makeup of the teeth. Placement of *Myledaphus* within the Rhinobatoidei has become quite widely accepted in recent years.

Here we report a nearly complete specimen of *Myledaphus* from Dinosaur Provincial Park complete with jaws that show the typical hexagonal teeth arranged in a tight, honeycomb formation and well-preserved vertebrae. The specimen is covered with skin denticles that outline the shape of the body and encrust the surface of the fossil. This fossil confirms the association of centra and denticles with the characteristic teeth.

Preliminary study identifies several features that support the association of *Myledaphus* with the rhinobatoids. The pectoral fins are moderately large and not expanded anterior to the eyes. They are more or less fused to the head, forming a somewhat angular disk. The pelvic fins are not divided into lobes and their origins are anterior to the free rear tips of the pectorals, such that there is overlap between these fins. The specimen is most similar to rhinobatoids in body shape and fin morphology.

The rostral region in from of the mouth is well preserved in the specimen under study, but is only partially prepared at this time. It does not resemble the rostral region of stingrays. It is slightly elongated, but not as much as in the typical guitarfishes (*Rhinobatos*), being more like the extant banded guitarfish *Zapteryx* and some of the thornbacks, like *Platyrhinoidis*. *Myledaphus* is very similar in this feature to the Cretaceous genus *Iansan* from Brazil. Further preparation and study will certainly uncover more clearly the relationships of *Myledaphus*.

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Recognition of annular growth on centra of Teleostei with application to Hiodontidae of the Cretaceous Dinosaur Park Formation

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Introduction

The oldest hiodontid fossils from North America are from the Campanian of Alberta and Saskatchewan but are represented only by isolated centra (Brinkman and Neuman, 2002). As such, very little is known about the taxonomic affinities, morphology, life history characteristics, and paleoecology of the taxon or taxa represented by the Cretaceous centra. Here we describe criteria for defining annular bone deposition on the fossil centra, which can be used to study the age and growth characteristics of Hiodontidae from the Cretaceous Dinosaur Park Formation.

Modern *Hiodon* exhibits a variety of growth-related characteristics useful for comparison to the Cretaceous centra including longevity, maximum size, growth rates, and sexual size dimorphism. In growth studies of extant *Hiodon*, scales or opercula are typically aged (Carlander, 1969; Donald et al., 1992) and growth can be estimated because growth of hard structures and total length are generally correlated (Carlander, 1969). Because the Dinosaur

Park Formation only produces isolated hiodontid centra, new criteria were needed to characterize annuli on both fossil and extant centra to allow a comparative analysis of growth. The objectives of this research are to: 1) use annuli on opercula to determine the age of dried museum skeletons of extant hiodontids; 2) examine centra from the same museum specimens to describe criteria for identification of annuli; 3) test the criteria by comparing age estimates based on various structures; and 4) use the new criteria to examine the Dinosaur Park Formation centra for annuli and determine the age and growth of the fossil individuals.

Materials and methods

Extant Taxa

Extant *Hiodon* is only found in North America and is represented by two freshwater species, *H. alosoides* Rafinesque and *H. tergisus* Lesueur. The genus ranges in latitude from the Arctic (68°N) to the Gulf Coast of Louisiana (30°N) (Lee et al., 1980). *Hiodon* can live to at least 16 years of age (Donald et al., 1992) and exhibit sexual size dimorphism, with females attaining larger sizes (Scott and Crossman, 1973).

Material Examined

Opercula and centra from 12 dried skeletons of *H. alosoides* were examined: two skeletons from the Natural History Museum and Biodiversity Research Center (KU), University of Kansas, 12728 and 12730; and 10 skeletons from the Bell Museum of Natural History (JFBM), University of Minnesota, 38800, 40126, 41718, 43306, 43308, 43310, 43311, 43312, 43313, and 43314. Opercula and centra from four skeletons of *H. tergisus* were also examined (JFBM 41120, 43320, 43331, 43332).

Nine fossil centra from the Dinosaur Park Formation (Brinkman and Neuman 2002) were examined in the Royal Tyrrell Museum (TMP) collection: 86.53.81, 86.179.6, 86.198.42, 87.153.39, 90.113.57b, 90.115.50a, 93.93.94, 95.163.44b, and 2000.6.3.

