266	Order Perciformes	Caudal centrum	
351	ROM 65267	Division Teleostei	Caudal centrum	Probably Cypriniformes or Ictaluridae
352	ROM 65268	Division Teleostei	Caudal centrum	Probably Cypriniformes or Ictaluridae
353	ROM 65269	Family ?Centrarchidae	First centrum	
354	ROM 65270	Subfamily Amiinae	Abdominal centrum	
355	ROM 65271	Subfamily Amiinae	Abdominal centrum	
356	ROM 65272	Subfamily Amiinae	Abdominal centrum	
357	ROM 65273	Subfamily Amiinae	Abdominal centrum	
358	ROM 65274	Subfamily Amiinae	Abdominal centrum	
359	ROM 65275	Subfamily Amiinae	Caudal centrum	
360	ROM 65276	Subfamily Amiinae	Caudal centrum	

361	ROM 65277	Subfamily Amiinae	Caudal centrum	
362	ROM 65278	Division Teleostei	Caudal centrum	Probably Cypriniformes or Ictaluridae
363	ROM 65279	Division Teleostei	Caudal centrum	Probably Cypriniformes or Ictaluridae
364	ROM 65280	Order Cypriniformes	First centrum	
365	ROM 65281	Order Cypriniformes: Taxon II	Fragmentary abdominal centrum	
366	ROM 65282	Family Ictaluridae	Fragmentary basioccipital	Either *Ictalurus* or *Ameiurus*
367	ROM 65283	Family Ictaluridae: *Ameiurus*	Pectoral fin spine	
368	ROM 65284	Family ?Esocidae	Isolated tooth	
369	ROM 65285	Family Esocidae: *Esox* (*Esox*)	Abdominal centrum	
370	ROM 65286	Family Esocidae: *Esox* (*Esox*)	Abdominal centrum	
371	ROM 65287	Order Perciformes	Median fin spine	

372	ROM 65288	Order Perciformes	Median fin spine
373	ROM 65289	Order Perciformes	Fragmentary basioccipital
374	ROM 65290	Order Perciformes	Caudal centrum
375	ROM 65291	Order Perciformes	Caudal centrum
376	ROM 65292	Order Perciformes	Caudal centrum
377	ROM 65293	Order Perciformes	Caudal centrum
378	ROM 65294	Order Perciformes	Caudal centrum
379	ROM 65295	Order Perciformes	Caudal centrum
380	ROM 65296	Family Centrarchidae: cf. *Pomoxis*	First centrum
381	ROM 65297	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum
382	ROM 65298	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum

383	ROM 65299	Family Centrarchidae: cf. *Pomoxis*	Anterior-most abdominal centrum
384	ROM 65300	Family Centrarchidae: cf. *Pomoxis*	Anterior abdominal centrum
385	ROM 65301	Family Centrarchidae: cf. *Pomoxis*	Posterior abdominal centrum
386	ROM 65302	Family Centrarchidae: cf. *Pomoxis*	Posterior abdominal centrum

Canadian Museum of Nature Specimens (N = 65). All specimens were recovered from the Yost Farm locality.

#	Specimen Number	Identification	Description
1	CMN 54920	Subfamily Amiinae	Abdominal centrum
2	CMN 54921	Subfamily Amiinae	Abdominal centrum
3	CMN 54922	Order Cypriniformes	Partial Weberian apparatus
4	CMN 54923	Subfamily Leuciscinae	Abdominal centrum
5	CMN 41935	Family Ictaluridae : cf. *Noturus*	Dorsal fin spine fragment
6	CMN 54920	Family ?Esocidae	Isolated tooth
7	CMN 54921	Family Esocidae : *Esox* (*Esox*) sp.	Abdominal centrum
8	CMN 54922	Family Esocidae : *Esox* (*Esox*) sp.	Caudal centrum
9	CMN 41936	Superorder Acanthopterygii	Spiny material
10	CMN 41939	Superorder Acanthopterygii	Spiny material
11	CMN 41940	Superorder Acanthopterygii	Spiny material
12	CMN 41941	Superorder Acanthopterygii	Spiny material
13	CMN 41944	Superorder Acanthopterygii	Spiny material
14	CMN 41946	Superorder Acanthopterygii	Spiny material
15	CMN 41947	Superorder Acanthopterygii	Spiny material
16	CMN 41948	Superorder Acanthopterygii	Spiny material

17	CMN 41949	Superorder Acanthopterygii	Spiny material
18	CMN 41950	Superorder Acanthopterygii	Spiny material
19	CMN 41951	Superorder Acanthopterygii	Spiny material
20	CMN 41953	Superorder Acanthopterygii	Spiny material
21	CMN 41955	Superorder Acanthopterygii	Spiny material
22	CMN 41956	Superorder Acanthopterygii	Spiny material
23	CMN 41957	Superorder Acanthopterygii	Spiny material
24	CMN 41958	Superorder Acanthopterygii	Spiny material
25	CMN 41959	Superorder Acanthopterygii	Spiny material
26	CMN 41961	Superorder Acanthopterygii	Spiny material
27	CMN 41962	Superorder Acanthopterygii	Spiny material
28	CMN 41964	Superorder Acanthopterygii	Spiny material
29	CMN 41967	Superorder Acanthopterygii	Spiny material
30	CMN 54927	Superorder Acanthopterygii	Spiny material
31	CMN 54928	Superorder Acanthopterygii	Spiny material
32	CMN 54929	Superorder Acanthopterygii	Spiny material
33	CMN 54930	Superorder Acanthopterygii	Spiny material
34	CMN 54931	Superorder Acanthopterygii	Spiny material
35	CMN 54932	Superorder Acanthopterygii	Spiny material
36	CMN 54933	Superorder Acanthopterygii	Spiny material
37	CMN 54934	Superorder Acanthopterygii	Spiny material
38	CMN 54935	Superorder Acanthopterygii	Spiny material
39	CMN 54936	Superorder Acanthopterygii	Spiny material
40	CMN 54937	Superorder Acanthopterygii	Spiny material
41	CMN 54938	Superorder Acanthopterygii	Spiny material

42	CMN 54939	Superorder Acanthopterygii	Spiny material
43	CMN 54940	Superorder Acanthopterygii	Spiny material
44	CMN 54941	Superorder Acanthopterygii	Spiny material
45	CMN 54942	Superorder Acanthopterygii	Spiny material
46	CMN 41934	Order Perciformes	Median fin spine fragment
47	CMN 41937	Order Perciformes	Right paired fin spine fragment
48	CMN 41938	Order Perciformes	Haemal spine fragment
49	CMN 41942	Order Perciformes	Right paired fin spine fragment
50	CMN 41943	Order Perciformes	Median fin spine fragment
51	CMN 41945	Order Perciformes	Median fin spine fragment
52	CMN 41952	Order Perciformes	Left paired fin spine fragment
53	CMN 41954	Order Perciformes	Median fin spine fragment
54	CMN 41960	Order Perciformes	Median fin spine fragment
55	CMN 41963	Order Perciformes	Median fin spine fragment
56	CMN 41965	Order Perciformes	Right paired fin spine fragment

57	CMN 41966	Order Perciformes	Right paired fin spine fragment
58	CMN 41968	Order Perciformes	Median fin spine fragment
59	CMN 54943	Order Perciformes	Caudal centrum
60	CMN 54944	Order Perciformes	Caudal centrum
61	CMN 54945	Family Centrarchidae : cf. *Pomoxis*	Anterior-most abdominal centrum
62	CMN 54946	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
63	CMN 54947	Family Centrarchidae : cf. *Pomoxis*	Anterior abdominal centrum
64	CMN 54948	Family Centrarchidae : cf. *Pomoxis*	Abdominal centrum
65	CMN 54209	Family Percidae : *Stizostedion*	Partial right premaxilla

APPENDIX III—CYPRESS HILLS FORMATION SPECIMENS

Royal Ontario Museum Specimens (N = 298)

