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Microstratigraphic variation in preservational patterns and meristic counts of *Amyzon aggregatum* (Teleostei: Catostomidae) from a 10 000-year interval of the Eocene varved lake deposits of Horsefly, British Columbia

by

Douglas G. Barton 

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

Department of Biological Sciences

University of Alberta

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Microstratigraphic variation in preservational patterns and meristic counts of *Amyzon aggregatum* (Teleostei: Catostomidae) from a 10 000-year interval of the Eocene varved lake deposits of Horsefly, British Columbia** submitted by **Douglas G. Barton** in partial fulfillment of the requirements for the degree of **Master of Science**.

Dr. M. V. H. Wilson, Supervisor

Dr. R. C. Fox

Dr. J. S. Nelson

Dr. N. Lovell

Date June 15, 1998

ABSTRACT

The 10 000-year H3 interval of the Eocene Horsefly locality in British Columbia is ideal for microstratigraphic studies. The sediments are preserved in yearly laminations, or varves, which allow study of variation in ecological and morphological characters with an exceptionally high temporal resolution. A taphonomic study of the fish supports a lake model for the H3 section in which the bottom waters are perennially anoxic (or hypoxic), but surface waters overturn regularly (monomictic or dimictic). Temporal trends in the preservation of fish suggest longer-term cycles of shallowing and deepening of the deposit. Phenotypic change in the most common species in this interval, *Amyzon aggregatum* (Cypriniformes: Catostomidae), is restricted to meristic elements. Numbers of meristic elements vary considerably through the interval, but much of this variation can likely be attributed to ecophenotypic effects. Periods of evolutionary stasis are suggested by the lack of phenotypic change which cannot be attributed to environmental change. Implications of these results on paleoenvironments, patterns and processes of phenotypic change, and temporal averaging are discussed.

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Firstly, special thanks are due to my supervisor, Mark V. H. Wilson, who got me started on this project, and who has provided support (financial and otherwise) throughout. Thanks are also due to the other members of my supervisory committee who have provided helpful comments on this thesis in various stages of preparation: R. C. Fox, J. S. Nelson, and N. Lovell. Other financial support has been provided by the Department of Biological Sciences in the form of a Graduate Teaching Assistantship, and a Graduate Studies and Research Scholarship. Travel to the Society of Vertebrate Paleontology annual meeting in Chicago in 1997 was funded by the J. Gordin Kaplan Graduate Studies Award.

I would like to thank an anonymous landowner for access to the Horsefly locality. Special thanks are also due to my field crew of Allan Lindoe and Gavin Hanke, for putting up with weeks of standing waist-deep in the frigid Horsefly River, and for their after-work conversations (verbal and otherwise) around the fire. Assistance in the field was also provided by my mom, Jean Barton (despite her difficulties in crossing the river). Allan Lindoe has also provided invaluable assistance in the lab, preparing many of the specimens collected in previous years, and providing me with expert assistance and advice.

I would also like to thank Ken Pugh of the Fraser Center for Non-Marine Eocene Research in British Columbia. Ken provided assistance while in the field, and I have benefited from numerous discussions with him on the Eocene fossils and localities of British Columbia. Richard Hebda at the Royal British Columbia Museum (RBCM) was very helpful in planning my field work and acquiring the necessary permissions. Joan Kerik, also at the Royal British Columbia Museum, has been very helpful in keeping me up to date on the specimens that we donated to the RBCM as part of our collecting agreement with the anonymous landowner. I would also like to thank Steve Cumbaa and Kieran Shepherd at the Museum of Nature (National Museum of Canada - NMC) for access to specimens in their collections, and for information on past collecting trips by the museum.

Throughout my thesis, I have benefited from the support and friendship of many colleagues and friends too numerous to mention individually. I would also like to thank my parents for their encouragement during this thesis. Finally, a special thanks to Davis Hill, who not only has supported and encouraged me throughout, but has also inspired me to work diligently and efficiently during the final stages of this thesis.

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LIST OF ABBREVIATIONS

Institutions:

RBCM - Royal British Columbia Museum

ROM - Royal Ontario Museum

UALVP - University of Alberta Laboratory for Vertebrate Paleontology

Counts and Measurements: (see p. 98-100 for explanations):

AFR - Anal fin rays

AP - Anal pterygiophores

BD - Body depth

CFR - Total caudal fin rays

CV - Caudal vertebrae

DFR - Dorsal fin rays

DV - Dorsal vertebrae

lCFR - Lower caudal fin rays

PAV - Post-anal vertebrae

PCV - Pre-caudal vertebrae

pDFR - Predorsal fin rays

PDV - Predorsal vertebrae

PFR - Pectoral fin rays

SL - Standard length

TV - Total vertebrae

uCFR - Upper caudal fin rays

VFR - Pelvic fin rays

CHAPTER 1: INTRODUCTION

Introduction

Over the past several decades, paleontologists have become increasingly interested in learning about patterns and rates of change in different biological and paleontological features over short time intervals in the fossil record (*e.g.* Bell et al. 1987; McCune 1987; Carroll 1997). Microstratigraphic studies, however, are rare because the temporal resolution of most of the fossil record is far too low to be able to identify all but the most broad patterns of change. There has therefore been a premium placed on fossil sites preserved with a high temporal resolution. Such sites can help to address questions of temporal variability in other fossil localities without such excellent temporal resolution. Microstratigraphic studies can also address other important biological questions such as patterns and magnitudes of environmental change through time. But perhaps the greatest current interest in microstratigraphic sites is in attempting to reconstruct patterns and rates of evolution in the fossil record.

Varved lacustrine sediments from the Eocene Horsefly locality of central British Columbia are among the most promising localities for such microstratigraphic studies. In this thesis, I present the results of the first microstratigraphic studies on both preservational patterns and phenotypic change in *Amyzon aggregatum* through a 10 000-year interval from these deposits. This chapter will serve as an introduction to the history and geology of the site, with a discussion of the formation of varves, and their importance in microstratigraphic studies.

History of the site

Fossils were first discovered near the Horsefly River in 1895 at Hobson's Horsefly placer gold mine (Lambe 1906; see Wilson 1996a for a history of fossil fish collection in British Columbia). J. B. Hobson, the owner of the mine, donated several specimens of

fossil fish recovered during mining operations to what is now the National Museum of Canada. At the museum, L. M. Lambe (1906) identified several of these fish as members of the sucker family (Catostomidae), with the majority of specimens identified as *Amyzon commune* Cope, and one individual identified as *A. brevipinne* Cope. Other fish fossils recovered from the mine include scales of an amiid and specimens of a hiodontid (see below). Fossils from the mine are preserved in two different matrices: specimens of *Amyzon* are preserved in a microlaminated sediment, while most specimens of other taxa are preserved in a dark shaly matrix.

Lambe himself visited the Horsefly Mine locality in 1906 (Lambe 1907), after the mining operations had ceased (Akins 1994). The site was not visited again by a professional collecting team until R. B. Campbell and his colleagues from the Geological Survey of Canada did a survey of British Columbia Cenozoic localities in 1959 and 1961. By this time, the mine locality itself was long-since grown over, and collection of fossils had shifted to the Horsefly River itself. There are some inconsistencies in the naming of localities in this area; therefore, I will specify locality names that I will be using for the remainder of this thesis. The original mine locality will be referred to as the Horsefly Mine locality; the exposure along the length of the river (near the mine) will be referred to as the Horsefly locality. Other conventions in naming of localities are presented later in this chapter. The Horsefly locality was visited again in 1963 by a field crew from the University of British Columbia (J. S. Nelson personal communication 1997). These visits stimulated a few papers (mostly on insects and plants of Horsefly and other British Columbia sites) (Rice 1959, 1968; Rouse *et al.* 1971), but it was not until M. V. H. Wilson visited the site as part of the research for his Ph.D. thesis in 1969, 1970 and 1971 that professional interest in the site really developed. Wilson's thesis (1974, summarized in Wilson 1977a) involved a detailed study of the fish fauna of all known Tertiary freshwater localities of British Columbia. Five of the eight species that Wilson identified from British Columbia are found at the Horsefly locality (Wilson 1974, 1977a). Some scales collected during early work at Horsefly by Lambe in 1906 were identified as an amiid (c.f. *"Amia" hesperia* Wilson, the only amiid known from British Columbia [Wilson 1982a, see also Grande and Bemis 1998]). Other Horsefly fishes include the perciform

Priscacara aquilonia (Wilson 1977a) and the hiodontids *Eohiodon rosei* (Wilson 1977a) and *E. woodruffi* (Wilson 1978a, see Li *et al.* 1997 for a review of *Eohiodon*). Finally, Wilson (1977a) described a new species of catostomid from Horsefly, which he named *Amyzon aggregatum*, and which includes the specimens that Lambe (1906) had identified (as *A. commune* and *A. brevipinne*) from the Horsefly locality. This makes *A. aggregatum* the only catostomid known from the Horsefly locality.

Following Wilson's thesis, there was a renewed interest in the Tertiary localities of British Columbia. Wilson published a series of papers on the insect fauna of Horsefly and other Tertiary localities of western North America (Wilson 1977b, 1978b, 1978c, 1982b). Several other authors have published on the flora of some of these localities (Janssens *et al.* 1979; Stockey and Manchester 1988). Wilson also studied the paleoecology of Eocene lakes of British Columbia in general (1980, 1987, 1988) and the Horsefly locality in particular (1977c, 1984). In the past decade, however, Wilson has turned his attention to the microlaminations that make up several intervals in the Horsefly deposits. Wilson realized the importance (and the rarity) of the precise stratigraphic control provided by microlaminations, which he demonstrated to be a result of yearly cycles of deposition (varves) for two different intervals in the site (Wilson 1993; Wilson and Bogen 1994). Each varve consists of a pale portion (composed mostly of diatom tests) and dark portion (composed mostly of clay), representing different material being deposited in the summer and winter, respectively. The first study that has taken advantage of the excellent temporal resolution provided by these varves was a study of the taphonomy of fishes preserved in a 715-year interval informally named H2 (Wilson and Barton 1996). In this study, however, I focus on the longest varved interval of the Horsefly locality, informally named H3 (Wilson and Bogen 1994; a further description of this interval is provided below).

Geological Age

Ever since its discovery, the geological age of the Horsefly locality has been debated. The site is one of several Tertiary freshwater sites in British Columbia each with somewhat similar faunas. These British Columbia sites are also somewhat similar in fossil

composition to several sites in the western United States, including Republic, Washington and the Green River Formation of Utah, Wyoming and Colorado.

Early dating of the Horsefly beds involved mostly biostratigraphic correlations with other sites of questionable age. Lambe (1906) was the first to attempt to estimate the age of the Horsefly locality, citing two biostratigraphic correlations: one with sediments of Eocene or Miocene age (Cope 1884), and another with middle Eocene sediments (Clark 1891). Handlirsch (1910) then correlated the Horsefly beds (among others) with some of presumed Oligocene age based on similar insect faunas. L. S. Russell (1935) was the first to conclusively establish a date of Eocene for one of the British Columbia freshwater sites (in Princeton) based on the presence of the genus *Trogosus* (Mammalia: Tillodontidae).

Modern dating of the site is based on much better biostratigraphic correlations with sites that have been well dated. In the 1960s, several lacustrine deposits in British Columbia were potassium-argon dated at 45-53 Ma, placing them in the early to middle Eocene (Rouse and Mathews 1961; Mathews 1964; Hills and Baadsgaard 1967). Symons and Wellings (1989) found that the paleomagnetic properties of the Kamloops Formation are consistent with an age of middle Eocene.