Meristic Data and Measurements

Opercula are commonly used to determine age of extant hiodontids. Opercula have been found to produce the most reliable age assignments (Donald et al., 1992) and thus we examined the effectiveness of ageing centra by comparing ages obtained from opercula and centra from various individuals. We identified opercular annuli as thin translucent bands that were separated by broad, more opaque bands, and then recorded the total number of annuli to determine age following methods described in Donald et al. (1992). Pairs of opaque and translucent bands were sometimes noted on opercula of individuals greater than three years of age; these bands combined dorsally and ventrally and were counted as a single annulus. To assess growth, the diagonal distance to the nearest 0.01 mm was recorded from the point just posterior to the hyomandibular articulation facet to each annulus toward the posteroventral margin (Fig. 1A). The validity of opercular age assignments was tested using the Von Bertalanffy (1938) growth equation in SYSTAT® version 10.0 (2002); valid age assignments typically produce realistic and significant maximum size (i.e., L_∞ and DD_∞) and K growth parameters at the 95% confidence interval (Burnham-Curtis and Bronte, 1996):

$$DD_t = DD_\infty\,[1 - e^{-K(t-t_0)}]$$

where:

DD_t = opercular diagonal distance (mm) at t (age in years);
DD_∞ = maximum diagonal distance;
K = the Brody growth coefficient;
t = time (i.e., age in years);
t_0 = time at age zero (time at theoretical zero distance).

Sixteen centra from extant individuals were examined for repeating patterns in circuli using a binocular microscope. To examine for annular features, light was angled at 45° across the surface to highlight relief. A preliminary assessment showed that broad opaque bands coinciding with raised, papilose surfaces often preceded thin translucent bands in a repeating pattern (Fig. 1B). Because growth during summer (i.e., raised bands) is presumed to be greater than that during winter in extant *Hiodon,* the thin translucent bands on the centra are hypothesized to be annuli. To assess growth, the center of the notochord foramen was marked using an ocular grid and radial distance (mm) to each translucent band toward the lateral margin was determined to the nearest 0.01 mm using a digital micrometer under a binocular dissecting microscope. To determine measurement error, we calculated the difference between two measurements for an annulus from 28 randomly selected annuli in 12 extant *Hiodon* centra; the mean measurement error was 0.06 ± 0.01 s.e. mm. To verify the validity of age estimates based on centra, we compared age estimates of centra to those based on opercula. To assess the feasibility of an age and growth study of fossil specimens, nine centra from the Dinosaur Park Formation were also examined for similar yearly markings (i.e., raised/papilose band followed by a thinner band) using the methodology applied to extant Hiodon centra.

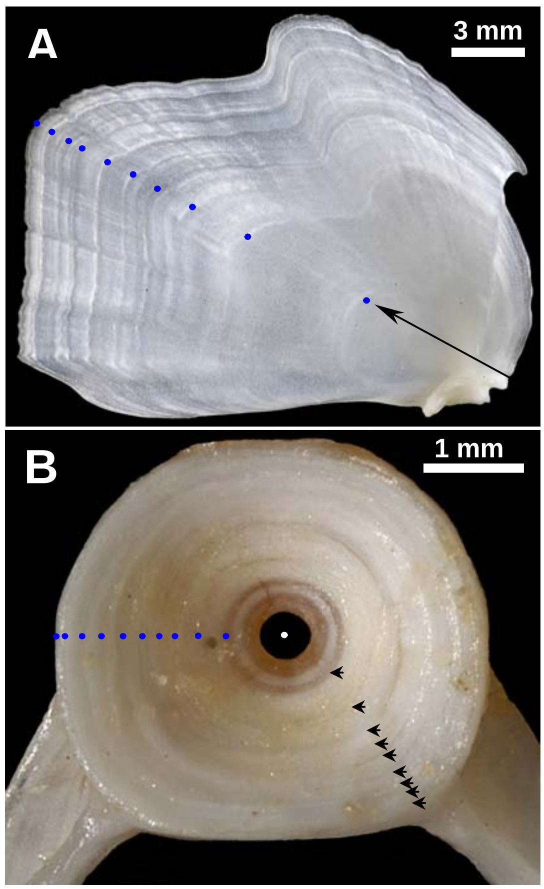

Figure 1. Operculum and centrum of extant *Hiodon alosoides* (KU 12730) collected 14 February 1968 from a latitude of 39°N: (A) medial view, posterior oriented toward the top, of the left operculum exhibiting 10 annuli and points of measurement used to determine growth; (B) anterior view of an abdominal centrum (dorsal side up), showing 10 annuli as translucent bands (arrows) and points of measurement (filled circles) used to determine growth.