#	Locality Information	Specimen number	ID
	L 41 Herman Pirson's Hill southeast 1/4 of southeast 1/4 of S 4 T 8 R 22		
1		66920	Amiine Maxilla
2		66921	Amiine abdominal
3		66922	Amiine abdominal
4		66923	Amiine abdominal
5		66924	Amiine caudal
6		66925	Catostomid 1st centrum
7		66926	Leusiscine abdominal
8		66927	*Astephus* A Pectoral Fin spine
9		66928	*Astephus* A Pectoral Fin spine
10		66929	*Astephus* A Pectoral Fin spine
11		66930	*Astephus* A Pectoral Fin spine
12		66931	*Astephus* A Abdominal
13		66932	*Astephus* A Abdominal
14		66933	Protacanthopterygian Abdominal
15		66934	Centrarchid Abdominal

	L40 Russell Hill 1949		
16		66935	Amiine caudal
17		66936	Catostomid or cyprinine 1st centrum
18		66937	Catostomid 1st centrum
19		66938	Catostomid 1st centrum
20		66939	Catostomid Weberian Fragment
21		66940	*Astephus* A Pectoral Fin spine
22		66941	*Astephus* A Pectoral Fin spine
23		66942	*Astephus* A Pectoral Fin spine
24		66943	*Astephus* A Pectoral Fin spine
25		66944	*Astephus* A Pectoral Fin spine
26		66945	*Astephus* A Pectoral Fin spine
27		66946	*Astephus* A Pectoral Fin spine
28		66947	*Astephus* A Pectoral Fin spine
29		66948	*Astephus* A Pectoral Fin spine
30		66949	*Astephus* A Abdominal
	Russell Hill on east side of Conglomerate Creek, northeast 1/4, Sec.4 Tp.8 Rg.22 1949		
31		66950	Catostomid Weberian Fragment
32		66951	*Astephus* A Pectoral Fin spine
33		66952	*Astephus* A Abdominal
34		66953	*Astephus* B Pectoral Spine

35		66954	*Astephus* B Pectoral Spine
36		66955	*Astephus* B Pectoral Spine
37		66956	Centrarchid First Centrum
	L40 Small Tooth Locality		
38		66957	*Astephus* A dorsal spine
39		66958	Catostomid or cyprinine first centrum
	L37 A573 Rodent Hill		
40		66959	Catostomid or cyprinine 1st centrum
41		66960	*Astephus* A Pectoral Fin spine
42		66961	*Astephus* A Pectoral Fin spine
43		66962	*Astephus* A Pectoral Fin spine
44		66963	*Astephus* A Abdominal
45		66964	Cypriniform ural centrum
	Found on Knowles + Slopes on NE Side of Conglomerate Creek 1949		
46		66965	Amiine abdominal
47		66966	Cypriniform abdominal
48		66967	*Astephus* A Pectoral Fin spine
49		66968	*Astephus* A Pectoral Fin spine
50		66969	*Astephus* A Pectoral Fin spine

Calf Creek near Hunter Quarry southwest 1/4 of Sec.8 Tp.8 Rge.22 1949

51	66970	Amiine abdominal
52	66971	Amiine abdominal
53	66972	Amiine caudal
54	66973	Catostomid 1st centrum
55	66974	Catostomid 1st centrum
56	66975	Cypriniform abdominal
57	66976	Leusiscine abdominal
58	66977	*Astephus* A dorsal spine
59	66978	*Astephus* A Pectoral Fin spine
60	66979	*Astephus* A Pectoral Fin spine
61	66980	*Astephus* A Pectoral Fin spine
62	66981	*Astephus* A Pectoral Fin spine
63	66982	Protacanthopterygian Abdominal
64	66983	Centrarchid Abdominal
65	66984	Centrarchid Abdominal

Hornell & Weare - Calf Creek Stewart Ranch 1949

66	66985	*Astephus* A Pectoral Fin spine
67	66986	Protacanthopterygian Abdominal

Weigel & Holman - Calf Creek Sec.7 Tp.8 R.22 W 3rd M 1967

68	66987	*Lepisosteus* Scale
69	66988	*Lepisosteus* Scale
70	66989	*Lepisosteus* Scale
71	66990	*Lepisosteus* Abdominal centrum
72	66991	*Lepisosteus* Abdominal centrum
73	66992	*Lepisosteus* Abdominal centrum
74	66993	Cypriniform abdominal
75	66994	*Astephus* A dorsal spine
76	66995	*Astephus* A dorsal spine
77	66996	*Astephus* A dorsal spine
78	66997	*Astephus* A dorsal spine
79	66998	*Astephus* A dorsal spine
80	66999	*Astephus* A Pectoral Fin spine
81	67000	*Astephus* A Pectoral Fin spine
82	67001	*Astephus* A Pectoral Fin spine
83	67002	*Astephus* A Pectoral Fin spine
84	67003	*Astephus* A Pectoral Fin spine
85	67004	*Astephus* A Pectoral Fin spine
86	67005	*Astephus* A Pectoral Fin spine
87	67006	*Astephus* A Pectoral Fin spine
88	67007	*Astephus* A Pectoral Fin spine
89	67008	*Astephus* A Abdominal
90	67009	*Astephus* A Abdominal

91	67010	*Astephus* A Abdominal
92	67011	Protacanthopterygian Abdominal

67 Party 19-VI-67 Ref GE 67-4 Surface collected 985-475 Dollard Hanson Ranch Eastend 1967

93	67012	*Astephus* A Pectoral Fin spine

Roadcut S. of Hanson Ranch Turnoff 1968 12-VI-68

94	67013	Amiine abdominal
95	67014	Amiine abdominal
96	67015	Amiine abdominal
97	67016	*Mioplosus* abdominal
98	67017	*Mioplosus* abdominal
99	67018	Cypriniform abdominal
100	67019	*Astephus* A Pectoral Fin spine
101	67020	*Astephus* A Pectoral Fin spine
102	67021	*Astephus* A Pectoral Fin spine
103	67022	*Astephus* A Abdominal
104	67023	Perciform Abdominal

15-V-68 surface collected Small Quarry Across the valley from Hunter Quarry Sec.5 T.8R.22 1968

105	67024	*Lepisosteus* scale frag.
106	67025	Amiine abdominal
107	67026	*Astephus* A Pectoral Fin spine

108	67027	*Astephus* A Pectoral Fin spine
109	67028	*Astephus* A Pectoral Fin spine
110	67029	*Astephus* A Abdominal

18-VI-68 Ref. GE-8-68 surface collected Calf Creek Area 1968

111	67030	unidentified tooth 1
112	67031	Amiine abdominal
113	67032	Amiine abdominal
114	67033	Amiine abdominal
115	67034	Amiine abdominal
116	67035	Amiine caudal
117	67036	Amiine caudal
118	67037	*Astephus* A Pectoral Fin spine
119	67038	*Astephus* A Pectoral Fin spine
120	67039	*Astephus* A Pectoral Fin spine
121	67040	*Astephus* A Pectoral Fin spine
122	67041	*Astephus* A Abdominal
123	67042	Percopsiform 1st Centrum
124	67043	Percopsiform Abdominal

Ref. 6E8-68 Small Tooth Quarry Calf Creek Hanson Ranch 1968 20-VI-68

125	67044	Cypriniform abdominal
126	67045	*Astephus* A Pectoral Fin spine
127	67046	*Astephus* A Pectoral Fin spine
128	67047	*Astephus* A Pectoral Fin spine
129	67048	*Astephus* A Pectoral Fin spine

130	67049	*Astephus* A Abdominal
131	67050	*Astephus* B Pectoral Spine

68 Party 25-16-VI-68 surface collected Various Outcrops N1/2 S.32 T.7 R.22 S1/2 S.5 T.8 R.22 Hanson Ranch 1968

132	67051	Amiine dentary
133	67052	Amiiine abdominal
134	67053	Catostomid 1st centrum
135	67054	*Astephus* A Basioccipital
136	67055	*Astephus* A Pectoral Fin spine
137	67056	*Astephus* A Pectoral Fin spine
138	67057	*Astephus* A Abdominal
139	67058	*Astephus* A Abdominal
140	67059	*Astephus* A Abdominal
141	67060	Protacanthopterygian Abdominal
142	67061	Percopsiform caudal
143	67062	Percopsiform caudal