The Horsefly locality, although it has not been directly dated, is biostratigraphically correlated with some of these well-dated beds. Some of the fishes from Horsefly (*Eohiodon woodruffi*, *Amyzon aggregatum*) are shared with the well-dated middle Eocene Republic (Washington) locality (Wilson 1977a, 1996b), and (based on recent revisions of genera and synonomyzation of species) are also shared with the well-known Green River Formation (Bruner 1991; Li *et al.* 1997). Interestingly, within the Green River Formation, *E. woodruffi* is known only from the end of the early Eocene in the Fossil Lake deposits, whereas *A. aggregatum* is known only from the first part of the middle Eocene in the Lake Gosiute deposits (Grande 1984, 1994), yet these species are found in sympatry in the Horsefly locality. *E. woodruffi*, however, is known from other middle (and possibly late) Eocene localities (see Li *et al.* 1997). The Kamploops Formation, which is also well-dated as middle Eocene, shares *A. aggregatum* and a different species of hiodontid (*E.rosei*) with the Horsefly locality (Wilson 1977a). *E. rosei* is also shared with the Allenby Formation in southern British Columbia, which has also been dated as middle Eocene. Finally, the

Horsefly deposit is biostratigraphically correlated with all of these British Columbia localities based on palynological studies (Rouse *et al.* 1971). We can therefore conclude that, based on a series of biostratigraphic correlations with well-dated beds, the best current age for the Horsefly locality is middle Eocene.

Locality

The Horsefly locality is situated in central British Columbia, about six kilometers north of the village of Horsefly (52°23.4'N; 121°24.5'W; Fig. 1-1). The fossil site is exposed along the Horsefly River, in and around a set of rapids referred to locally as "the steps" (Fig. 1-2). The entire section is composed of lacustrine sediments, but fossils are most abundant in three microlaminated intervals, referred to informally as H1 (University of Alberta Laboratory for Vertebrate Paleontology [UALVP] locality 66), H2 (UALVP locality 67) and H3 (the focus of this study, UALVP localities 68 and 69; locality 68 was described as being just below the H3 interval, but with the extension of the section in this paper [see below], H3 now includes UALVP localities 68 and 69). Although the microlaminated intervals were each assigned different locality numbers, they are part of a continuous depositional sequence, and I will therefore consider them as intervals within a single (Horsefly) locality.

Stratigraphic section.--In the summer of 1996, L. A. Lindoe and I did a preliminary measurement and drawing of the stratigraphic section for the entire interval of lacustrine sediments that make up the Horsefly locality (illustrated in Figure 1-3). Our measurements were rough and we made no attempt to look for fossils in any of the strata. Any further study of the entire interval should certainly include a remeasurement of this section. This section does, however, put the the varved intervals into their stratigraphic context. This description of the section includes several different lithologies, but it should be noted that the deposition of the entire deposit is continuous, and each of the lithologies (with the exception of the event layers) grade into each other. Divisions between lithologies is often somewhat arbitrary.

At the bottom of the H3 interval, the Horsefly sediments dip upstream at an angle of

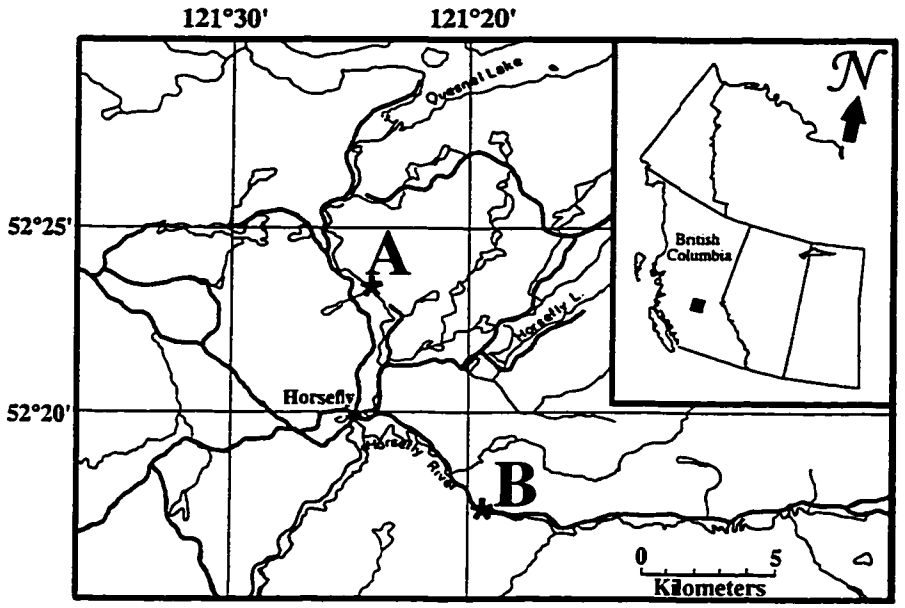


Figure 1-1: Map showing location of Eocene lacustrine sediments in the vicinity of Horsefly, British Columbia. The Horsefly locality (A) is the focus of this thesis. Other Eocene lacustrine sediments are exposed upstream of the Horsefly locality along the Black Creek Road (B). Adapted from Wilson 1977c.

A

B

Figure 1-2: Exposure of the Horsefly locality, British Columbia. A, Exposure of the lower part of the lacustrine deposits along the west bank of the Horsefly River. Arrow indicates the base of the measured section described in the text. This exposure contains the H1 and H2 intervals. B, Exposure of the top of the lacustrine deposits is limited to the river itself. Exposure of the H3 interval begins at the right edge of the photo and extends upstream to the boulders in the middle of the photo.

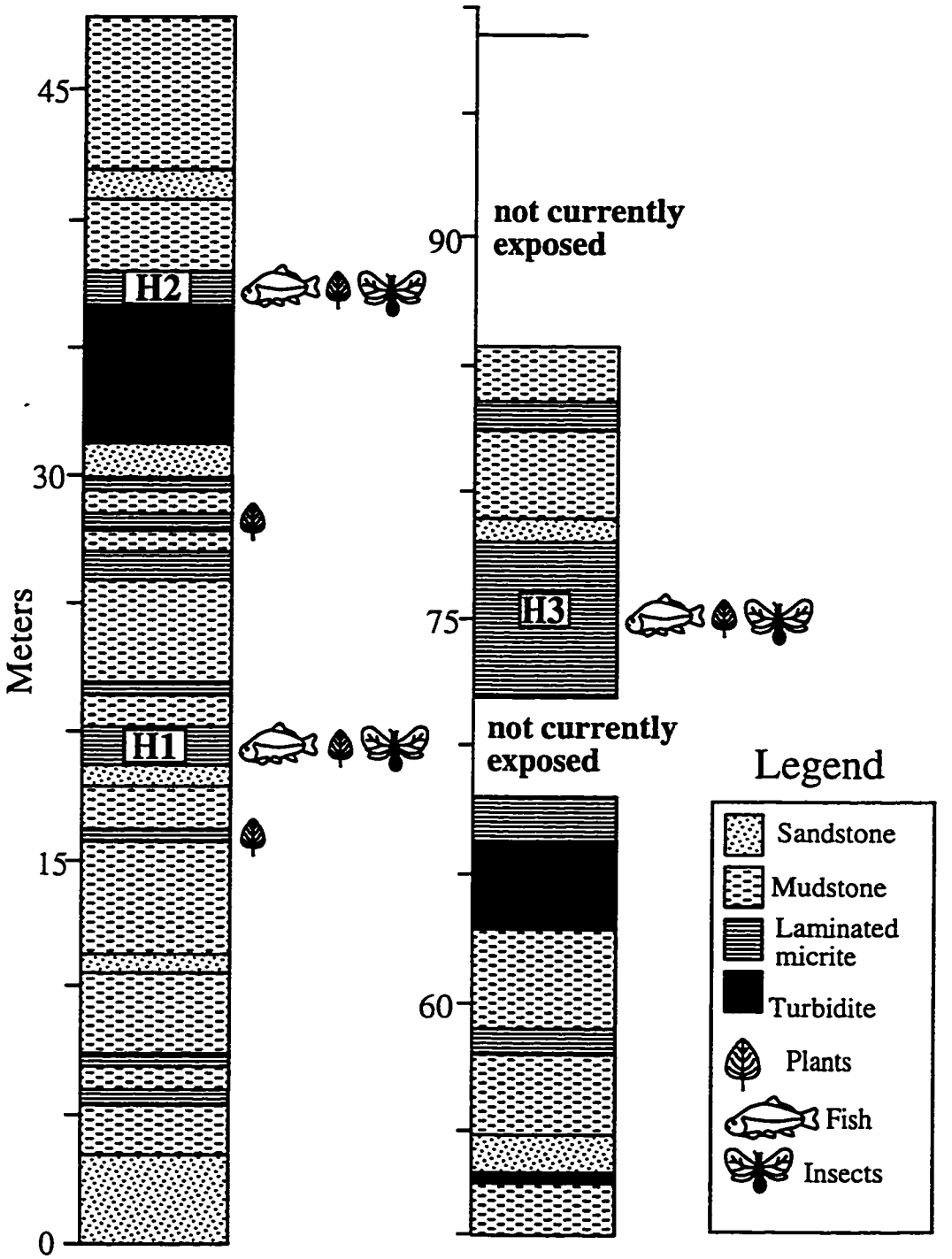


Figure 1-3: Stratigraphic section of the Horsefly locality indicating the relative postions of the varved intervals H1, H2 and H3. Sandstones and mudstones in this section are often laminated, but only intervals preserved with microlaminations are indicated as laminated micrites. Only the H2 and H3 sections have been demonstrated to preserved in yearly laminations, or varves. Lithologies (except turbidites) tend to grade into each other, and divisions are often somewhat arbitrary.

25°, but strata become progressively flatter upsection to nearly horizontal at the top of the H3 interval. All references to meters in this discussion of the stratigraphic section refer to stratigraphic meters above the bottom of the measured section. The very bottom of the lacustrine sediments are badly deformed. The beds at the bottom of the section are tectonically broken up into large blocks and rotated to point in all directions. We started measuring the section on the west bank of the river from the bottom of the first beds that are nearly horizontal and continuous with the rest of the Horsefly section (upstream and upsection) (see Fig. 1-2). The starting point for our measurements is easy to find because it consists of a fairly thick layer of very coarse sand that is the first nearly horizontal (undeformed) strata of the section. This sandy layer is immediately upstream of the deformed beds. The lowest 20 meters of the measured section is mostly laminated sandstone interspersed by mudstone. There are several intervals in this 20 meter section with fine laminations that might represent varves. At about 19 meters from the bottom of the section is the interval that most likely represents the H1 interval. Descriptions of the position of the H1 interval are vague, but the interval at 19 meters is the most obvious sequence of finely laminated sediments of any length below the H2 section. This could be verified in the future by comparing the sequence of varves and event layers of specimens that have been previously collected from the H1 interval to those of this particular interval. There follows an interval of laminated mudstones from about 20 meters to about 30 meters. Just below 30 meters is an interval of very dense fossil vegetation (mostly woody tissue) that is easily recognized. Just above 30 meters, there is a thick (about 5 meter) section of unlaminated sediment representing an instantaneous (probably turbiditic) event. The H2 interval, the most intensely studied interval of the Horsefly section, is located about 36 meters from the bottom of the section.

Above the H2 section, there is a series of mudstones occasionally interspersed by sandy beds. There is another distinctive event layer containing concretions at about 63 meters, followed by a section of finely laminated sediments that likely represent varves. This is followed by four meters of section which were not exposed along the shoreline and which were too deep in the river to collect; therefore, we could not examine the lithology.

The H3 interval begins 72 meters above the bottom of the section. The bottom of the

H3 interval is limited by exposure; it might indeed be microlaminated all the way down to the previous interval (around the 66 meter measure). If these intermediate layers ever become accessible and the microlaminations extend all the way through, the H3 interval will be able to be extended by several meters. A cursory examination, however, did not reveal any fish fossils from the lower microlaminations.