Results

Ages obtained from opercula and centra of extant *Hiodon* individuals ranged from 5-11 years. Opercular measurements and age estimates produced significant Von Bertalanffy growth parameters (95% confidence interval from lowest to highest of all opercula: DD_{∞}, 14.213 to 31.872; K, 0.098 to 0.796), indicating proper age assignments and asymptotic growth curves (Fig. 2). Extant *Hiodon* centra provided the same age estimates as opercula, confirming our interpretation of annuli on centra as illustrated in Figure 3. Growth patterns of centra tended to be more linear than that of opercula and growth in centra tapered off after age 9 e.g., KU 12730 (Fig. 4).

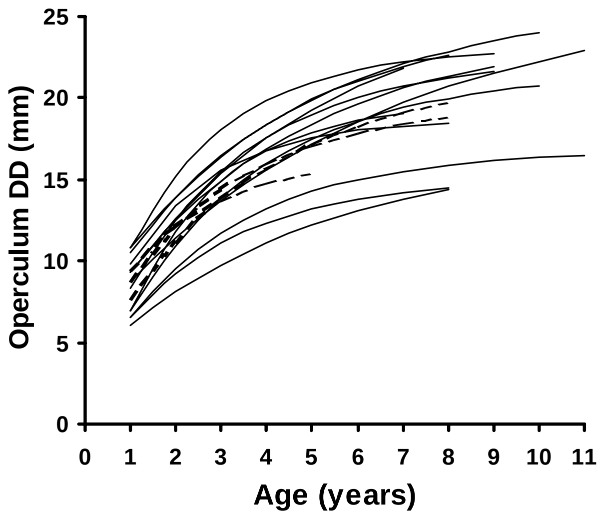

Figure 2. Von Bertalanffy growth curves from opercula of extant *Hiodon alosoides* (solid lines) and *H. tergisus* (broken lines) based on operculum diagonal distances (DD); all growth curves have significant DD_{∞} and K growth parameters (n = 16).

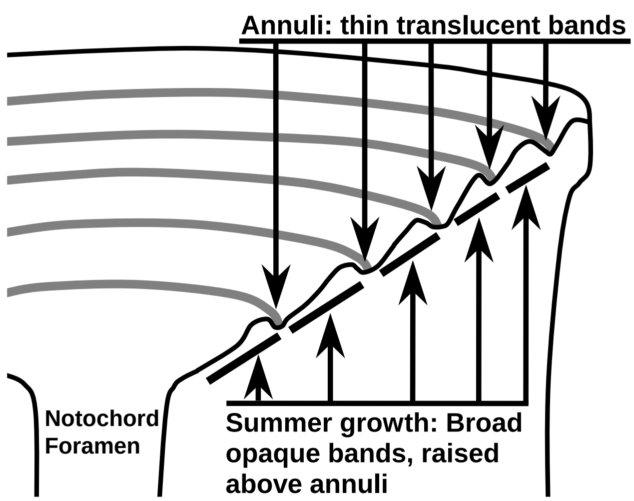

Figure 3. A hypothetical longitudinal section through a centrum of extant *Hiodon* in lateral view, anterior oriented toward the top, showing the pattern of annuli with respect to summer growth. Magnification is about 40X.

Similar to the annuli in extant *Hiodon*, centra from the Dinosaur Park Formation exhibit dark colored bands, a fine-papilosed surface, and circular ridges (Fig. 5). Annuli following the ridges were nondescript, so measurements were taken at points immediately following the ridges. Individual Dinosaur Park Formation centra that exhibit numerous repetitive ridges and bands tended to show crowding near the margin similar to extant *Hiodon* that approach asymptotic growth (Figs. 1B, 2B).