North Edge of S.32 T.7 R.22 Hanson Ranch 196827-VI-68

144	67063	Amiine abdominal
145	67064	Amiine abdominal
146	67065	Amiine caudal
147	67066	Cypriniform abdominal
148	67067	*Astephus* A Pectoral Fin spine
149	67068	*Astephus* A Pectoral Fin spine

150	67069	*Astephus* A Pectoral Fin spine
151	67070	*Astephus* A Abdominal
152	67071	Protacanthopterygian Abdominal
153	67072	Percopsiform caudal

Hanson Ranch N. edge of S.32 T.7 R.22, S. edge of S.5 T.8 R.22 28-VI-68 surface collected

154	67073	Amiine abdominal
155	67074	Amiine caudal
156	67075	*Mioplosus* abdominal (large)
157	67076	Cypriniform abdominal
158	67077	*Astephus* A Dentary
159	67078	*Astephus* A Pectoral Fin spine
160	67079	*Astephus* A Pectoral Fin spine
161	67080	*Astephus* A Pectoral Fin spine
162	67081	*Astephus* A Pectoral Fin spine
163	67082	*Astephus* A Pectoral Fin spine
164	67083	*Astephus* A Pectoral Fin spine
165	67084	*Astephus* A Pectoral Fin spine
166	67085	*Astephus* A Pectoral Fin spine
167	67086	*Astephus* A Pectoral Fin spine
168	67087	*Astephus* A Pectoral Fin spine

169	67088	*Astephus* A Web Ap Frag
170	67089	*Astephus* A First Centrum after Web. Ap.
171	67090	*Astephus* A Abdominal
172	67091	*Astephus* B Pectoral Fin spine
173	67092	Protacanthopterygian Abdominal

N. Side of Coulee, N.W. Corner of S.32 T.7 R.22 1968

174	67093	Protacanthopterygian Abdominal

Vicinity of Hanson Bros Ranch, NW of Eastend Detailed Locality not recorded 1968

175	67094	Amiine Abdominal
176	67095	*Mioplosus* anterior-most abdominal
177	67096	Cypriniform abdominal
178	67097	*Astephus* A dorsal spine
179	67098	*Astephus* A Pectoral Fin spine
180	67099	*Astephus* A Pectoral Fin spine
181	67100	*Astephus* A Pectoral Fin spine
182	67101	*Astephus* A Pectoral Fin spine
183	67102	*Astephus* A Pectoral Fin spine
184	67103	*Astephus* A Pectoral Fin spine
185	67104	*Astephus* A Pectoral Fin spine

186	67105	*Astephus* A Pectoral Fin spine
187	67106	*Astephus* A First centrum
188	67107	*Astephus* A Abdominal
189	67108	*Astephus* B Pectoral Spine
190	67109	Percopsiform 1st Centrum

W. of ?Center of Sec.3 T.8 R.22 "Farily High" 68-Party

191	67110	*Lepisosteus* scale Frag.
192	67111	Amiine abdominal
193	67112	Amiine abdominal
194	67113	Amiine abdominal
195	67114	*Mioplosus* abdominal (small)
196	67115	Catostomid or cyprinine 1st centrum
197	67116	Catostomid 1st centrum
198	67117	Catostomid 1st centrum
199	67118	Cypriniform abdominal
200	67119	*Astephus* A Pectoral Fin spine
201	67120	*Astephus* A Pectoral Fin spine
202	67121	*Astephus* A Pectoral Fin spine
203	67122	*Astephus* B Pectoral Spine
204	67123	*Astephus* B Pectoral Spine
205	67124	*Astephus* B Pectoral Spine
206	67125	*Astephus* B Pectoral Spine

26.VI.71 Dollard Sec.7 T.8 R.22 Dollard street

207	67126	Amiine abdominal
208	67127	*Astephus* A Pectoral Fin spine
209	67128	*Astephus* A Pectoral Fin spine
210	67129	*Astephus* A Pectoral Fin spine
211	67130	*Astephus* A Pectoral Fin spine
212	67131	*Astephus* A Pectoral Fin spine

26-VI-71 Gyrmov Sec.7 T.8 R.22 Dollard street 1971

213	67132	Amiine abdominal
214	67133	*Hiodon* posterior abdominal
215	67134	Cypriniform abdominal
216	67135	Cypriniform abdominal
217	67136	*Astephus* A Pectoral Fin spine
218	67137	Protacanthopterygian Abdominal

Sec.18 T.8 R.22 Gyrmov 26-VI-71

219	67138	unidentified tooth 2
220	67139	Leusiscine abdominal
221	67140	*Astephus* A Pectoral Fin spine
222	67141	Perciform Abdominal

Gyrmov?? 28-VI-71 Sec.16 T.3 R.22 Dollard street

223	67142	Amiine abdominal
224	67143	Catostomid 1st centrum
225	67144	Catostomid 1st centrum
226	67145	*Astephus* A Pectoral Fin spine
227	67146	*Astephus* A Pectoral Fin spine
228	67147	*Astephus* A Pectoral Fin spine
229	67148	*Astephus* A Pectoral Fin spine
230	67149	*Astephus* B Pectoral Spine
231	67150	Protacanthopterygian Abdominal
232	67151	Protacanthopterygian Abdominal
233	67152	Moronid Abdominal

Gyrmov 29-VI-71 Sec.4 T.8 R.22

234	67153	Amiine abdominal
235	67154	Amiine abdominal
236	67155	Amiine abdominal
237	67156	Amiine caudal
238	67157	Cypriniform abdominal
239	67158	*Astephus* A dorsal spine
240	67159	*Astephus* A dorsal spine
241	67160	*Astephus* A Pectoral Fin spine
242	67161	*Astephus* A Pectoral Fin spine

243	67162	*Astephus* A Pectoral Fin spine
244	67163	*Astephus* A Pectoral Fin spine
245	67164	*Astephus* A Pectoral Fin spine
246	67165	*Astephus* A Abdominal
247	67166	*Astephus* A Abdominal
248	67167	Protacanthopterygian Abdominal

Tillie ?S of 8/71? Sec.16 T.9 R.20 South Edge of Section @ Roadcut

249	67168	amiine abdominal
250	67169	*Astephus* A Pectoral Fin spine

Sec.16 T.9 R.20 southern Edge of Sec.16 @ Roadcut (Tillie, R.) 8-VII-71

251	67170	Amiine abdominal
252	67171	Catostomid or cyprinine 1st centrum

Sec.5 T.8 R.22 (Tillie, R.) 9-VII-71

253	67172	Amiine abdominal
254	67173	Cypriniform abdominal

Sec.16 T.8 R.22 (Tillie, R.) 1971

255	67174	Amiine caudal
256	67175	Cypriniform abdominal
257	67176	*Astephus* A Pectoral Fin spine
258	67177	*Astephus* A Pectoral Fin spine

Cypress Hills Sk. ?Pickings from Concentrate? 1972 W. Side of Calf Creek

Michael Torsgok/Roger Kidlark

259	67178	unidentified tooth morph 1
260	67179	Cypriniform abdominal
261	67180	Moronid Abdominal

Small Bones Quarry SE 1/4 of SE 1/4 Sec.7 T.8 R.22

262	67181	*Astephus* A Pectoral Fin spine

Grymov & Fisk Sec.6 T.8 R.22 on Dollard Sheet

263	67182	Amiine abdominal
264	67183	*Astephus* A Pectoral Fin spine
265	67184	*Astephus* A Pectoral Fin spine
266	67185	*Astephus* A Pectoral Fin spine
267	67186	*Astephus* A Pectoral Fin spine
268	67187	*Astephus* A Pectoral Fin spine
269	67188	*Astephus* B Pectoral Spine

Entrance to Hanson Ranch on R. Side on his Driveway

270	67189	Catostomid 1st centrum
271	67190	*Astephus* A Pectoral Fin spine
272	67191	Protacanthopterygian Abdominal

E. Side of Trail Next to HQ N. of Quarry

273	67190	Amiine abdominal

1/4 Mile S. on E. Side of Calf Creek Campsite

274	67191	Catostomid 1st centrum
275	67192	Catostomid Weberian Fragment
276	67193	Leusiscine abdominal
277	67194	Leusiscine abdominal
278	67195	*Astephus* A dorsal spine
279	67196	*Astephus* A Pectoral Fin spine
280	67197	*Astephus* A Pectoral Fin spine

1/4 Mile N., E. Side of Calf Creek Camp Site

281	67198	Centrarchid First Centrum

Only Info is "Cypress Hills, Sk."