Immediately above the H3 interval is a layer of slightly laminated sandstone, followed by mudstone, another layer of microlaminations, and more mudstones. Above this point (86 m), the sediments are no longer exposed along the river. The banks are covered with overburden, the shoreline is very steep, and the middle of the river is too deep to allow access to the sediments. Many little fragments of lacustrine sediment, however, are washed up on the banks of the river all the way upstream to about 100 stratigraphic meters above the bottom of the section, at which point they suddenly end. This sudden end of lacustrine sediments suggests that they are not being washed downstream from a different lacustrine deposit. These fragments of sediment suggest that the Horsefly section, although not exposed for the top 14 meters, extends about 100 stratigraphic meters from the bottom of the measured section.

In our measurement and examination of the Horsefly stratigraphic section, we did not come across any lithology that corresponds to the brown shaly matrix in which some of the original specimens from the mine are preserved. The microlaminated matrix in which other specimens from the mine are found likely represents one of the varved intervals of our measured section (M. V. H. Wilson personal communication 1998). The location of the mine itself is about 100 meters west of the river. The lack of correlation between the brown shaly matrix and any layer in our measured section suggests either a very high spatial variability of some layers over that 100 meters (but see below), or that the mine contains strata that we did not sample in our section (either the deformed sediments below the measured section, or a separate stratigraphic unit altogether). Unfortunately, the mine is now completely overgrown and these sediments are no longer exposed, so we could not attempt any further correlation.

There is another exposure of lacustrine sediments along the Black Creek Road, south-east of Horsefly, about 10 km from the Horsefly locality (Fig. 1-1; UALVP locality 70).

Wilson (1977c; Wilson and Bogen 1994) mentions that these beds might be laterally equivalent to the Horsefly beds. However, after measuring and examining the Horsefly section, I could find no lithological correlation between the Horsefly locality and the Black Creek Road locality. The differences could very well represent lateral variation within a lake, but in the absence of any evidence, I see no reason to assume that these sediments represent the same lake deposit.

Sedimentation rates.--Sedimentation rates (post-compaction) for the two well-studied varved intervals (H2 and H3) can be easily determined by directly counting years from the sediment and measuring the interval. The duration of the Horsefly lacustrine sediments can then be estimated by extrapolating these sedimentation rates over the entire section. This method of estimating total time represented by stratigraphic intervals (varve-calibration) is used fairly commonly in the fossil record (*e.g.* Bell and Haglund 1982; Bell *et al.* 1985; Olsen 1986), usually without mention of the inherent assumptions. One of the main assumptions is that sedimentation rates over the entire history of the lake are equivalent to those of the varved intervals. Sedimentation rates, however, are lowest in the deeper parts of lakes (Digerfeldt 1986), which are also where varves are most likely to be formed and preserved. It is therefore likely that varve-calibrated sedimentation rates underestimate rates of deposition of non-varved sediments (and therefore overestimate the time represented by stratigraphic intervals). Varve-calibrated sedimentation rates also assume no interruptions in deposition. By their nature, varves are very unlikely to be subject to such interruptions (without first going through stages of decreased lamination). Non-microlaminated intervals do not have the same attribute; therefore, gaps in sedimentation (unconformities) will not be as obvious. Because of these assumptions, varve-calibrated sedimentation rates can provide only a rough estimate (and probably only an upper time limit) of the total time represented by a stratigraphic section.

The H3 interval consists of 10 176 years (see below), and measures 3.66 meters; therefore, the (post-compaction, dewatered) sedimentation rate is 360 Bubnoff units (1B. = 1 μm/yr; see Schindel 1980). The H2 interval consists of 715 years, and measures 0.337 meters (471 B.). These rates are on the low end of the lacustrine sedimentation rates listed by Schindel (1980), probably because Schindel's rates are based on sedimentation in both

shallow and deep parts of modern lakes, and are based on largely compacted, but not dewatered, sediments. The total length of the Horsefly section is about 100 meters (see above), and therefore represents 212 314 years (if the H2 rate is used) or 277 777 years (if the H3 rate is used). Considering the assumptions, the actual time represented by the entire Horsefly locality is therefore likely less than 200 000 years.

H3 section

Collection and preparation of reference column.--The H3 interval, the focus of this thesis, was originally described by Wilson and Bogen (1994) based on a limited exposure of sediments on the east bank of the Horsefly River. The bottom of this exposure is covered with overburden. Fossils are found within the riverbank: small fragments of rock are individually removed and later glued back together. In the summer of 1996, we took advantage of a better exposure of the H3 section on the west side of the river (discovered in a previous year by L. A. Lindoe). Strata are exposed along a set of rapids in the river, so there is little overburden to limit exposure (Fig. 1-2). Fossils are collected by removing large slabs from the deposits in the river and splitting them to reveal fossils. The increased exposure of the section on the west side of the river allowed us to extend the original H3 stratigraphic column (consisting of 6375 couplets) by 3801 couplets below the bottom of the original section.

We collected and assembled a stratigraphic column of the newly discovered 3801 layers to allow study of the complete H3 section. We pulled samples of the section out of the river and identified their relative position on the original H3 column from Wilson and Bogen (1994) until we found the layers corresponding to the base of the original H3 section. We then followed the laminated interval as far downstream as we could (access is limited by fast and deep water, as mentioned above). We then collected oriented rock samples from the river starting at the bottom and proceeding upstream until we reached the bottom of the original H3 column. We allowed several centimeters of overlap between the samples and the original column to ensure that no layers were missed. The collected samples of section were labeled sequentially from the bottom, wrapped in paper towels,

and returned to the laboratory where they were assembled into a stratigraphic column. I trimmed the oriented samples to fit into a wooden tray lined with thin plastic that had been previously prepared for this purpose. I then poured epoxy around the rock samples (within the plastic) to fill all the gaps between rocks and to hold the section together. Several days later, after the epoxy had cured, I removed the plastic and wrapped the epoxy-coated column in fiberglass for reinforcement. After this cured, the column was sawed with a rock saw to expose a fresh cross-section of the laminations, and then sanded to remove saw lines. The stratigraphic column is in a total of 11 pieces, four of which are from the new layers (Fig. 1-4). Individual pieces of the section are continuous with each other, and breaks between the pieces are in event layers to ensure that no varves are missed.

The procedure for naming layers in the stratigraphic column followed that of Wilson and Bogen (1994). Wilson and Bogen assigned numbers to major event layers (turbidites and ash) in the original section, beginning with 1. I also assigned numbers to major layers of the new section numbers starting with 1, but preceeded by "x" to differentiate them from Wilson and Bogen's original (1994) section (some of these layers are visible in Fig. 1-4 and Fig. 1-5). Between these major layers, all other recognizable layers (ash, turbidites, etc.) were assigned a letter (starting with "a" at the major numbered layer; therefore the first minor layer after the major layer is designated "b"). Each couplet was then numbered starting with 1 after each minor layer. For example, the third couplet after the first major layer of the new section would be named x1a3, the 10th layer after the third minor layer following the coarse layer 26 (of the original section) would be named 26d10. This method ensures that each couplet has a unique combination of numbers and letters, and also allows the published naming of the original layers (Wilson and Bogen 1994) to be conserved. The entire H3 stratigraphic column is shown in Figure 1-4 (photograph) and Figure 1-5 (stylized stratigraphic section). The numbering of years does not directly correspond with stratigraphic distance because of the presence of event layers and changes in sedimentation rate through the interval.

Hypothesis of annual deposition.--Wilson and Bogen (1994) performed a series of tests on the original 6375 couplets to show that these couplets represented yearly cycles of deposition (varves). A spectral analysis of the couplets revealed no periodicity, as would

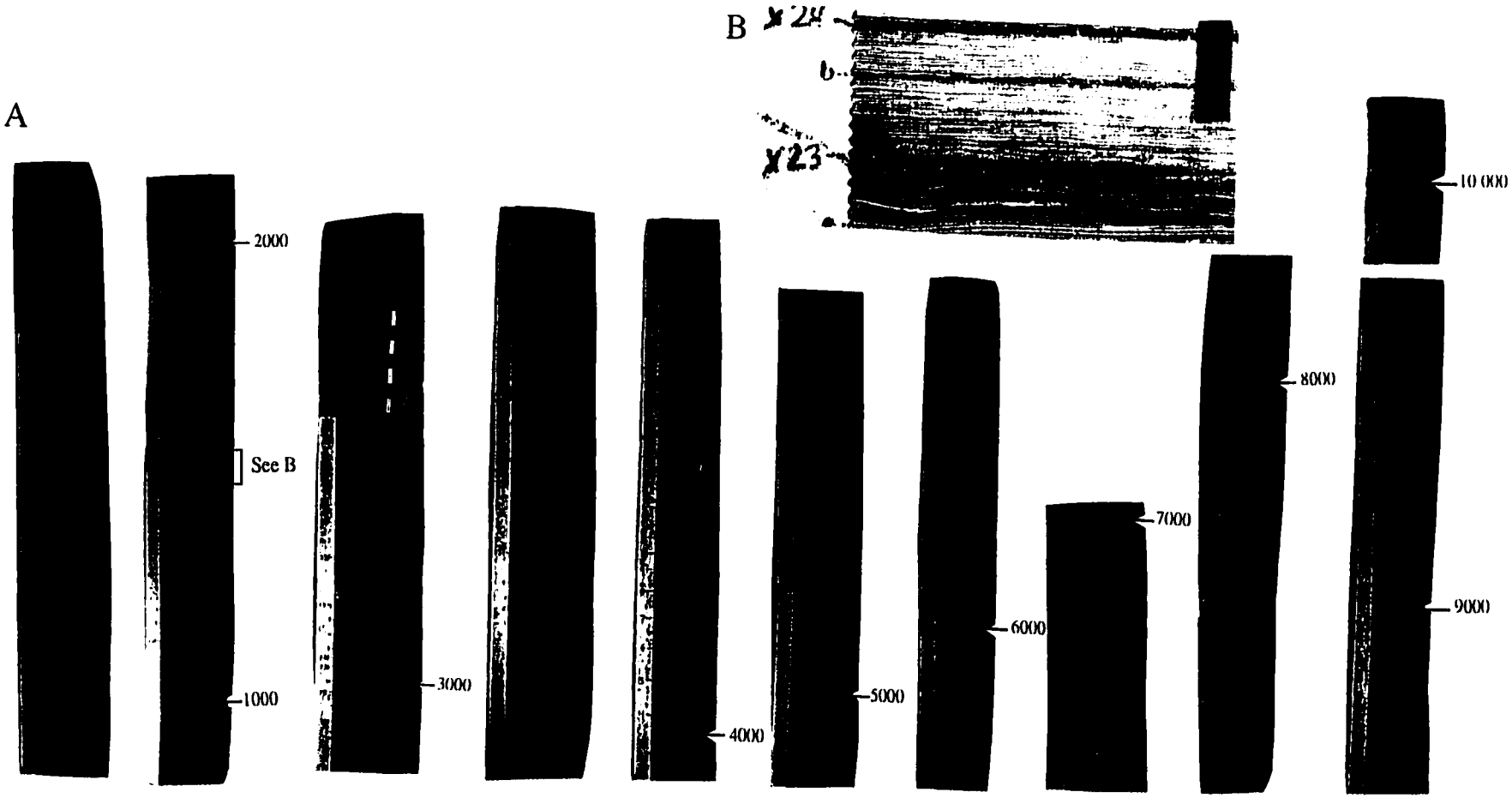


Figure 1-4: A, Reference stratigraphic column for the H3 interval of the Horsefly locality. The complete stratigraphic history starts at the bottom left, and continues sequentially up each of the 11 pieces of the column. All pieces of the column are continuous with each other (maximum overlap 4 cm.). Relative year (as described in the text) is indicated on the right side of the section at every 1000 years. A stylized version of this column appears in Figure 1-5. B, Close-up of varved interval including the layers x22e through x24a (see text for naming of varves). Scale bar is 1 cm.