The data from extant *Hiodon* show a maximum longevity of up to 12 years, but preliminary data from the Cretaceous hiodontids show they only lived to six years of age. The mean centrum radial distance in extant *Hiodon* at age 2 was 0.86 ± 0.03 s.e. mm, but the Dinosaur Park Formation centra at age 2 were smaller, 0.41 ± 0.04 s.e. mm. In extant *Hiodon*, mean centrum radial distance at age 2 was 52% larger than those of the Cretaceous centra at the same age (Fig. 6).

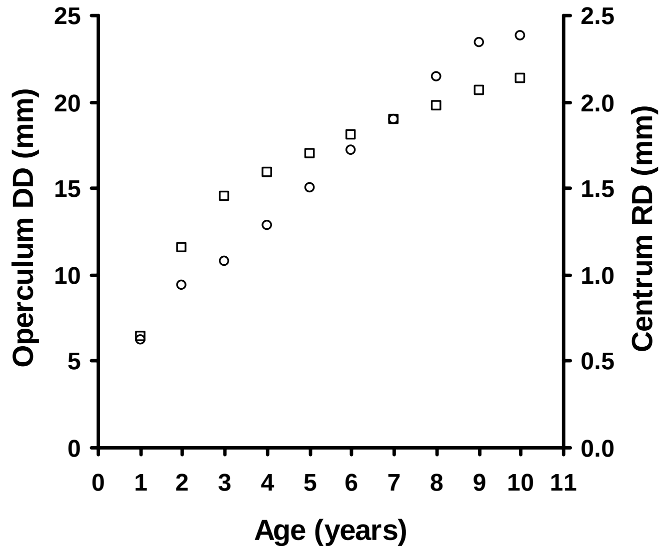

Figure 4. A comparison of growth patterns in extant *Hiodon alosoides* (KU 12730) derived from left operculum diagonal distance (DD) (squares) and centrum radial distance (RD) (circles).