282	67199	Amiine abdominal
283	67200	*Hiodon* anterior abdominal
284	67201	Cypriniform abdominal

Only Info is "Cypress Hills"

285	67202	Amiine abdominal
286	67203	Amiine abdominal
287	67204	Amiine abdominal

288	67205	Amiine caudal
289	67206	Cypriniform abdominal
290	67207	*Astephus* A dorsal Spine
291	67208	*Astephus* A dorsal Spine
292	67209	*Astephus* A Pectoral Fin spine
293	67210	*Astephus* A Pectoral Fin spine
294	67211	*Astephus* A Pectoral Fin spine
295	67212	*Astephus* A Pectoral Fin spine
296	67213	*Astephus* A Abdominal
297	67214	Percopsiform caudal
298	67215	Percopsiform caudal

APPENDIX IV—BRIDGER FORMATION SPECIMENS

University of California Museum of Paleontology Specimens (N = 439)

#	Specimen Number	Identification
1	V193208	*Astephus* pectoral fin spine A
2	V193209	*Astephus* Weberian
3	V193210	*Astephus* Weberian
4	V193211	*Astephus* Weberian
5	V193212	*Astephus* Weberian
6	V193213	*Phareodus* maxilla
7	V193214	*Phareodus* basibranchial fragment
8	V193215	*Phareodus* basibranchial fragment
9	V193216	*Astephus* dentary
10	V193217	*Astephus* basioccipital
11	V193218	*Astephus* basioccipital
12	V193219	*Astephus* basioccipital
13	V193220	*Astephus* basioccipital
14	V193221	*Astephus* basioccipital
15	V193222	*Astephus* first Weberian centrum
16	V193223	*Astephus* first Weberian centrum
17	V193224	*Astephus* first Weberian centrum
18	V193225	*Astephus* abdominal
19	V193226	*Astephus* abdominal
20	V193227	*Astephus* abdominal
21	V193228	*Astephus* abdominal

22	V193229	*Astephus* abdominal
23	V193230	*Astephus* abdominal
24	V193231	*Astephus* abdominal
25	V193232	*Astephus* abdominal
26	V193233	*Astephus* abdominal
27	V193234	*Astephus* abdominal
28	V193235	*Astephus* abdominal
29	V193236	*Phareodus* first centrum
30	V193237	*Phareodus* abdominal
31	V193238	*Phareodus* abdominal
32	V193239	*Phareodus* abdominal
33	V193240	Caudal centrum
34	V193241	Caudal centrum
35	V193242	Caudal centrum
36	V193243	Caudal centrum
37	V193244	Caudal centrum
38	V193245	Caudal centrum
39	V193246	Caudal centrum
40	V193247	Caudal centrum
41	V193248	Caudal centrum
42	V193249	Unid. centrum
43	V193250	Unid. centrum
44	V193251	Unid. centrum
45	V193252	Unid. centrum

46	V193253	Unid. centrum
47	V193254	Unid. centrum
48	V193255	Unid. centrum
49	V193256	Unid. centrum
50	V193257	Unid. centrum
51	V193258	Unid. centrum
52	V193259	Unid. centrum
53	V193260	Unid. centrum
54	V193261	Unid. centrum
55	V193262	*Phareodus* pharyngeal
56	V193263	*Phareodus* premaxilla
57	V193264	*Phareodus* premaxilla
58	V193265	*Phareodus* premaxilla
59	V193266	*Phareodus* dentary
60	V193267	*Phareodus* dentary
61	V193268	*Phareodus* dentary
62	V193269	*Phareodus* dentary
63	V193270	*Phareodus* dentary
64	V193271	*Phareodus* maxilla (anterior)
65	V193272	*Phareodus* maxilla (posterior)
66	V193273	*Phareodus* maxilla
67	V193274	*Phareodus* maxilla
68	V193275	*Phareodus* maxilla
69	V193276	*Phareodus* maxilla

70	V193277	*Phareodus* maxilla
71	V193278	*Phareodus* maxilla
72	V193279	*Phareodus* maxilla
73	V193280	*Phareodus* maxilla
74	V193281	*Phareodus* maxilla
75	V193282	*Phareodus* maxilla
76	V193283	*Astephus* cleithrum fragment
77	V193284	*Astephus* dentary
78	V193285	*Astephus* dentary
79	V193286	*Astephus* dentary
80	V193287	*Astephus* dentary
81	V193288	*Astephus* dentary
82	V193289	*Astephus* dentary
83	V193290	*Astephus* dentary
84	V193291	*Astephus* dentary
85	V193292	*Astephus* dentary
86	V193293	*Astephus* dentary
87	V193294	*Astephus* dentary
88	V193295	*Phareodus* basioccipital + first centrum
89	V193296	Lepisosteid abdominal
90	V193297	*Astephus* post-temporal
91	V193298	*Phareodus* abdominal
92	V193299	*Phareodus* abdominal
93	V193300	*Phareodus* abdominal

94	V193301	*Phareodus* abdominal
95	V193302	*Phareodus* abdominal
96	V193303	*Phareodus* abdominal
97	V193304	*Phareodus* abdominal
98	V193305	*Phareodus* abdominal
99	V193306	*Phareodus* abdominal
100	V193307	*Phareodus* abdominal
101	V193308	*Phareodus* abdominal
102	V193309	*Phareodus* abdominal
103	V193310	*Phareodus* abdominal
104	V193311	*Phareodus* abdominal
105	V193312	*Astephus* abdominal
106	V193313	*Astephus* abdominal
107	V193314	*Astephus* basioccipital
108	V193315	Caudal centrum
109	V193316	Caudal centrum
110	V193317	Caudal centrum
111	V193318	Caudal centrum
112	V193319	Caudal centrum
113	V193320	Caudal centrum
114	V193321	Caudal centrum
115	V193322	Caudal centrum
116	V193323	Caudal centrum
117	V193324	Caudal centrum

118	V193325	Caudal centrum
119	V193326	Caudal centrum
120	V193327	Caudal centrum
121	V193328	Caudal centrum
122	V193329	Caudal centrum
123	V193330	Caudal centrum
124	V193331	Caudal centrum
125	V193332	Caudal centrum
126	V193333	Caudal centrum
127	V193334	Caudal centrum
128	V193335	Caudal centrum
129	V193336	*Phareodus* basioccipital + first centrum
130	V193337	*Phareodus* basioccipital + first centrum
131	V193338	*Phareodus* basioccipital + first centrum
132	V193339	*Phareodus* first centrum
133	V193340	*Phareodus* first centrum
134	V193341	*Phareodus* first centrum
135	V193342	*Phareodus* first centrum
136	V193343	*Phareodus* abdominal
137	V193344	*Phareodus* abdominal
138	V193345	*Phareodus* abdominal
139	V193346	*Phareodus* abdominal
140	V193347	*Phareodus* abdominal
141	V193348	*Phareodus* abdominal

142	V193349	*Phareodus* abdominal
143	V193350	*Phareodus* abdominal
144	V193351	*Phareodus* abdominal
145	V193352	*Phareodus* abdominal
146	V193353	*Phareodus* abdominal
147	V193354	*Phareodus* abdominal
148	V193355	*Phareodus* abdominal
149	V193356	*Phareodus* abdominal
150	V193357	*Phareodus* abdominal
151	V193358	*Phareodus* abdominal
152	V193359	*Astephus* abdominal
153	V193360	*Astephus* abdominal
154	V193361	*Astephus* abdominal
155	V193362	*Astephus* abdominal
156	V193363	*Astephus* abdominal
157	V193364	*Astephus* abdominal
158	V193365	*Astephus* abdominal
159	V193366	*Astephus* abdominal
160	V193367	*Astephus* abdominal
161	V193368	*Astephus* abdominal
162	V193369	*Astephus* abdominal
163	V193370	*Astephus* abdominal
164	V193371	*Astephus* abdominal
165	V193372	*Astephus* abdominal