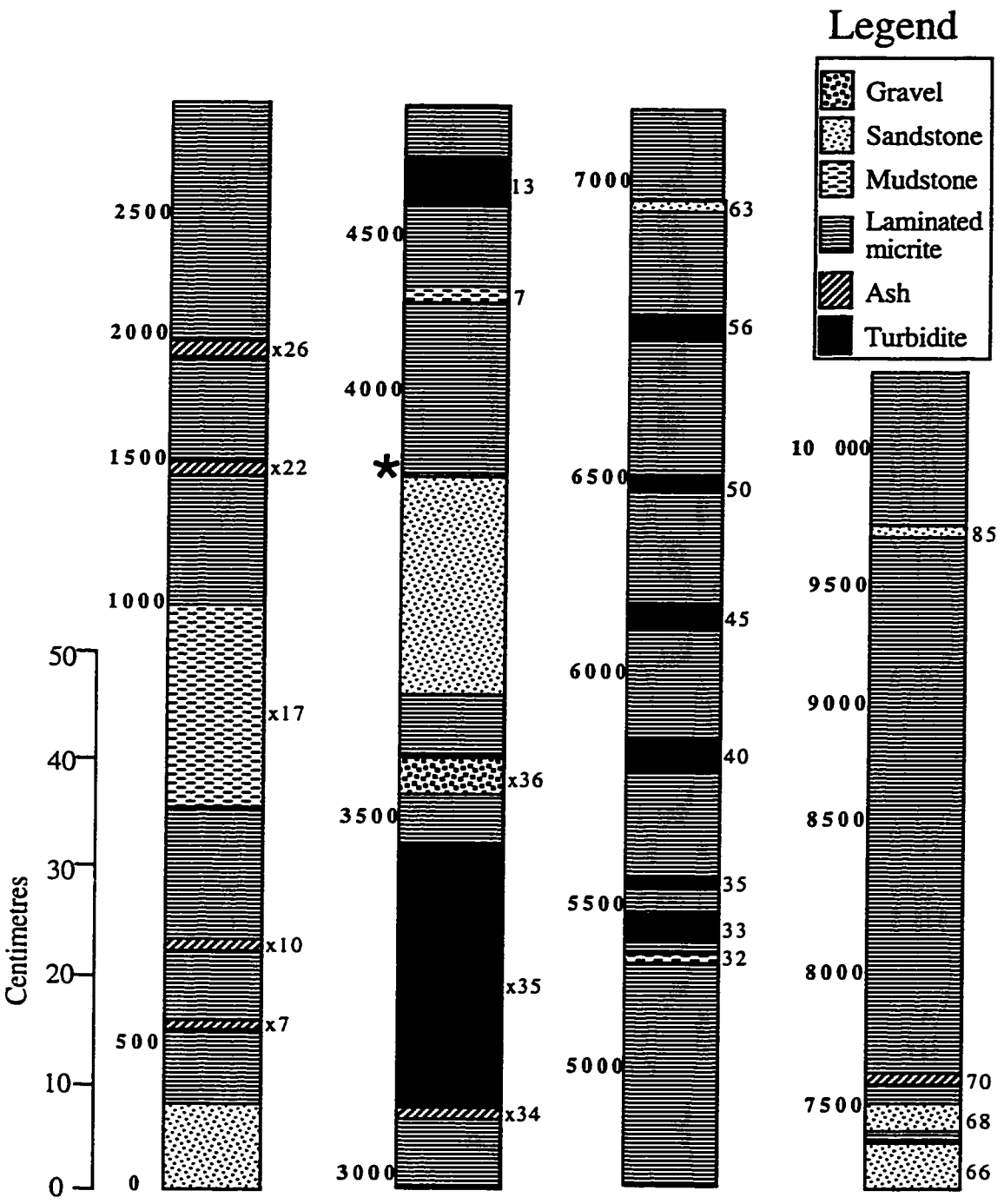


Figure 1-5: Detailed stratigraphic section of the H3 section of the Horsefly locality. Lithologies are not usually distinct, but tend to grade into each other (with the exception of ash and turbidites which are event layers). Asterix indicates the bottom of the old H3 section (Wilson and Bogen 1994). Numbers along left side of section indicate relative year (as described in the text). Along the right side of the section are the numbers of any named layers (mostly ash and turbidtes, see text) thicker than about half a centimeter. Breaks between parts of the section here are arbitrary and do not correspond with pieces of the reference column (see Fig. 1-4).

be expected by an irregular deposition of couplets (*e.g.* if they were caused by turbidity currents). The size distribution of couplets is unimodal, which suggests that a single couplet is deposited each year. Scanning electron microscopy demonstrated the the pale parts of the couplets are composed "almost totally of diatom fragments, while the dark parts of the couplets are composed mostly of clay particles along with pyrite and gypsum" (Wilson and Bogen 1994: p. 334) representing summer and winter deposition, respectively. The distribution of fossils is another strong indication of the seasonality of deposition at the site, with fishes most common in the dark parts of the lamina, and insects and plants most common in the pale parts of the lamina (see Wilson 1977c). The combination of all of these tests is irrefutable evidence that these layers represent yearly cycles of deposition.

The new layers have not been subject to the same analyses of seasonality. As a preliminary test, I measured the thickness of couplets and then plotted them as a frequency distribution (Fig. 1-6). The new couplets are significantly thicker than the couplets of the original H3 section (*t*-test, t=14.5, d.f.=10174, $p<0.001$). This might reflect a true difference in size of the couplets, or it could simply be due to inter-observer variability. The unimodal, slightly skewed shape of the frequency distribution of the new couplets is, however, almost identical to that of the original section (compare Fig. 1-6 to Wilson and Bogen 1994: Fig. 3). The new layers are stratigraphically continuous with the original section (although there are 20 cm of sediment near the top of the new layers in which varves grade into a more coarse sandstone, which quickly grades back into varves), and a cursory examination cannot differentiate the new layers from the old in terms of grain size, colour, composition, or thickness of varves. Other than a 0.01 mm. difference in mean thickness, therefore, there is nothing to distinguish the new layers from the original. There is no reason to believe that these new layers do not also represent varves; their varved nature will be assumed for the rest of this paper.

Collection and preparation of fossils.--Fossils were collected from the H3 section over several field seasons. The relative position of the fossils on the stratigraphic column was determined in the laboratory by lining up sequences of turbidites, ash layers, and varves on rocks containing fossils with the reference column. The characteristic appearances of

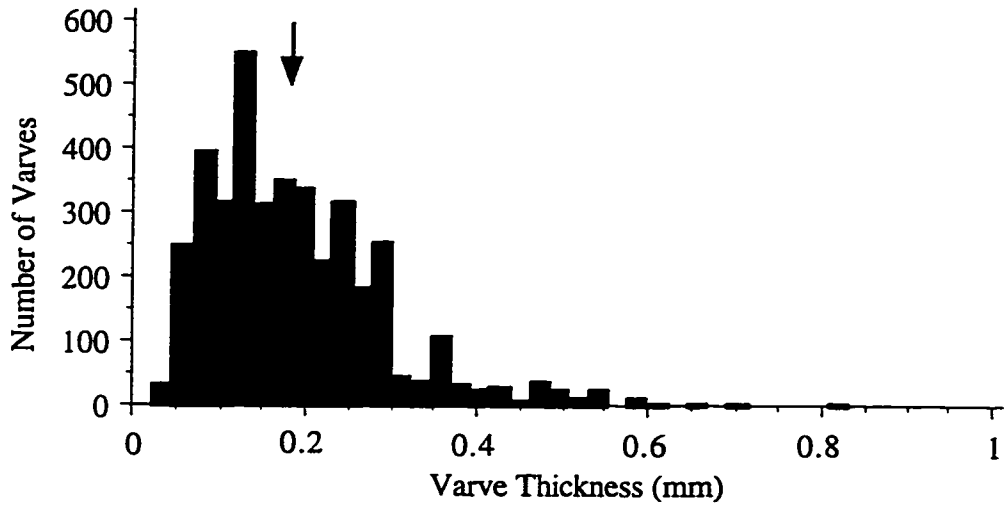


Figure 1-6: Frequency distribution of thicknesses of the 3801 couplets that have been added to the H3 section since it was studied by Wilson and Bogen (1994). The unimodal positively skewed distribution is very similar to the distribution of the original layers (compare to Wilson and Bogen 1994: Fig.3). Arrow indicates mean value of 0.178 mm.

turbidites or ash layers, thicknesses and colours of varves, and number of varves between major or minor layers are all useful tools to help pinpoint the exact position of a sample on the reference column. As specimens were collected in the field, their vertical orientation and a rough estimate of their position on the section were recorded to facilitate this process. After the major and minor layers bracketing the fossil are identified, the number of varves separating the fossil from the nearest layer can be counted (either counted down from the layer above, or up from the layer below, or in most cases both to ensure accuracy). Most specimens could be assigned to their exact varve in the reference column, especially when a thin part of the fossil (*e.g.* the ends of the fins) is visible in cross-section. Occasionally a cross-section is not visible, or cannot be prepared out (this is especially true of the occasional isolated bone). Relative ages on some specimens might, therefore, have a margin of error of ±1 or 2 years. Deposition of varves and event layers are consistent enough across the exposure that specimens collected on either bank of the river can easily be assigned to their position in the section (dated) in this way. In fact, there is almost no lateral variation across the river (about 30 meters), which seems to suggest that the strata in which some of the specimens from the Mine locality are preserved (another 100 meters away) are not represented in the presently exposed Horsefly section. Specimens collected from the river in previous years can also be dated on the reference column with ease.

Only 33 of the 698 specimens of *Amyzon aggregatum* collected from the H3 interval could not be positioned on the stratigraphic section. Most of these specimens are preserved on very thin rock samples with few or no characteristic layers to assist dating.

Nearly all of the fossils were prepared manually. Sometimes rock samples are split to reveal fossils, but usually fossils are found in cross-section in the rock, and have to be prepared out. Manual preparation involves splitting the rock as much as possible, and chipping or picking off the matrix on top of the fossil with dental tools. Recently L. A. Lindoe attempted acid preparation of some specimens from the H3 interval to dissolve the bone away from the matrix. He then made latex peels of these specimens. These techniques produced some excellent results and should be considered for future studies on the fishes of the Horsefly site.

Specimens of *Amyzon* and other genera that were recovered from the H3 section over

several collecting seasons (*Priscacara*, *Eohiodon*) are not distributed uniformly through the H3 section (Fig. 1-7). Part of the cause of this uneven distribution is likely sampling bias: some parts of the section were only exposed in deep and fast waters, whereas others parts were exposed in shallow slow-moving waters (where collection is much easier). The polymodal temporal distribution of *Amyzon* is likely an artifact of collection methods: as slabs are removed from the river, fossils in the middle layers of such slabs are more likely to recovered. The peaks in the distribution therefore likely represents intervals that could be removed from the river in slabs, with gaps between the peaks representing layers that are not included in such large slabs, or layers on the edges of such slabs that are more likely to be lost during removal of the slabs. Based on my collecting experiences, however, there does appear to be a true temporal heterogeneity of specimens through the entire H3 section. The top 3000 years of the section were sampled exclusively for about three days with only a few fish recovered. In contrast, sampling around the year 4000 generates about one fish per collector hour. Sampling biases also cannot account for the different distributions of different species through the section. Specimens of *Priscacara* are concentrated near the top of the section, whereas specimens of *Eohiodon* are slightly more common than expected (relative to *Amyzon*) in the first 3000 years and at the end of the section. Fossil insects also seem to be more common at the top of the H3 section. Distributions of different taxa have major implications on the paleoecology of the H3 site (see Wilson 1980, 1988). These will be discussed in more detail in Chapter 2.