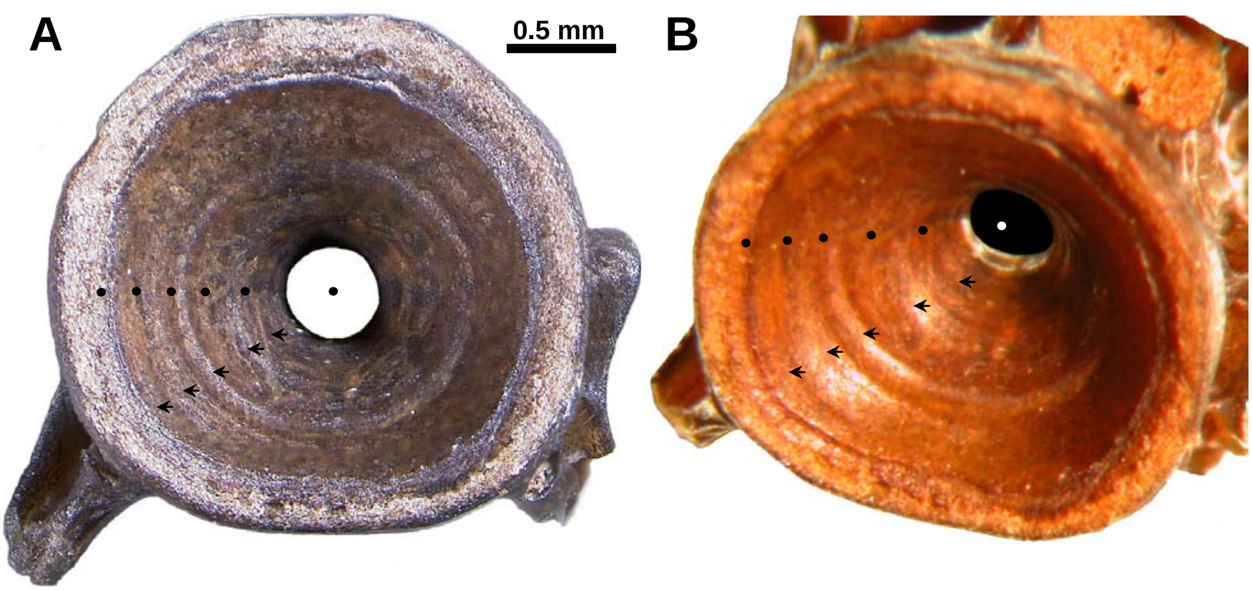

Figure 5. A hiodontid centrum (TMP 86.198.42) from the Dinosaur Park Formation; five seasons of summer growth are indicated by arrows; filled circles indicate the points of measurement after summer growth; (A) anterior view from which the measurements were made; (B) circular ridges (i.e., summer growth) are highlighted with angled light.

Discussion

Circular ridges and dark bands on the Dinosaur Park Formation centra were assumed to represent summer deposition of bone as in extant *Hiodon*. Cretaceous hiodontid annuli were probably produced during cooler seasons and periods of lower productivity, which were both modulated by annual variability in solar radiation at the moderately high paleolatitude of the fossil localities. It can be argued that in tropical systems annuli may be difficult to detect due to the lack of seasonality (Tesch, 1971). At low latitudes, growth is relatively constant throughout the year, with day and night length relatively equal year round and with minimal seasonal temperature fluctuation. The problems with depositing annuli in the Cretaceous tropical to subtropical systems could also be a factor in detecting annuli. For example, Cretaceous water temperatures have been reported to be about 13-25°C, indicating subtropical to tropical conditions (He et al., 2005), but these temperatures probably didn't affect the deposition of annuli. The fossil localities in Alberta and Saskatchewan are currently located at ~50°N, but occurred farther north in the Cretaceous at a paleolatitude of ~59°N (calculated from PLATES, Ian Dalziel, University of Texas). At 59°N solar radiation would have varied in a seasonal manner similar to that at Lake Athabasca, Saskatchewan today. Lake Athabasca currently experiences approximately six hours of daylight in December and 18 hours in June. Temperature in the Cretaceous aquatic systems would have varied with seasonal changes in solar radiation and affected fish growth similar to the effects of seasonality and temperature on extant fish growth (Le Cren, 1958; Gerking, 1966). Seasonal changes in solar radiation also affect primary productivity and subsequently yearly fish growth (Weatherley, 1972).