166	V193373	*Astephus* abdominal
167	V193374	*Astephus* abdominal
168	V193375	*Astephus* abdominal
169	V193376	*Astephus* abdominal
170	V193377	*Astephus* abdominal
171	V193378	*Astephus* first Weberian centrum
172	V193379	*Astephus* first Weberian centrum
173	V193380	*Astephus* first Weberian centrum
174	V193381	*Astephus* first post-Weberian centrum
175	V193382	*Astephus* first post-Weberian centrum
176	V193383	*Phareodus* abdominal
177	V193384	*Phareodus* abdominal
178	V193385	*Phareodus* abdominal
179	V193386	*Phareodus* abdominal
180	V193387	*Phareodus* abdominal
181	V193388	*Astephus* first Weberian centrum
182	V193389	*Astephus* first post-Weberian centrum
183	V193390	*Astephus* Weberian
184	V193391	*Astephus* Weberian
185	V193392	*Astephus* Weberian
186	V193393	*Astephus* Weberian
187	V193394	*Astephus* Weberian
188	V193395	*Astephus* Weberian
189	V193396	*Astephus* basioccipital

190	V193397	*Astephus* basioccipital
191	V193398	*Astephus* basioccipital
192	V193399	*Astephus* basioccipital
193	V193400	*Astephus* basioccipital
194	V193401	*Astephus* basioccipital
195	V193402	*Astephus* basioccipital
196	V193403	*Astephus* basioccipital
197	V193404	*Astephus* basioccipital
198	V193405	*Astephus* basioccipital
199	V193406	*Astephus* basioccipital
200	V193407	*Astephus* basioccipital
201	V193408	*Astephus* pectoral fin spine B
202	V193409	*Astephus* articular
203	V193410	*Astephus* articular
204	V193411	*Astephus* articular
205	V193412	*Astephus* articular
206	V193413	*Phareodus* dentary
207	V193414	*Phareodus* dentary
208	V193415	*Phareodus* dentary
209	V193416	*Phareodus* dentary
210	V193417	*Phareodus* dentary
211	V193418	*Phareodus* premaxilla
212	V193419	*Phareodus* premaxilla
213	V193420	*Phareodus* premaxilla

214	V193421	*Phareodus* maxillary
215	V193422	*Phareodus* maxillary
216	V193423	*Phareodus* maxillary
217	V193424	*Phareodus* maxillary
218	V193425	*Phareodus* maxillary
219	V193426	Lepisosteid lacrimomaxillar
220	V193427	*Astephus* toothplate
221	V193428	*Astephus* toothplate
222	V193429	*Phareodus* basibranchial
223	V193430	*Phareodus* basibranchial
224	V193431	*Phareodus* maxilla
225	V193432	*Astephus* dentary
226	V193433	*Astephus* dentary
227	V193434	*Astephus* dentary
228	V193435	*Astephus* dentary
229	V193436	*Astephus* dentary
230	V193437	*Astephus* dentary
231	V193438	*Astephus* dentary
232	V193439	*Astephus* dentary
233	V193440	*Astephus* dentary
234	V193441	*Astephus* dentary
235	V193442	*Astephus* dentary
236	V193443	*Astephus* dentary
237	V193444	*Astephus* dentary

238	V193445	*Astephus* dentary
239	V193446	*Astephus* dentary
240	V193447	*Astephus* articular fragment
241	V193448	*Astephus* pectoral spine A
242	V193449	*Astephus* pectoral spine A
243	V193450	*Astephus* pectoral spine A
244	V193451	*Astephus* pectoral spine B
245	V193452	*Astephus* pectoral spine B
246	V193453	*Astephus* pectoral spine B
247	V193454	*Astephus* pectoral spine B
248	V193455	*Astephus* pectoral spine B
249	V193456	*Astephus* Weberian
250	V193457	*Astephus* Weberian
251	V193458	*Astephus* Weberian
252	V193459	*Astephus* Weberian
253	V193460	*Astephus* Weberian
254	V193461	*Astephus* Weberian
255	V193462	*Astephus* Weberian
256	V193463	*Astephus* Weberian
257	V193464	*Astephus* Weberian
258	V193465	*Astephus* Weberian
259	V193466	*Astephus* Weberian
260	V193467	*Astephus* Weberian
261	V193468	*Astephus* Weberian

262	V193469	*Astephus* Weberian
263	V193470	*Astephus* Weberian
264	V193471	*Astephus* Weberian
265	V193472	*Astephus* Weberian
266	V193473	*Astephus* Weberian
267	V193474	*Astephus* Weberian
268	V193475	*Astephus* Weberian
269	V193476	*Astephus* Weberian
270	V193477	*Astephus* Weberian
271	V193478	*Astephus* Weberian
272	V193479	*Astephus* abdominal
273	V193480	*Astephus* abdominal (posterior)
274	V193481	*Astephus* abdominal
275	V193482	*Astephus* abdominal
276	V193483	*Astephus* abdominal
277	V193484	*Astephus* abdominal
278	V193485	*Astephus* abdominal
279	V193486	*Astephus* abdominal
280	V193487	*Astephus* abdominal
281	V193488	*Astephus* abdominal
282	V193489	*Astephus* abdominal
283	V193490	*Astephus* abdominal
284	V193491	*Astephus* abdominal
285	V193492	*Astephus* abdominal

286	V193493	*Astephus* abdominal
287	V193494	*Astephus* abdominal
288	V193495	*Astephus* abdominal
289	V193496	*Astephus* abdominal
290	V193497	*Astephus* abdominal
291	V193498	*Astephus* abdominal
292	V193499	*Astephus* abdominal
293	V193500	*Astephus* abdominal
294	V193501	*Astephus* abdominal
295	V193502	*Astephus* abdominal
296	V193503	*Astephus* abdominal
297	V193504	*Astephus* abdominal
298	V193505	*Astephus* abdominal
299	V193506	*Astephus* abdominal
300	V193507	*Astephus* abdominal
301	V193508	*Astephus* abdominal
302	V193509	*Astephus* abdominal
303	V193510	*Astephus* abdominal
304	V193511	*Astephus* abdominal
305	V193512	*Astephus* abdominal
306	V193513	*Astephus* abdominal
307	V193514	*Astephus* abdominal
308	V193515	*Astephus* abdominal
309	V193516	*Astephus* abdominal

310	V193517	*Astephus* abdominal
311	V193518	*Astephus* abdominal
312	V193519	*Astephus* abdominal
313	V193520	*Astephus* abdominal
314	V193521	*Astephus* abdominal
315	V193522	*Astephus* abdominal
316	V193523	*Astephus* abdominal
317	V193524	*Astephus* abdominal
318	V193525	*Astephus* abdominal
319	V193526	*Astephus* abdominal
320	V193527	*Astephus* abdominal
321	V193528	*Astephus* abdominal
322	V193529	*Astephus* abdominal
323	V193530	*Astephus* abdominal
324	V193531	*Astephus* abdominal
325	V193532	*Astephus* abdominal
326	V193533	*Astephus* abdominal
327	V193534	*Astephus* abdominal
328	V193535	*Astephus* abdominal
329	V193536	*Astephus* abdominal
330	V193537	*Astephus* abdominal
331	V193538	*Astephus* abdominal
332	V193539	*Astephus* abdominal
333	V193540	*Astephus* abdominal

334	V193541	*Astephus* abdominal
335	V193542	*Astephus* abdominal
336	V193543	*Astephus* abdominal
337	V193544	*Astephus* abdominal
338	V193545	*Astephus* abdominal
339	V193546	*Astephus* abdominal
340	V193547	*Astephus* abdominal
341	V193548	*Astephus* abdominal
342	V193549	*Astephus* abdominal
343	V193550	*Astephus* abdominal
344	V193551	*Astephus* abdominal
345	V193552	*Astephus* first Weberian centrum
346	V193553	*Astephus* first Weberian centrum
347	V193554	*Astephus* first Weberian centrum
348	V193555	*Astephus* first Weberian centrum
349	V193556	*Astephus* first Weberian centrum
350	V193557	*Astephus* first Weberian centrum
351	V193558	*Astephus* first post-Weberian centrum
352	V193559	*Astephus* first post-Weberian centrum
353	V193560	*Astephus* first post-Weberian centrum
354	V193561	*Astephus* first post-Weberian centrum
355	V193562	*Astephus* first post-Weberian centrum
356	V193563	*Astephus* basioccipital
357	V193564	*Astephus* basioccipital