Varves

Formation.--Much of our knowledge of the formation of lacustrine varves comes from studies on modern lakes (see Anderson *et al.* 1985; Anderson and Dean 1988). Two main conditions are required for the formation and subsequent preservation of varves in a lake: a seasonal cycle in which clearly distinct material is deposited in the summer and winter, and preservation of the integrity of the microlaminations. The first condition is relatively easily met. As Anderson and Dean (1988) mention, sediments in many lakes are formed in microlaminations; they are simply not usually preserved. Wetzel (1983), however,

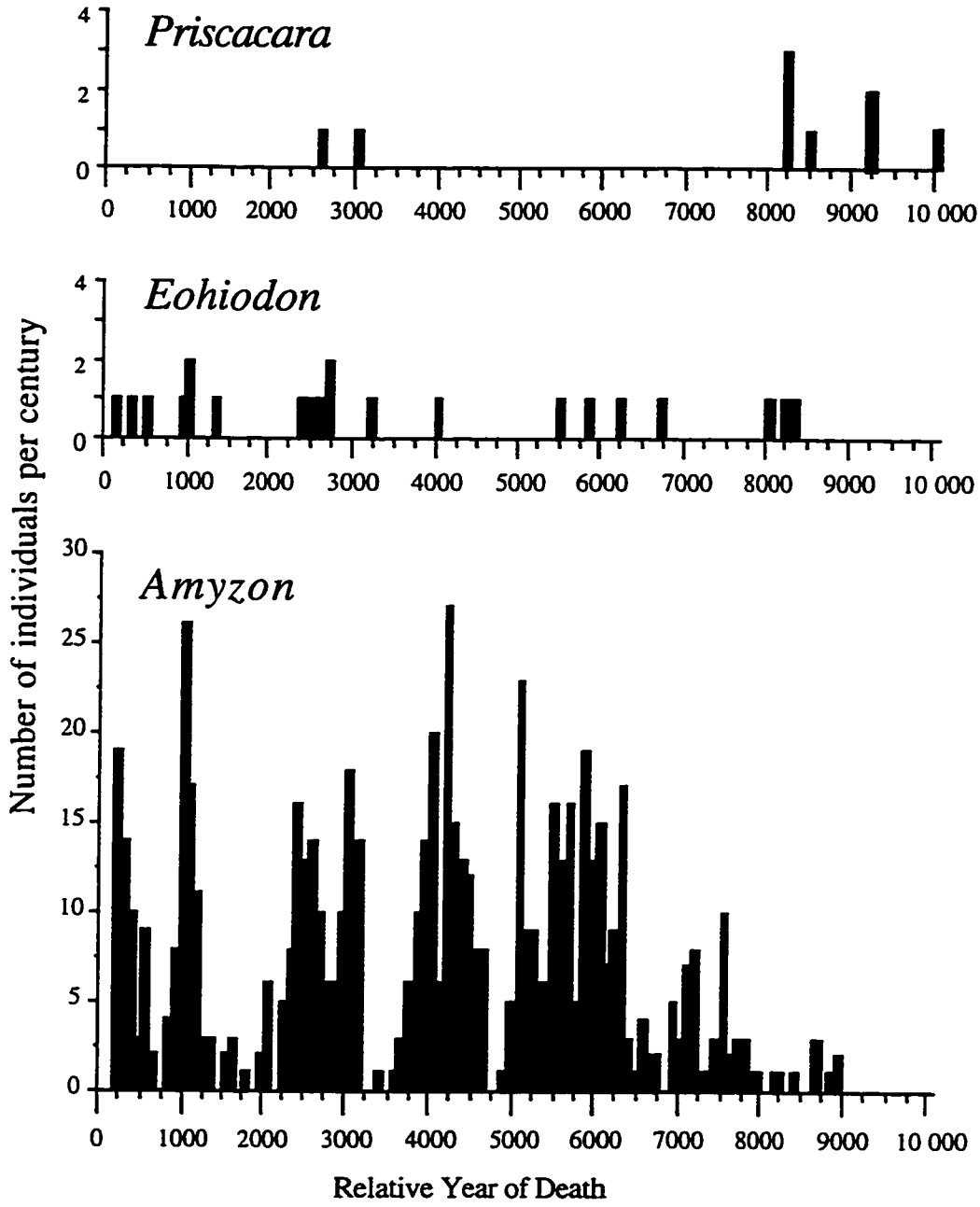


Figure 1-7: Distribution of specimens of *Amyzon*, *Eohiodon* and *Priscacara* through the 10 000 years represented by the H3 section of the Horsefly locality, British Columbia. Polymodality of distribution of *Amyzon* can likely be explained by sampling biases (see text), but such biases cannot explain the different distributions of the three genera through time.

mentions that for seasonal laminations to form, the seasonal influx of material to the lake must coincide with stratification of the water column.

It is the second condition, the preservation of these microlaminations, that requires very specific conditions. Two major barriers to the preservation of microlaminations are bioturbation and re-suspension. The effects of bioturbation are fairly obvious: benthic organisms have an effect on the sediment in which they live. A little bioturbation can easily destroy very fine microlaminations. Re-suspension is an equally large, if not larger, barrier to the preservation of microlaminations. Sediments in many lakes (especially those with reasonably high organic content) tend to have a consistency of a "gel or floc" with up to 90% water content (Anderson and Dean 1988). Often simple circulation of a lake (during an overturn event) is enough to re-suspend these sediments, and therefore destroy microlaminations (Anderson and Dean 1988).

The specific conditions for varve formation and preservation are met most frequently in meromictic lakes, in which sediments are perennially anoxic, usually separated from the rest of the water column by a chemical (usually salt) gradient (Anderson *et al.* 1985). The water column above the chemical gradient in meromictic lakes can be thermally stratified, and can overturn once (monomictic), twice (dimictic) or several times per year (polymictic). Lack of oxygen on the bottom of meromictic lakes precludes the existence of benthic organisms (and therefore bioturbation). Chemical stratification helps to ensure that the bottom waters never mix, so microlaminations are not disturbed.

Rarely, non-meromictic lakes can also preserve varved sediments. For example, lakes with very low organic content and high proportions of chemical precipitates will have sediments which are more solid, and can therefore retain microlaminations under slightly more oxic conditions, or conditions of slightly more circulation (Anderson and Dean 1988). Other exceptional conditions can also lead to the preservation of varves. For example, Elk Lake, Minnesota, is not meromictic, but has excellent varve preservation (Anderson *et al.* 1985; Anderson and Dean 1988). Varves are formed in a deep hole in the middle of this lake. This hole has very weak circulation, and is partly oxygenated for part of the year. Oxygen levels, however, are too low to allow benthic organisms to become established, and circulation is so gentle that sediments do not mix. So although the vast

majority of varved sediments are formed in meromictic lakes, there are occasionally exceptional conditions in other (non-meromicitic) lakes that can also lead to the formation and preservation of varves.

Importance of varves.--The preservation of varves in ancient lakes is interesting not just from an ecological (or environmental) viewpoint (*e.g.* Anderson and Dean 1988), but also from an evolutionary perspective. In the past few decades, there has been a great interest in the study of stratigraphic sequences with high temporal resolution (*e.g.* McCune 1987; Carroll 1997), in the hopes of better understanding processes of both temporal averaging (Kidwell and Behrensmeyer 1993a) and evolutionary change (see Carroll 1997 for a summary). Most stratigraphic sequences have maximum temporal resolutions between thousands and millions of years (Schindel 1980; Kidwell and Behrensmeyer 1993b), and can therefore only address long-term patterns of change in the fossil record. Temporal averaging, or the process by which organic remains from different time intervals come to be preserved together (Kidwell and Behrensmeyer 1993b), is perhaps the most fundamental barrier to these microstratigraphic studies. Temporal averaging can have one of two main causes: either an actual physical mixing or reworking of sediments (and fossils within), or low generation times of organisms living within the depositional environment relative to the net sedimentation rate (Kidwell and Behrensmeyer 1993b). Nearly all fossil sites are subject to these processes of temporal averaging; therefore, there is a premium on fossil sites with temporal resolutions high enough to examine the scale of variation that occurs within other sequences.

Fossil sites preserved with varves can provide among the highest possible temporal resolutions. Most varves are formed in lakes, which have one of the most continuous sedimentation rates of any depositional environment (Schindel 1980). Studies on varved sites have several advantages over other sites, even those with extremely high resolution (*e.g.* deep sea cores) including a built-in proof of a lack of temporal averaging, and a built-in temporal calibration.

Several intervals of the Horsefly locality in British Columbia are preserved with varves. Fossils in these intervals are abundant and morphologically complex. Fossils can be assigned to their relative position on the stratigraphic section, and therefore their relative

year of death can be determined.

The precise temporal precision provided by these varves will be used in this thesis to study patterns of changes in fossils through time. In Chapter 2, I examine microstratigraphic variation in taphonomic processes of fishes from the site, with a discussion of what this variation indicates about environmental changes in and around the lake. In Chapter 3, I examine microstratigraphic changes in meristic counts of fishes from the site, and discuss the most likely causes of these changes.

Literature Cited

Akins, C. 1994. One of Horsefly's best kept secrets. Horsefly Buzz 24:10.

Anderson, R. Y., and W. E. Dean. 1988. Lacustrine varve formation through time. Palaeogeography, Palaeoclimatology, Palaeoecology 62:215-235.

Anderson, R. Y., W. E. Dean, J. P. Bradbury, and D. Love. 1985. Meromictic lakes and varved lake sediments in North America. U.S. Geological Survey Bulletin 1607:1-19.

Bell, M. A., and T. R. Haglund. 1982. Fine-scale temporal variation of the Miocene stickleback *Gasterosteus doryssus*. Paleobiology 8:282-292.

Bell, M. A., J. V. Baumgartner, and E. C. Olson. 1985. Patterns of temporal change in single morphological characters of a Miocene stickleback. Paleobiology 11:258-271.

Bell, M. A., M. S. Sadagursky, and J. V. Baumgartner. 1987. Utility of lacustrine deposits for the study of variation within fossil samples. Palaios 2:455-466.

Bruner, J. C. 1991. Comments on the genus *Amyzon* (Family Catostomidae). Journal of Paleontology 65:678-686.

Carroll, R. L. 1997. Patterns and processes of vertebrate evolution. Cambridge University Press, Cambridge.

Clark, W. B. 1891. Correlation papers: Eocene. U.S. Geological Survey Bulletin 83:1-173.

Cope, E. D. 1884. The Vertebrata of the Tertiary formations of the West, Book 1. Report, U.S. Geological Survey of the Territories 3:1-1009.

Digerfeldt, G. 1986. Studies on past lake-level fluctuations. Pp. 127-143 *in* B. E. Berglund, ed. Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley and Sons, New York.

Grande, L. 1984. Paleontology of the Green River Formation with a review of the fish fauna (second edition). Geological Survey of Wyoming Bulletin 63:1-333.

——— 1994. Studies of paleoenvironments and historical biogeography in the Fossil Butte and Laney members of the Green River Formation. University of Wyoming Contributions to Geology 30:15-32.

Grande, L., and W. E. Bemis. 1998. A comparative phylogenetic study of Amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Journal of Vertebrate Paleontology 18 (supplement to number 1):1-690.

Handlirsch, A. 1910. Canadian fossil insects. Contributions to Canadian Palaeontology 2. Insects from the Tertiary lake deposits of the southern interior of British Columbia, collected by Mr. Laurence M. Lambe in 1906. Geological Survey of Canada Memoir 12:93-129.

Hills, L. V., and H. Baadsgaard. 1967. Potassium-Argon dating of some Lower Tertiary strata in British Columbia. Bulletin of Canadian Petroleum Geology 15:138-149.

Janssens, J. A., D. G. Horton, and J. F. Basinger. 1979. *Aulacomnium heterostichoides* sp. nov., an Eocene moss from south central British Columbia. Canadian Journal of Botany 57:2150-2161.

Kidwell, S. M., and A. K. Behrensmeyer (eds.) 1993a. Taphonomic approaches to time resolution in fossil assemblages. Short Courses in Paleontology Series, Number 6. S. J. Culver, series ed.

——— 1993b. Taphonomic approaches to time resolution in fossil assemblages: introduction. Pp. 1-8 *in* S.M. Kidwell and A.K. Behrensmeyer, eds.

Lambe, L. M. 1906. On *Amyzon brevipinne*, Cope, from the *Amyzon* beds of the Southern Interior of British Columbia. Transactions of the Royal Society of Canada series 2; Volume 12, section 4, article 11: 151-157.