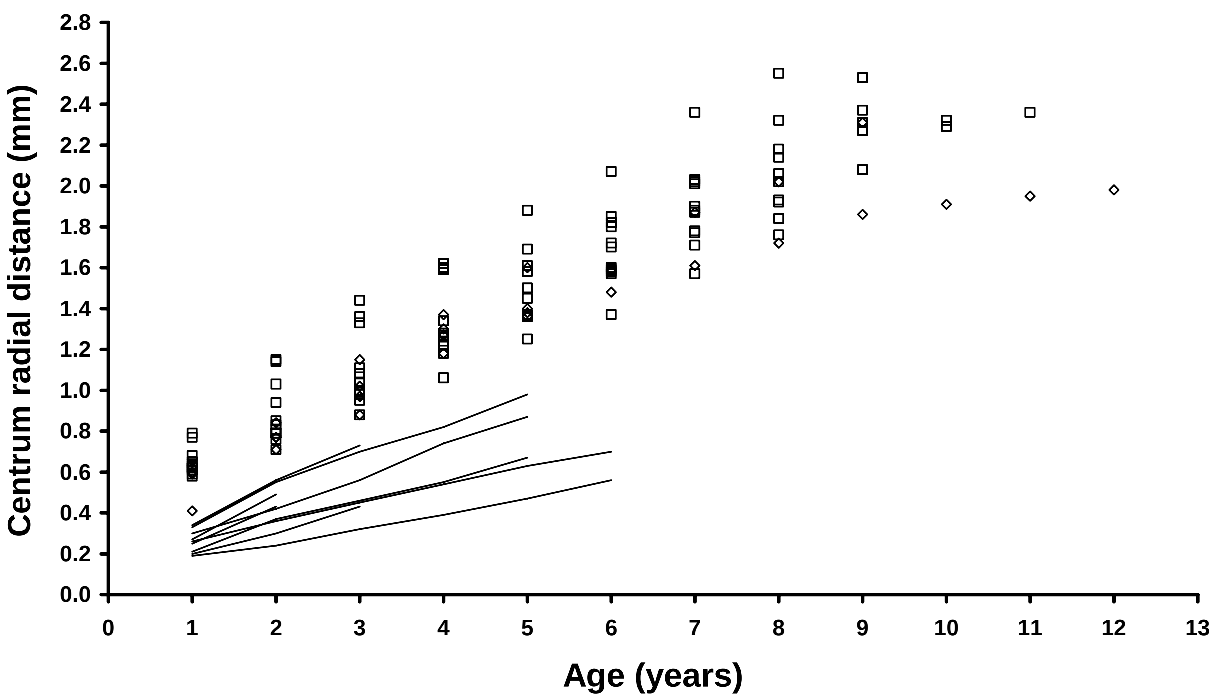

Figure 6. The relationship between age and centrum radial distance for *Hiodon alosoides* (squares) and *H. tergisus* (diamonds) in contrast to the Dinosaur Park Formation hiodontids studied (lines).

We observed variability in color of annular bands among Dinosaur Park Formation centra. Some fossil centra exhibited circular ridges with dark brown bands while others lacked dark brown bands. We believe this to be a preservation artifact because no taxonomically distinctive morphological features could be detected between the various centra.

The growth patterns of Dinosaur Park Formation centra are generally similar to those on extant centra of *Hiodon*. In extant *Hiodon*, the growth patterns of centra appear to be more linear than that of opercula. Centra do not show an asymptotic growth pattern as clearly as opercula because centra continue to grow even after an individual reaches asymptotic total length, unlike opercula, which grow in a more deterministic manner. Casselman (1990) documented similar growth differences between cleithra, scales, and otoliths in *Esox*. Nevertheless, one specimen of *Hiodon* (KU 12730) reveals that centrum growth slowed considerably after age 9.

This preliminary research suggests that body size and longevity differences may exist between the extant and Cretaceous forms of *Hiodon* and thus demonstrates a potential application and importance for age and growth studies in Cretaceous ecosystems. The Dinosaur Park Formation hiodontid centra are 48% smaller than those of Recent *Hiodon* and the longevity of Cretaceous hiodontids appears to have been shorter than modern *Hiodon*. However, a larger sample size is necessary before definitive conclusions about growth can be made. Future research will entail the examination of approximately 80 hiodontid centra from the Dinosaur Park Formation for age and growth characteristics. Furthermore, future research will also include an analysis of the age and growth characteristics of Eocene hiodontids.

The described method also has applications to other fossil fish taxa found in the Dinosaur Park Formation. Brinkman and Neuman (2002) reported numerous morphotypes of centra representing a variety of teleost taxa (e.g., esocoid, osteoglossid, gonorynchid, etc.). These taxa also are reported from other fossil localities in the geologic record and have extant representatives that would enable comparisons for age and growth studies. In the future, research into the age and growth of other taxa from the Dinosaur Park Formation will be necessary to learn more about the evolution and paleoecology of its fishes.

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Developing a digital atlas from well-preserved materials: centrosaurine ceratopsian foot morphology based on nearly complete and articulated materials

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A nearly complete right hind limb of a centrosaurine ceratopsian from the Sage Creek Locality of the Late Cretaceous (Campanian) Dinosaur Park Formation of southern Alberta provides important information regarding the structure and function of the pelvic limb in this group. As preservation of complete and articulated manual or pedal components of the appendicular skeleton is rare in ceratopsians, the presence of a nearly complete right pes in the Sage Creek centrosaurine has the potential to add important information to our understanding of the centrosaurine pes morphology, hind limb posture, and realistic range of locomotor behavior. The elements of the right foot indicate that metatarsals I-IV were closely packed and tightly bound. Fortuitous preservation of metatarsals I and II, and complete preparation of metatarsal IV indicate that the metatarsals articulated with one another medio-laterally with high congruence, creating a very tight union and allowing little, if any, splay. Each of the completely prepared elements was subjected to three-dimensional digital scanning in order to: (1) create a digital atlas of the skeletal elements, and (2) provide a means to more readily test differing hypotheses of pedal morphology and posture.