358	V193565	*Astephus* basioccipital
359	V193566	*Astephus* basioccipital
360	V193567	*Astephus* basioccipital
361	V193568	*Astephus* basioccipital
362	V193569	*Astephus* basioccipital
363	V193570	*Astephus* basioccipital
364	V193571	*Astephus* basioccipital
365	V193572	*Astephus* basioccipital
366	V193573	*Astephus* basioccipital
367	V193574	*Astephus* basioccipital
368	V193575	*Astephus* basioccipital
369	V193576	*Astephus* basioccipital
370	V193577	*Astephus* basioccipital
371	V193578	*Astephus* basioccipital
372	V193579	*Astephus* basioccipital
373	V193580	*Astephus* basioccipital
374	V193581	*Astephus* basioccipital
375	V193582	*Astephus* basioccipital
376	V193583	*Astephus* basioccipital
377	V193584	*Astephus* basioccipital
378	V193585	*Astephus* basioccipital
379	V193586	*Astephus* basioccipital
380	V193587	*Astephus* basioccipital
381	V193588	*Astephus* basioccipital

382	V193589	*Astephus* basioccipital
383	V193590	*Astephus* basioccipital
384	V193591	*Astephus* basioccipital
385	V193592	*Astephus* basioccipital
386	V193593	*Astephus* basioccipital
387	V193594	*Astephus* basioccipital
388	V193595	*Astephus* basioccipital
389	V193596	*Astephus* basioccipital
390	V193597	*Astephus* basioccipital
391	V193598	*Astephus* basioccipital
392	V193599	*Astephus* basioccipital
393	V193600	*Phareodus* first centrum
394	V193601	*Phareodus* first centrum
395	V193602	*Phareodus* abdominal (posterior)
396	V193603	*Phareodus* abdominal
397	V193604	*Phareodus* abdominal
398	V193605	*Phareodus* abdominal
399	V193606	*Phareodus* abdominal
400	V193607	*Phareodus* abdominal
401	V193608	*Phareodus* abdominal
402	V193609	*Phareodus* abdominal
403	V193610	*Phareodus* abdominal
404	V193611	*Phareodus* abdominal
405	V193612	*Phareodus* abdominal

406	V193613	*Phareodus* abdominal
407	V193614	*Phareodus* abdominal
408	V193615	*Phareodus* abdominal
409	V193616	*Phareodus* abdominal
410	V193617	*Phareodus* abdominal
411	V193618	*Phareodus* abdominal
412	V193619	*Phareodus* abdominal
413	V193620	*Phareodus* abdominal
414	V193621	*Phareodus* abdominal
415	V193622	*Phareodus* abdominal
416	V193623	*Phareodus* abdominal
417	V193624	*Phareodus* abdominal
418	V193625	*Phareodus* abdominal
419	V193626	*Phareodus* abdominal
420	V193627	*Phareodus* abdominal
421	V193628	*Phareodus* abdominal
422	V198894	*Phareodus* basibranchial
423	V198895	*Phareodus* premaxilla
424	V198896	*Phareodus* maxilla (mid)
425	V198897	*Phareodus* dentary
426	V198898	*Astephus* dentary
427	V198899	*Astephus* dentary
428	V198900	*Astephus* dentary
429	V198901	*Phareodus* basioccipital

430	V198902	*Astephus* basioccipital
431	V198903	*Astephus* basioccipital
432	V198904	*Astephus* basioccipital
433	V198905	*Astephus* abdominal centra (9 mid-abdominal specimens)
434	V198906	*Astephus* first Weberian centrum (4 specimens)
435	V198907	*Phareodus* posterior abdominal centra (2 specimens)
436	V198908	*Astephus* first Weberian centra (5 specimens)
437	V198909	*Astephus* abdominal (1) + *Astephus* Weberian (2)
438	V198910	*Astephus* posterior abdominals (3 specimens)
439	V198911	*Phareodus* abdominal (anterior)

APPENDIX V—WASATCH FORMATION SPECIMENS

University of California Museum of Paleontology Specimens (N = 271)

#	Specimen Number	Identification
1	V198887 Ia	Centrarchid or "*Priscacara*" vomer
2	V198887 Ib	Centrarchid or "*Priscacara*" vomer
3	V198887 Ic	Centrarchid or "*Priscacara*" vomer
4	V198887 II	Centrarchid or "*Priscacara*" fifth ceratobranchial
5	V198887 IIIa	Unid. tooth-bearing element
6	V198887 IIIb	Unid. tooth-bearing element
7	V198887 IIIc	Unid. tooth-bearing element
8	V198887 IIId	Unid. tooth-bearing element
9	V198887 IIIe	Unid. tooth-bearing element
10	V198887 Iva	*Diplomystus* dentary
11	V198887 Ivb	*Diplomystus* dentary
12	V198887 Va	Centrarchid dentary
13	V198887 Vb	Centrarchid dentary
14	V198887 Vc	Centrarchid dentary
15	V198887 Via	Centrarchid or "*Priscacara*" dentary
16	V198887 Vib	Centrarchid or "*Priscacara*" dentary
17	V198888 Ia	Centrarchid or "*Priscacara*" abdominal centrum
18	V198888 Ib	Centrarchid or "*Priscacara*" abdominal centrum
19	V198888 Ic	Centrarchid or "*Priscacara*" abdominal centrum

20	V198888 Id	Centrarchid or "*Priscacara*" abdominal centrum
21	V198888 Ie	Centrarchid or "*Priscacara*" abdominal centrum
22	V198888 If	Centrarchid or "*Priscacara*" abdominal centrum
23	V198888 Ig	Centrarchid or "*Priscacara*" abdominal centrum
24	V198888 Ih	Centrarchid or "*Priscacara*" abdominal centrum
25	V198888 Ii	Centrarchid or "*Priscacara*" abdominal centrum
26	V198888 Ij	Centrarchid or "*Priscacara*" abdominal centrum
27	V198888 Ik	Centrarchid or "*Priscacara*" abdominal centrum
28	V198888 Il	Centrarchid or "*Priscacara*" abdominal centrum
29	V198888 Im	Centrarchid or "*Priscacara*" abdominal centrum
30	V198888 In	Centrarchid or "*Priscacara*" abdominal centrum
31	V198888 Io	Centrarchid or "*Priscacara*" abdominal centrum
32	V198888 Ip	Centrarchid or "*Priscacara*" abdominal centrum
33	V198888 Iq	Centrarchid or "*Priscacara*" abdominal centrum
34	V198888 Ir	Centrarchid or "*Priscacara*" abdominal centrum
35	V198888 Is	Centrarchid or "*Priscacara*" abdominal centrum
36	V198888 It	Centrarchid or "*Priscacara*" abdominal centrum
37	V198888 Iu	Centrarchid or "*Priscacara*" abdominal centrum
38	V198888 Iv	Centrarchid or "*Priscacara*" abdominal centrum
39	V198888 Iw	Centrarchid or "*Priscacara*" abdominal centrum
40	V198888 Ix	Centrarchid or "*Priscacara*" abdominal centrum
41	V198888 IIa	*Diplomystus* abdominal centrum
42	V198888 IIb	*Diplomystus* abdominal centrum
43	V198888 IIc	*Diplomystus* abdominal centrum