——— 1907. Monographs of the U.S. Geological Survey, Washington, D.C. 49:178-179.

Li, G.-Q., M. V. H. Wilson, and L. Grande. 1997. Review of *Eohiodon* (Teleostei: Osteoglossomorpha) from western North America, with a phylogenetic reassessment of Hiodontidae. Journal of Paleontology 71:1109-1124.

Mathews, W. H. 1964. Potassium-Argon age determination of Cenozoic volcanic rocks from British Columbia. University of British Columbia Department of Geology Report 2.

McCune, A. R. 1987. Lakes as laboratories of evolution: endemic fishes and environmental cyclicity. Palaios 2:446-454.

Olsen, P. E. 1986. A 40-million-year lake record of early Mesozoic orbital climate forcing. Science 234:842-849.

Rice, H. M. A. 1959. Fossil Bibionidae (Diptera) from British Columbia. Geological Survey of Canada Bulletin 55:1-37.

——— 1968. Two Tertiary sawflies (Hymenoptera: Tenthredinidae) from British Columbia. Geological Survey of Canada Papers 67-69:1-21.

Rouse, G. E., and W. H. Mathews. 1961. Radioactive dating of Tertiary plant-bearing deposits. Science 133:1079-1080.

Rouse, G. E., W. S. Hopkins, and K. M. Piel. 1971. Palynology of some late Cretaceous and early Tertiary deposits in British Columbia and adjacent Alberta. Geological Survey of America, Special Paper 127:213-246.

Russell, L. S. 1935. A middle Eocene mammal from British Columbia. American Journal of Science 29:54-55.

Schindel, D. E. 1980. Microstratigraphic sampling and the limits of paleontological resolution. Paleobiology 6:408-426.

Stockey, R. A., and S. R. Manchester. 1988. A fossil flower with *in situ Pistillipillenites* from the Eocene of British Columbia. Canadian Journal of Botany 66:313-318.

Symons, D. T. A., and M. R. Wellings. 1989. Paleomagnetism of the Eocene Kamloops Group and the cratonization of Terraine I of the Canadian Cordillera. Canadian Journal of Earth Sciences 26:821-828.

Wetzel, R.G. 1983. Limnology (second edition). Saunders College Publishing, Fort Worth.

Wilson, M. V. H. 1974. Fossil fishes of the Tertiary of British Columbia. Unpublished PhD thesis; University of Toronto; Toronto, Ontario.

——— 1977a. Middle Eocene freshwater fishes from British Columbia. Life Sciences Contributions, Royal Ontario Museum 113:1-61.

——— 1977b. New records of insect families from the freshwater middle Eocene of British Columbia. Canadian Journal of Earth Sciences 14:1139-1155.

——— 1977c. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. Canadian Journal of Earth Sciences 14:953-962.

——— 1978a. *Eohiodon woodruffi* n. sp. (Teleostei, Hiodontidae), from the middle Eocene Klondike Mountain Formation near Republic, Washington. Canadian Journal of Earth Sciences 15:679-686.

——— 1978b. Paleogene insect faunas of western North America. Quaestiones Entomologicae 14:13-34.

——— 1978c. Evolutionary significance of North American Paleogene insect faunas. Quaestiones Entomologicae 14:35-42.

——— 1980. Eocene lake environments: depth and distance-from-shore variation in fish, insect and plant assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology 32:21-44.

——— 1982a. A new species of the fish *Amia* from the middle Eocene of British Columbia. Paleontology 25:413-424.

——— 1982b. Early Cenozoic insects: paleoenvironmental biases and evolution of the North American insect fauna. Third North American Paleontological Convention Proceedings 2:585-588.

——— 1984. Year classes and sexual dimorphism in the Eocene catostomid fish *Amyzon aggregatum*. Journal of Vertebrate Paleontology 3:137-142.

——— 1987. Predation as a source of fish fossils in Eocene lake sediments. Palaios 2:497-504.

——— 1988. Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 62:609-623.

——— 1993. Calibration of Eocene varves at Horsefly, British Columbia, Canada, and temporal distribution of specimens of the Eocene fish *Amyzon aggregatum* Wilson. Kaupia - Darbstädter Beiträge zur Naturgeschichte 2:27-38.

——— 1996a. Fishes from the Eocene lakes of the Interior. Pp. 212-224 *in* R. Ludvigsen, ed. Life in stone: a natural history of British Columbia's fossils. UBC Press, Vancouver.

——— 1996b. Eocene fishes of Republic, Washington. Washington Geology 24:30-31.

Wilson, M. V. H., and D. G. Barton. 1996. Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. Paleobiology 22:535-542.

Wilson, M. V. H., and A. Bogen. 1994. Tests of the annual hypothesis and temporal calibration of a 6375-varve fish-bearing interval, Eocene Horsefly Beds, British Columbia. Historical Biology 7:325-339.

CHAPTER 2:

TAPHONOMIC VARIABILITY AND THE PALEOENVIRONMENT OF THE H3 INTERVAL

"The fish, an organized assembly of soft and bony tissues surrounding a float structure sensitive to temperature, will be thought of as a recording device dropped into a lake to be recovered later with imprinted information about temperature, depth, energy, scavengers, and oxygen concentration." (Elder 1985: pp. 13-14)

Introduction

Paleontologists have been interested in the study of preservation of fossils since the early part of the 20th century (Abel 1912; Richter 1928) and even into the 19th century (Walther 1894). Taphonomy, literally the system of laws governing death, was not defined until 1940 by Efremov as the "science of the laws of embedding". Early taphonomic studies dealt mostly with information lost from the fossil record, for example, estimates of the percentages of biota missing from the fossil record because of the rarity of preservation of soft tissues (Johnson 1960; Fagerstrom 1964). It was not until the late 1970s, when the scope of taphonomic studies increased, that the field of taphonomy progressed much beyond this point. More recent definitions reflect this broader scope. For example, Behrensmeyer and Kidwell (1985) define taphonomy as the "study of processes of preservation and how they affect information in the fossil record". A major part of the increase in scope has been the incorporation of information that can be gained from the study of differential preservation. Brett and Baird (1986) laid the foundations for the study of "comparative taphonomy" (how differential preservation relates to different depositional environments). A recent study on *Archaeopteryx* (Kemp and Unwin 1997) provides a good example of the applications of comparative taphonomy. Wilson (1988a) reviews the history of the study of taphonomy and an increasing emphasis on information that can be obtained from comparative taphonomy ("taphonomic gain").

Because of the many definitions of taphonomy that are currently in use, I should specify the exact definitions which I will be using for the remainder of this chapter.

"Taphonomy" is often used to refer to the general study of preservation, including causes and patterns of disarticulation (see definition of Behrensmeyer and Kidwell above), or the study of how organisms (or traces of organisms) come to be buried and preserved in the fossil record. I will use the term "taphonomic studies" or "taphonomy" to refer to this broad application of the term. "Taphonomy" also has a more narrow definition: processes occurring between death (or necrolysis) of an organism and its discovery as a fossil (Valentine 1973). According to this definition, taphonomy refers only to processes that result in particular patterns of preservation. This more narrow definition is also useful, but I will use the term "taphonomic processes" to specifically refer to these processes.

Even with the increasing scope of taphonomy, there are still some major biases in terms of the groups that are being studied. About 30% of papers dealing with taphonomy listed in "Georef" (a database of papers in geological journals) between 1975 and 1985 involved studies on vertebrates (Behrensmeyer and Kidwell 1985). The vast majority of these, however, focus specifically on terrestrial vertebrates (Wilson 1988a). Up until the mid 1980s, aside from an important work by Schäfer (1962) and a few others (Zangerl and Richardson 1963; McGrew 1975; Gaudant 1983), little has been published on the taphonomy of fishes, largely because of a lack of knowledge of basic processes of aquatic taphonomy. In the early 1980s, however, R. L. Elder, as part of her Ph.D. thesis research (along with her supervisor G. R. Smith) conducted a series of experiments and studies that became the foundation of our knowledge of taphonomy of fishes (Elder 1985; Elder and Smith 1984, 1988; Smith and Elder 1985). Following Elder's thesis, there was a great increase in numbers of taphonomic studies specifically on fishes (*e.g.* Wilson 1987; Mörs 1993; Wells *et al.* 1993; Ferber and Wells 1995; Burrow 1996; Wilson and Barton 1996).

The specific objectives of this paper are to apply this knowledge of taphonomic processes of fishes in a microstratigraphic study of changes in preservational patterns. The middle Eocene varved lacustrine beds at Horsefly, British Columbia, are ideal for microstratigraphic studies because of their fine time resolution (see Chapter 1) (Wilson 1977a, 1993; Wilson and Bogen 1994; Wilson and Barton 1996; see Bell *et al.* 1987 for a discussion of the utility of lacustrine [and especially varved] deposits in time resolution studies). Preservational patterns of different body regions will be analyzed for changes

through a 10 000-year interval. Changes in these patterns of preservation are indicative of changes in taphonomic processes, which, in turn, are indicative of broader paleoenvironmental changes in and around the lake represented by these sediments. First, however, a brief review of the basics of the taphonomy of fishes will be presented.

Taphonomy and preservational patterns of fish

The basic approach of Elder's thesis research (1985; Smith and Elder 1985) was to subject fish carcasses to a variety of environmental conditions, and to examine the effects these conditions have on both taphonomic processes and the preservational patterns that they produce. Actualistic studies such as these are important and are becoming more and more common for different taxa (*e.g.* Blob 1997; Davis and Briggs 1998) because they form the basis for further work on taphonomy of fossil members of those taxa. Elder's main objective was to identify unique preservational patterns that could be recognized in the fossil record. If a particular environmental condition (causing a particular taphonomic process) produces a unique pattern of preservation, this pattern of preservation, if found in a fossil specimen, can be used to infer the environmental conditions upon death of that specimen. Relationships between environment, taphonomic processes, and their preservational patterns will be briefly reviewed, followed by a brief discussion of some of the assumptions and limitations of Elder's work, followed by a description of the specific approach taken in this study.

Temperature.--One of the most fundamental taphonomic processes of fish is the tendency for carcasses to float above a certain threshold temperature, or more accurately, a certain function of temperature and time (Fig. 2-1) (for a more complete discussion of threshold temperatures, see Elder 1985; Smith and Elder 1985). A carcass will float when enough decay gas has built up in its tissues to render it slightly more than neutrally buoyant. These gases build up more quickly at increased temperatures. Time to flotation (and indeed the likelihood of floating at all), therefore, depends on the temperatures to which the carcasses are subjected (Fig. 2-1). Fishes at or near the threshold temperature (within the gray line on Fig. 2-1) undergo a process Elder (1985; Smith and Elder 1985)