44	V198888 IIIa	*Notogoneus* abdominal centrum
45	V198888 IIIb	*Notogoneus* abdominal centrum
46	V198888 IIIc	*Notogoneus* abdominal centrum
47	V198888 IIId	*Notogoneus* abdominal centrum
48	V198888 IIIe	*Notogoneus* abdominal centrum
49	V198888 IVa	Centrarchid first centrum
50	V198888 IVb	Centrarchid first centrum
51	V198888 IVc	Centrarchid first centrum
52	V198888 V	*Notogoneus* basioccipital
53	V198888 VIa	*Diplomystus* basioccipital
54	V198888 VIb	*Diplomystus* basioccipital
55	V198888 VIc	*Diplomystus* basioccipital
56	V198888 VId	*Diplomystus* basioccipital
57	V198888 VII a	*Notogoneus* Weberian centrum
58	V198888 VII b	*Notogoneus* Weberian centrum
59	V198888 VII c	*Notogoneus* Weberian centrum
60	V198888 VIII a	aff. Amblyopsidae first centrum
61	V198888 VIII b	aff. Amblyopsidae first centrum
62	V198888 VIII c	aff. Amblyopsidae first centrum
63	V198888 VIII d	aff. Amblyopsidae first centrum
64	V198888 VIII e	aff. Amblyopsidae first centrum
65	V198888 IX	*Notogoneus* abdominal centrum
66	V198888 X a	*Diplomystus* abdominal centrum
67	V198888 X b	*Diplomystus* abdominal centrum

68	V198888 X c	*Diplomystus* abdominal centrum
69	V198888 X d	*Diplomystus* abdominal centrum
70	V198888 X e	*Diplomystus* abdominal centrum
71	V198888 X f	*Diplomystus* abdominal centrum
72	V198888 X g	*Diplomystus* abdominal centrum
73	V198888 X h	*Diplomystus* abdominal centrum
74	V198888 X i	*Diplomystus* abdominal centrum
75	V198888 X j	*Diplomystus* abdominal centrum
76	V198888 XI a	Centrarchidae or "*Priscacara*" abdominal centrum
77	V198888 XI b	Centrarchidae or "*Priscacara*" abdominal centrum
78	V198888 XI c	Centrarchidae or "*Priscacara*" abdominal centrum
79	V198888 XI d	Centrarchidae or "*Priscacara*" abdominal centrum
80	V198888 XI e	Centrarchidae or "*Priscacara*" abdominal centrum
81	V198888 XI f	Centrarchidae or "*Priscacara*" abdominal centrum
82	V198888 XI g	Centrarchidae or "*Priscacara*" abdominal centrum
83	V198888 XI h	Centrarchidae or "*Priscacara*" abdominal centrum

84	V198888 XI i	Centrarchidae or "*Priscacara*" abdominal centrum
85	V198888 XI j	Centrarchidae or "*Priscacara*" abdominal centrum
86	V198888 XI k	Centrarchidae or "*Priscacara*" abdominal centrum
87	V198888 XI l	Centrarchidae or "*Priscacara*" abdominal centrum
88	V198888 XI m	Centrarchidae or "*Priscacara*" abdominal centrum
89	V198888 XI n	Centrarchidae or "*Priscacara*" abdominal centrum
90	V198888 XI o	Centrarchidae or "*Priscacara*" abdominal centrum
91	V198888 XI p	Centrarchidae or "*Priscacara*" abdominal centrum
92	V198888 XI q	Centrarchidae or "*Priscacara*" abdominal centrum
93	V198888 XI r	Centrarchidae or "*Priscacara*" abdominal centrum
94	V198888 XI s	Centrarchidae or "*Priscacara*" abdominal centrum
95	V198888 XII a	*Notogoneus* abdominal centrum
96	V198888 XII b	*Notogoneus* abdominal centrum

97	V198888 XII c	*Notogoneus* abdominal centrum
98	V198888 XII d	*Notogoneus* abdominal centrum
99	V198888 XII e	*Notogoneus* abdominal centrum
100	V198888 XIII a	aff. Amblyopsidae abdominal centrum
101	V198888 XIII b	aff. Amblyopsidae abdominal centrum
102	V198888 XIII c	aff. Amblyopsidae abdominal centrum
103	V198888 XIII d	aff. Amblyopsidae abdominal centrum
104	V198888 XIII e	aff. Amblyopsidae abdominal centrum
105	V198889 I a	Centrarchidae or "*Priscacara*" first centrum
106	V198889 I b	Centrarchidae or "*Priscacara*" first centrum
107	V198889 I c	Centrarchidae or "*Priscacara*" first centrum
108	V198889 II	aff. Amblyopsidae first centrum
109	V198889 III a	*Notogoneus* Weberian centrum
110	V198889 III b	*Notogoneus* Weberian centrum
111	V198889 IV a	*Diplomystus* basioccipital
112	V198889 IV b	*Diplomystus* basioccipital
113	V198889 IV c	*Diplomystus* basioccipital
114	V198889 V a	*Diplomystus* abdominal centrum
115	V198889 V b	*Diplomystus* abdominal centrum
116	V198889 V c	*Diplomystus* abdominal centrum
117	V198889 V d	*Diplomystus* abdominal centrum
118	V198889 V e	*Diplomystus* abdominal centrum
119	V198889 V f	*Diplomystus* abdominal centrum
120	V198889 VI a	Centrarchidae or "*Priscacara*" abdominal centrum

121	V198889 VI b	Centrarchidae or "*Priscacara*" abdominal centrum
122	V198889 VI c	Centrarchidae or "*Priscacara*" abdominal centrum
123	V198889 VI d	Centrarchidae or "*Priscacara*" abdominal centrum
124	V198889 VI e	Centrarchidae or "*Priscacara*" abdominal centrum
125	V198889 VI f	Centrarchidae or "*Priscacara*" abdominal centrum
126	V198889 VI g	Centrarchidae or "*Priscacara*" abdominal centrum
127	V198889 VI h	Centrarchidae or "*Priscacara*" abdominal centrum
128	V198889 VI i	Centrarchidae or "*Priscacara*" abdominal centrum
129	V198889 VI j	Centrarchidae or "*Priscacara*" abdominal centrum
130	V198889 VI k	Centrarchidae or "*Priscacara*" abdominal centrum
131	V198889 VI l	Centrarchidae or "*Priscacara*" abdominal centrum
132	V198889 VI m	Centrarchidae or "*Priscacara*" abdominal centrum

133	V198889 VI n	Centrarchidae or "*Priscacara*" abdominal centrum
134	V198889 VI o	Centrarchidae or "*Priscacara*" abdominal centrum
135	V198889 VI p	Centrarchidae or "*Priscacara*" abdominal centrum
136	V198889 VI q	Centrarchidae or "*Priscacara*" abdominal centrum
137	V198889 VI r	Centrarchidae or "*Priscacara*" abdominal centrum
138	V198889 VI s	Centrarchidae or "*Priscacara*" abdominal centrum
139	V198889 VII a	*Notogoneus* abdominal centrum
140	V198889 VII b	*Notogoneus* abdominal centrum
141	V198889 VII c	*Notogoneus* abdominal centrum
142	V198889 VII d	*Notogoneus* abdominal centrum
143	V198889 VII e	*Notogoneus* abdominal centrum
144	V198889 VII f	*Notogoneus* abdominal centrum
145	V198889 VII g	*Notogoneus* abdominal centrum
146	V198889 VII h	*Notogoneus* abdominal centrum
147	V198889 VII i	*Notogoneus* abdominal centrum
148	V198890 I a	*Diplomystus* abdominal centrum
149	V198890 I b	*Diplomystus* abdominal centrum
150	V198890 II a	*Diplomystus* abdominal centrum

151	V198890 II b	*Diplomystus* abdominal centrum
152	V198890 II c	*Diplomystus* abdominal centrum
153	V198890 II d	*Diplomystus* abdominal centrum
154	V198890 III a	*Notogoneus* abdominal centrum
155	V198890 III b	*Notogoneus* abdominal centrum
156	V198890 III c	*Notogoneus* abdominal centrum
157	V198890 IV	*Notogoneus* abdominal centrum
158	V198890 V	*Notogoneus* basioccipital
159	V198890 VI a	*Notogoneus* Weberian centrum
160	V198890 VI b	*Notogoneus* Weberian centrum
161	V198890 VII a	Centrarchidae or "*Priscacara*" abdominal centrum
162	V198890 VII b	Centrarchidae or "*Priscacara*" abdominal centrum
163	V198890 VII c	Centrarchidae or "*Priscacara*" abdominal centrum
164	V198890 VII d	Centrarchidae or "*Priscacara*" abdominal centrum
165	V198890 VII e	Centrarchidae or "*Priscacara*" abdominal centrum
166	V198890 VII f	Centrarchidae or "*Priscacara*" abdominal centrum
167	V198890 VII g	Centrarchidae or "*Priscacara*" abdominal centrum