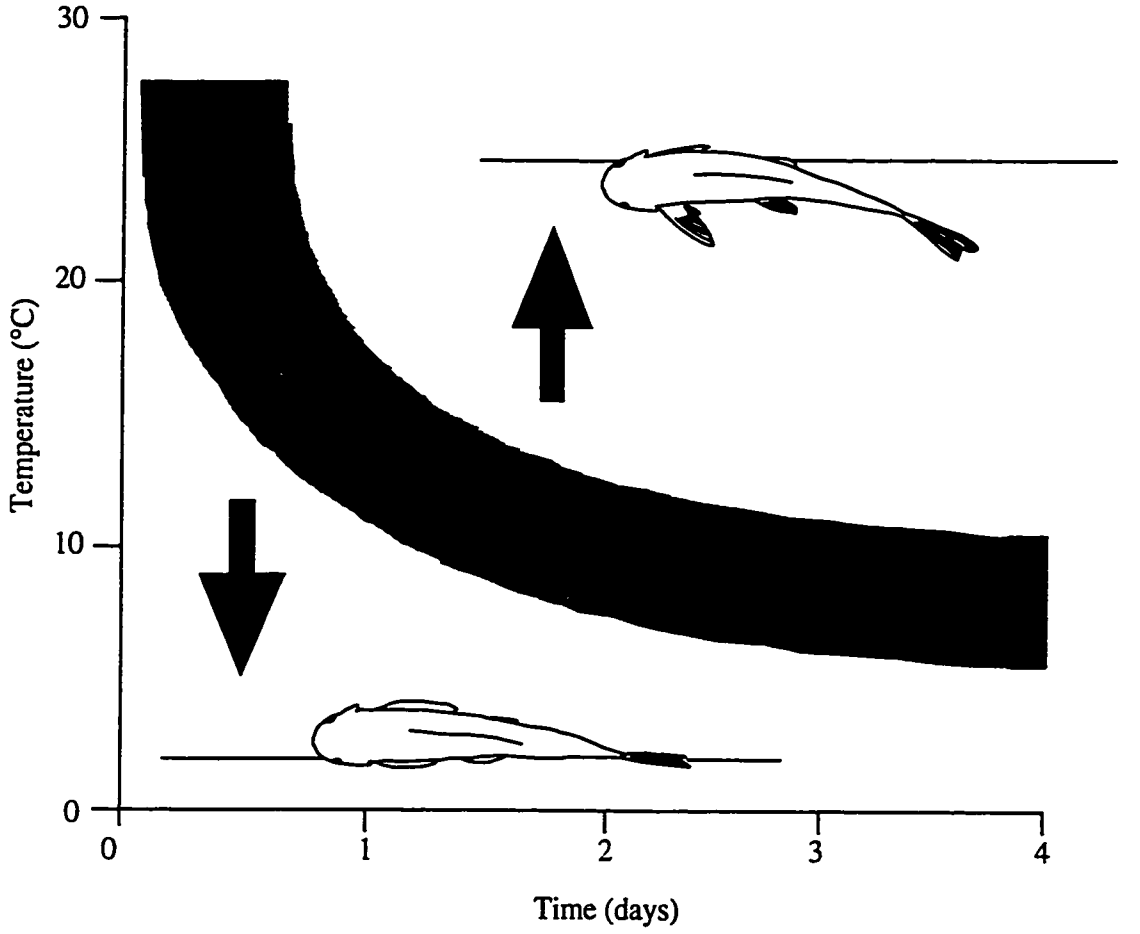


Figure 2-1: Summary of Elder's (1985) and Smith and Elder's (1985) experiments of buoyancy responses of fish carcasses to various temperatures through time. Above the gray line indicates conditions in which carcasses float to the surface, below the gray line indicates conditions in which carcasses sink, and within the gray line indicates conditions in which carcasses are almost neutrally buoyant and partially lift off the sediment ("partial flotation"). Adapted from Smith and Elder (1985).

called partial flotation, in which the carcass partially rises from the sediment as the build-up of decay gas is sufficient lift the abdomen, but insufficient to lift the head and tail off the sediment. Eventually this gas ruptures through the skin and escapes, causing the carcass to fall back down to the sediment surface. The relationship between temperature, time and flotation is not always as straightforward as illustrated in Figure 2-1. In Elder's actual data (1985: Fig. 2), some specimens sank at high temperatures, and others floated at low temperatures. The relationships illustrated by Figure 2-1, do, however, approximate the general trends of fish carcasses, and will be used as a model for the rest of this chapter.

All of Elder's (1985; Smith and Elder 1985) experiments were conducted in controlled laboratory settings. In natural settings, many other factors (some of which Elder addressed in further studies) can complicate these relationships. Many lakes have temperature profiles that can result in great temperature differences between the surface waters and the bottom waters of a lake. The immediate tendency for a carcass to sink or float depends on the temperature at the level in the lake in which the fish died, but the long-term tendency to sink or float depends on the temperature at the bottom of the lake. Both of these temperatures have to be considered when analyzing trends of flotation. A second complication is increased pressure (as is found at the bottom of deep lakes) which increases the temperature necessary to float carcasses (Elder 1985). Even at warm temperatures, specimens at great depths are not at all likely to float. In other words, the threshold temperature (gray line in Fig. 2-1) is shifted upwards with increased pressure. A third complication on the tendency for a carcass to sink or float is the effects of changing temperature. Fishes dying in changing temperatures can act somewhat like Cartesian divers such that fishes dying in rising temperatures are likely to float, and those dying in decreasing temperatures are more likely to sink (see Seilacher and Labarbera 1995). Most teleosts control their depth in the water column by regulating the amount of gas in their swim bladder. Changes in ambient temperatures alter the volume of gas contained within the swim bladder, causing a fish to either sink or float (unless it compensates for such changes). It should be noted that although the swim bladder is important in the initial response of a carcass to float or sink, it is gases building up in tissues of the rest of the body that determine the ultimate floating or sinking of carcasses (fishes with swim bladders removed behaved similarly in constant

temperatures to those with swim bladders intact) (Elder 1985).

The previous experiments were designed to examine relationships between environment of death (temperature) and taphonomic processes (flotation, partial flotation or sinking). Elder (1985; Elder and Smith 1985) then examined the relationships between these taphonomic processes and the preservational patterns that they produce.

Floating carcasses tend to lose skeletal elements in a consistent and predictable sequence:

> "the lower jaw bones are the first elements to disarticulate from the body along with the tiny lepidotrichia from the fins [followed by the] maxillae, premaxillae, scales, opercular series, shoulder girdle, suspensorium, pterygoids, pelvic ptergiophores [sic], hyoid series, ceratotrichia, and loss of body regions such as breakage between the skull and vertebral column or breakage of the caudal peduncle" (Elder 1985: p. 30).

After many of these elements have fallen off, decay gas can easily escape from the carcass, causing it to sink (regardless of temperature). There are therefore two main patterns of preservation that can be produced by floating carcasses: headless (and finless) carcasses, and isolated bones that have fallen off the floating carcass (bones listed earliest in the above sequence should be most common). Isolated bones can be produced by numerous taphonomic processes; therefore, they are of limited use in paleoenvironmental reconstruction. Both scavenging (see below) and flotation can result in disarticulation of the skull, but flotation is the only process in which disarticulated elements should not be found anywhere near the source (scavengers scatter elements but generally in the near vicinity of the carcass).

Partial flotation, in which build-up of decay gas is not sufficient to completely float the carcass, is associated with a diagnostic pattern of disarticulation. As decay gas escapes the body, it ruptures through the skin, often causing displacement of mid-body elements (vertebrae and ribs) (Elder 1985; Smith and Elder 1985). Results of this process, especially when elements are severely disarticulated (with ribs and vertebrae displaced out of the body cavity) are sometimes called "gas explosions" (Schäfer 1962). Displaced vertebrae and ribs, however, are found on the same bedding plane, generally not far from their original position on the carcass. Partial flotation is a common occurrence in the fossil record (see, for example, Grande 1984: Fig. II.27; Frickhinger 1985: p. 580; Wilson

1988a: Fig. 10 B). Patterns of preservation caused by this process are distinctive; therefore, their presence in the fossil record is a good indication that environmental conditions were conducive to partial flotation.

At temperatures below threshold (or at high pressure), build-up of decay gas is insufficient to lift the carcass off the sediment. Disarticulation under these conditions is slow, with little or no scatter of any elements. After about eight weeks of Elder's controlled experiments, connective tissue holding the lepidotrichia together began to decay, causing a slight disarticulation of these elements. In natural conditions, the time to disarticulation of fins will likely be much greater than eight weeks. Fossils showing minor lepidotrichial displacement, but no other sign of any other sources of disarticulation, are therefore indicative of decay without a sediment cover for (at least) 8 weeks. The opposite, however, is not necessarily true: lack of lepidotrichial damage does not indicate rapid burial. Fossils with no lepidotrichial displacement could have been buried immediately, or conditions could have been such that they remained unburied for many months.

Figure 2-2 is a graphic summary of the relationships between different temperatures, taphonomic processes associated with these temperatures, and the preservational patterns that they produce.

Scavengers.--Scavengers are another major factor in aquatic taphonomy. Elder examined the effects of different macroscavengers (snails, crayfish, fish) on fish carcasses, but she did not attempt to specify inter-taxa differences.

Macroscopic scavengers tend to attack "distal parts of fins, especially the caudal fin, the eyes, the jaws, and the abdominal cavity first, then disarticulating the hyoid and opercular bones before moving on to disturb the rest of the scales, fins, and mid-body musculature" (Elder 1985: p. 55). Like partial flotation, scavengers cause a multi-directional scatter of elements, but the patterns caused by partial flotation are localized around the abdominal area, while those of scavengers are more generalized.

The presence of scavengers is generally thought to indicate a high level of oxygen in the water. However, Rahel and Nutzman (1994) showed that a species of mudminnow (*Umbra limi*) regularly ventures into an hypoxic hypolimnion (a normally lethal environment) to forage and returns to oxygenated water to respire. Although the

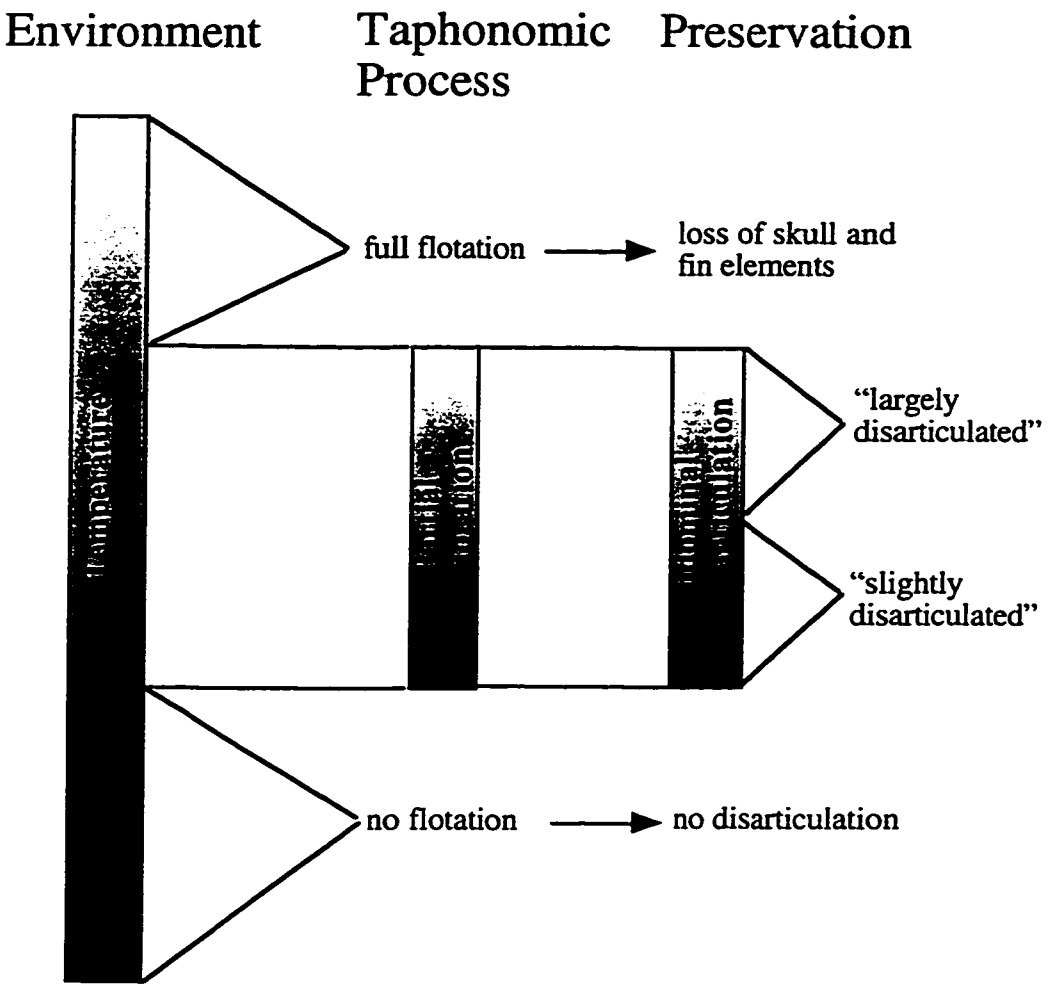


Figure 2-2: Summary of relationships between environment, taphonomic processes and preservational patterns, as illustrated by temperature. The environmental variable, temperature, is continuous. Different temperatures, however, can result in only three distinct taphonomic processes, two of which are discrete patterns, and one is (likely) a continuous pattern. For example, at low temperatures, specimens do not float, and unless there are other taphonomic processes occurring, will show no disarticulation. Within some range of intermediate temperatures, specimens will tend to undergo partial flotation, in which the abdomen lifts off the sediment with the accumulation of decay gas. As this gas eventually is released, it causes some degree of disarticulation of abdominal elements (ribs and vertebrae). At higher temperatures, gas build-up should be greater, and the subsequent release more violent, causing more abdominal disarticulation. In this study, I used two distinct categories separated by a somewhat arbitrary division to code abdominal disarticulation. Finally, at high temperatures, accumulation of decay gas will lift carcasses right off the sediment to the surface of the lake. Preservational patterns are very different from the other processes, with individual bones falling off the floating carcass until there is little left to contain the decay gases, at which point the carcass sinks back down to the bottom. This figure also illustrates the approach of this paper: with a good knowledge of these processes, preservational patterns can provide paleoenvironmental information. For example, a largely disarticulated abdomen is an indication of death or decay in some moderate temperature range.