168	V198890 VII h	Centrarchidae or "*Priscacara*" abdominal centrum
169	V198890 VII i	Centrarchidae or "*Priscacara*" abdominal centrum
170	V198890 VII j	Centrarchidae or "*Priscacara*" abdominal centrum
171	V198890 VII k	Centrarchidae or "*Priscacara*" abdominal centrum
172	V198890 VII l	Centrarchidae or "*Priscacara*" abdominal centrum
173	V198890 VII m	Centrarchidae or "*Priscacara*" abdominal centrum
174	V198890 VII n	Centrarchidae or "*Priscacara*" abdominal centrum
175	V198890 VII o	Centrarchidae or "*Priscacara*" abdominal centrum
176	V198890 VII p	Centrarchidae or "*Priscacara*" abdominal centrum
177	V198890 VII q	Centrarchidae or "*Priscacara*" abdominal centrum
178	V198890 VII r	Centrarchidae or "*Priscacara*" abdominal centrum
179	V198890 VII s	Centrarchidae or "*Priscacara*" abdominal centrum

180	V198890 VII t	Centrarchidae or "*Priscacara*" abdominal centrum
181	V198890 VII u	Centrarchidae or "*Priscacara*" abdominal centrum
182	V198890 VII v	Centrarchidae or "*Priscacara*" abdominal centrum
183	V198890 VII w	Centrarchidae or "*Priscacara*" abdominal centrum
184	V198890 VII x	Centrarchidae or "*Priscacara*" abdominal centrum
185	V198890 VIII	aff. Amblyopsidae first centrum
186	V198890 IX	Centrarchidae or "*Priscacara*" first centrum
187	V198890 X	aff. Amblyopsidae abdominal
188	V198891 I a	*Diplomystus* abdominal centrum
189	V198891 I b	*Diplomystus* abdominal centrum
190	V198891 I c	*Diplomystus* abdominal centrum
191	V198891 I d	*Diplomystus* abdominal centrum
192	V198891 I e	*Diplomystus* abdominal centrum
193	V198891 I f	*Diplomystus* abdominal centrum
194	V198891 II a	Centrarchidae or "*Priscacara*" abdominal centrum
195	V198891 II b	Centrarchidae or "*Priscacara*" abdominal centrum
196	V198891 II c	Centrarchidae or "*Priscacara*" abdominal centrum

197	V198891 II d	Centrarchidae or "*Priscacara*" abdominal centrum
198	V198891 II e	Centrarchidae or "*Priscacara*" abdominal centrum
199	V198891 II f	Centrarchidae or "*Priscacara*" abdominal centrum
200	V198891 II g	Centrarchidae or "*Priscacara*" abdominal centrum
201	V198891 II h	Centrarchidae or "*Priscacara*" abdominal centrum
202	V198891 II i	Centrarchidae or "*Priscacara*" abdominal centrum
203	V198891 II j	Centrarchidae or "*Priscacara*" abdominal centrum
204	V198891 II k	Centrarchidae or "*Priscacara*" abdominal centrum
205	V198891 II l	Centrarchidae or "*Priscacara*" abdominal centrum
206	V198891 II m	Centrarchidae or "*Priscacara*" abdominal centrum
207	V198891 II n	Centrarchidae or "*Priscacara*" abdominal centrum
208	V198891 II o	Centrarchidae or "*Priscacara*" abdominal centrum

209	V198891 II p	Centrarchidae or "*Priscacara*" abdominal centrum
210	V198891 II q	Centrarchidae or "*Priscacara*" abdominal centrum
211	V198891 II r	Centrarchidae or "*Priscacara*" abdominal centrum
212	V198891 II s	Centrarchidae or "*Priscacara*" abdominal centrum
213	V198891 III a	*Notogoneus* abdominal centrum
214	V198891 III b	*Notogoneus* abdominal centrum
215	V198891 III c	*Notogoneus* abdominal centrum
216	V198891 IV a	Centrarchidae first centrum
217	V198891 IV b	Centrarchidae first centrum
218	V198891 IV c	Centrarchidae first centrum
219	V198891 V a	*Notogoneus* Weberian centrum
220	V198891 V b	*Notogoneus* Weberian centrum
221	V198891 V c	*Notogoneus* Weberian centrum
222	V198891 VI a	*Notogoneus* abdominal centrum
223	V198891 VI b	*Notogoneus* abdominal centrum
224	V198891 VI c	*Notogoneus* abdominal centrum
225	V198891 VII	*Notogoneus* basioccipital
226	V198891 VIII a	aff. Amblyopsidae first centrum
227	V198891 VIII b	aff. Amblyopsidae first centrum
228	V198891 VIII c	aff. Amblyopsidae first centrum

229	V198891 VIII d	aff. Amblyopsidae first centrum
230	V198891 VIII e	aff. Amblyopsidae first centrum
231	V198891 VIII f	aff. Amblyopsidae first centrum
232	V198891 VIII g	aff. Amblyopsidae first centrum
233	V198891 IX a	aff. Amblyopsidae abdominal centrum
234	V198891 IX b	aff. Amblyopsidae abdominal centrum
235	V198891 X a	Centrarchidae or "*Priscacara*" abdominal centrum
236	V198891 X b	Centrarchidae or "*Priscacara*" abdominal centrum
237	V198891 X c	Centrarchidae or "*Priscacara*" abdominal centrum
238	V198891 X d	Centrarchidae or "*Priscacara*" abdominal centrum
239	V198891 X e	Centrarchidae or "*Priscacara*" abdominal centrum
240	V198891 X f	Centrarchidae or "*Priscacara*" abdominal centrum
241	V198891 X g	Centrarchidae or "*Priscacara*" abdominal centrum
242	V198891 X h	Centrarchidae or "*Priscacara*" abdominal centrum
243	V198891 X i	Centrarchidae or "*Priscacara*" abdominal centrum

244	V198891 X j	Centrarchidae or "*Priscacara*" abdominal centrum
245	V198892 I	*Notogoneus* abdominal centrum
246	V198892 II a	*Notogoneus* abdominal centrum
247	V198892 II b	*Notogoneus* abdominal centrum
248	V198892 III a	*Diplomystus* abdominal centrum
249	V198892 III b	*Diplomystus* abdominal centrum
250	V198892 III c	*Diplomystus* abdominal centrum (pathological; fused to d)
251	V198892 III d	*Diplomystus* abdominal centrum (pathological; fused to c)
252	V198892 IV a	*Diplomystus* abdominal centrum
253	V198892 IV b	*Diplomystus* abdominal centrum
254	V198892 V a	*Notogoneus* abdominal centrum
255	V198892 V b	*Notogoneus* abdominal centrum
256	V198892 VI	Centrarchidae first centrum
257	V198892 VII a	Centrarchidae or "*Priscacara*" abdominal centrum
258	V198892 VII b	Centrarchidae or "*Priscacara*" abdominal centrum
259	V198892 VII c	Centrarchidae or "*Priscacara*" abdominal centrum
260	V198892 VII d	Centrarchidae or "*Priscacara*" abdominal centrum

261	V198892 VII e	Centrarchidae or "*Priscacara*" abdominal centrum
262	V198892 VII f	Centrarchidae or "*Priscacara*" abdominal centrum
263	V198892 VII g	Centrarchidae or "*Priscacara*" abdominal centrum
264	V198892 VII h	Centrarchidae or "*Priscacara*" abdominal centrum
265	V198892 VII i	Centrarchidae or "*Priscacara*" abdominal centrum
266	V198892 VII j	Centrarchidae or "*Priscacara*" abdominal centrum
267	V198892 VII k	Centrarchidae or "*Priscacara*" abdominal centrum
268	V198892 VII l	Centrarchidae or "*Priscacara*" abdominal centrum
269	V198893 I a	Centrarchid or "*Priscacara*" vomer
270	V198893 I b	Centrarchid or "*Priscacara*" vomer
271	V198893	Unid. jaw elements