mudminnow is not a scavenger, it does provide evidence that fishes can tolerate normally lethal environments for short periods of time, especially to exploit a plentiful food resource. Rahel and Nutzman suggest that "foraging in hypoxic water may be common among some fishes when food abundance is low in surface waters" (1994: p. 1246). Carcasses in highly oxic waters are obviously more vulnerable to scavengers (because scavengers do not need to limit the lengths of their trips to feed), but the presence of scavengers is not limited to oxygenated waters.

Oxygen.--Other preservational features of fish fossils are more directly indicative of the relative abundance of oxygen. Of the several causes of death (*e.g.* starvation, anoxia, heat stress) that Elder examined (1985; Smith and Elder 1985), only anoxia produced a distinctive pattern that would be visible on fossil fishes: fishes dying in low or no oxygen display tetany of fins and mouths. No other known taphonomic process causes preservational patterns similar to those of low oxygen; therefore, tetany is a clear indication of death in anoxic or hypoxic conditions.

Other factors.--Several other taphonomic processes, including wave action and currents, can be important in studies of preservation of fossil fishes. These processes, however, are not important in the preservation of the fishes from the site in this study, therefore they will not be discussed in any detail here.

Further Research

There are a few specific areas that Elder did not address in her thesis (1985) that are important for future work on fish taphonomy. Firstly, a quantitative study of different preservational patterns caused by different scavengers would be useful for paleoecological reconstructions. A knowledge of these differences will help to determine the major types of scavengers (even in the absence of body fossils) in different environments. Secondly, particularly small and large individuals tend to be less predictable in their responses to environment, but Elder (1985) made no attempt to examine or quantify these differences. Finally, Elder made no attempt to quantify or even qualitatively address differences in taphonomic processes in different groups (other than a few remarks on exceptional groups;

for example, heavily armoured groups tend to not float, even at high temperatures). These differences could potentially be large, and should be addressed in future actualistic studies on fishes. Many of Elder's studies were on catostomids, the focus of this paper, so these interspecific differences should not be a large concern in this study.

Approach

Elder's approach was to manipulate the environment, and to examine taphonomic processes and the resulting preservational patterns (Fig. 2-2). The framework is now in place to allow taphonomists to use these relationships to infer environmental conditions from preservational patterns. These relationships depend in a large part on a one-to-one relationship between patterns of preservation and taphonomic processes. Not every preservational pattern, however, is unique. For example, largely disarticulated fossils with elements scattered around on the bedding plane can be caused by several factors including scavengers, partial flotation ("gas explosion") and currents. The patterns of currents are easy to recognize because they result in unidirectional scatter of elements, and some sorting with respect to bone size and density (Elder 1985; Smith and Elder 1985). Both scavenging and partial floatation are specific to certain parts of fish carcasses. If the disarticulation is concentrated in the head region it is unlikely that this pattern was caused the the buildup and subsequent release of decay gases, and it therefore strongly suggests scavengers. Likewise, if the head region is relatively intact, but the abdomen is the center of disarticulation, it is likely that partial flotation caused the pattern of disarticulation. There are many specimens for which the specific cause of disarticulation cannot be determined. The approach that I will take here is to look for disarticulation of three main body regions (abdomen, skull and fins), each affected by different taphonomic processes. The preservation of these will be examined for temporal trends, and the environmental trends that most likely caused these changes will be discussed.

This study is somewhat similar to that of Wilson and Barton (1996) in that it is a microstratigraphic analysis of changes in preservational patterns through time. This study differs, however, in that it includes an attempt to explain those changes with specific

reference to taphonomic processes and the environmental conditions that produced them. The environmental conditions that produced these changes will be analyzed for temporal trends, and compared to other features of the fossils that can also provide paleoenvironmental data. The temporal span of this study is also much longer than that of Wilson and Barton (1996), allowing study of changes over much longer periods of time.

Materials and Methods

Locality.--The Horsefly locality is exposed along the banks of the Horsefly River in central British Columbia. The site is biostratigraphically correlated with many other Cenozoic deposits of central British Columbia based on both palynological (Rouse *et al.* 1971) and paleoichthyological (Wilson 1977) studies. Some of these other sites, in turn, have been dated as middle Eocene using both radiometric (Rouse and Mathews 1961; Mathews 1964; Hills and Baadsgaard 1967) and paleomagnetic (Symons and Wellings 1989) methods. The Horsefly locality represents a lacustrine deposit (*e.g.* Wilson 1977). Exposure of the Horsefly site is restricted to the banks of the river, and therefore, the size of the original lake cannot be determined.

The entire Horsefly site (approximately 100 vertical metres of section) has fossils throughout (plant, insects and fishes), but there are several sequences of microlaminations rich in fossil fishes. Three of these intervals have been informally named H1, H2 and H3 (see Chapter 1). H3, the longest of these intervals, is the focus of this study (Fig. 2-3).

Wilson and Bogen (1994) demonstrated that the roughly 6000 microlaminations that make up the originally described H3 section represent yearly layers, or varves (Wilson [1993] previously demonstrated the same of the 715-varve H2 interval). Since this study, the H3 section has been extended by about 4000 laminations below the original 6000 due to the discovery of a more complete exposure. The additional layers are very similar in overall general appearance (thickness and composition of laminations) to the originally described layers, and for the purpose of this study, will be assumed to be varves (see Chapter 1). The distinctiveness of sequences of varves (colour, grain size, varve

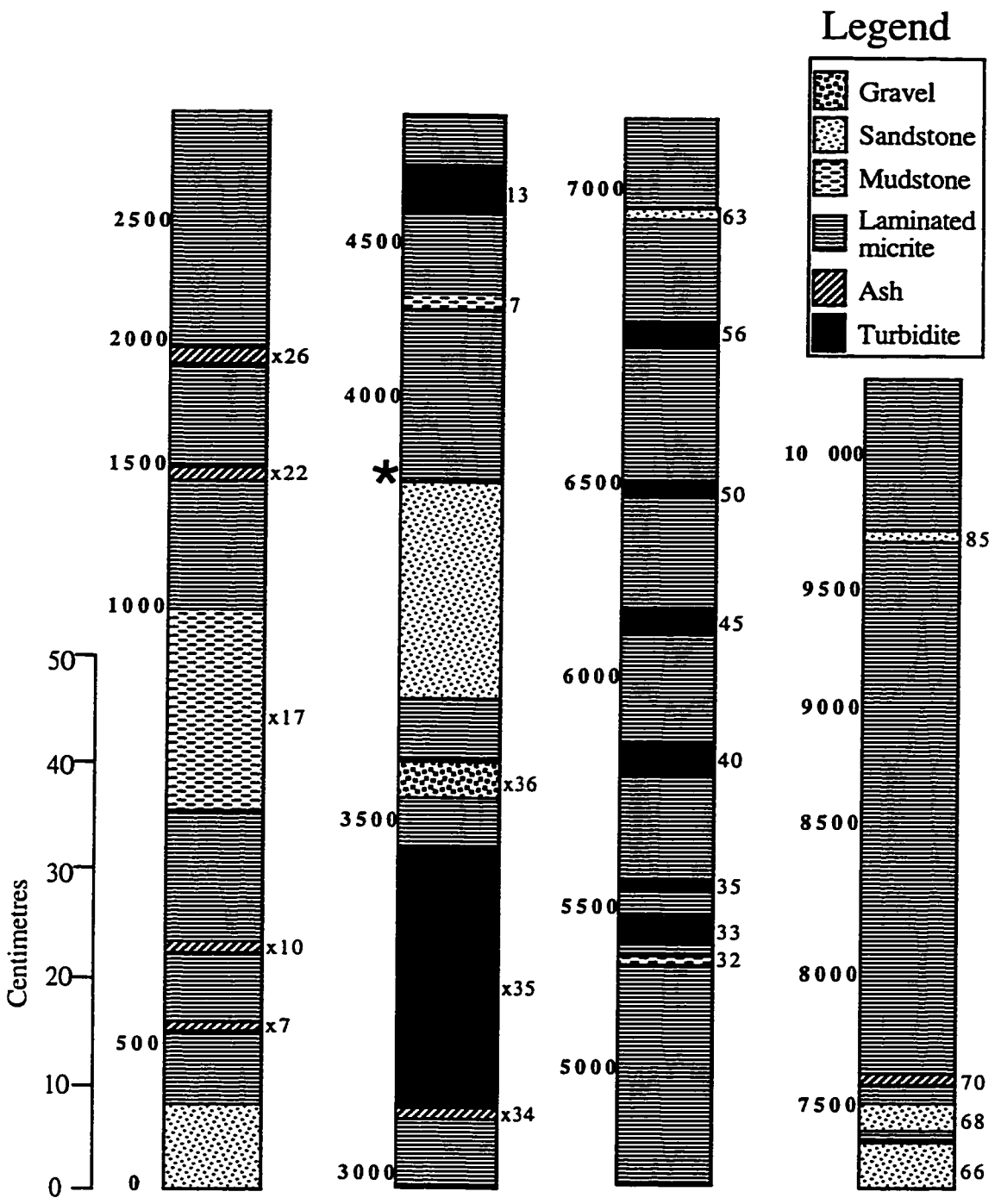


Figure 2-3: Detailed stratigraphic section of the H3 section of the Horsefly locality. Lithologies are not usually distinct, but tend to grade into each other (with the exception of ash and turbidites which are interpreted as event layers). Laminated micrite layers are interpreted as annually laminated (varved). Asterix indicates the bottom of the old H3 section (Wilson and Bogen 1994). Numbers along left side of section indicate relative year (as described in the text). Breaks between parts of the section here are arbitrary.

thickness) and event layers (turbidites and ash layers that are distributed throughout the column) allow the assignment of individual rock fragments and fossils to their precise orientation and vertical position in the stratigraphic column as described in Chapter 1 and by Wilson and Bogen (1994).

Previous work on the paleoecology of the Horsefly locality has been almost exclusively on the H2 interval (Wilson 1977; see also Wilson 1980, 1984, 1988b, 1993; Wilson and Barton 1996), with only one study specifically on the H3 section (Wilson and Bogen 1994). The H2 section was deposited in the deeper parts of a normally stratified lake in a warm temperate climate (Wilson 1977, 1980). Several possible yearly cycles have been proposed for the layers represented by the H2 section: meromictic (bottom perennially anoxic or hypoxic), monomictic (circulating once a year), dimictic (circulating twice a year) or polymictic (overturning several times a year) (Wilson 1977, 1980; Wilson and Barton 1996). It is also possible that bottom sediments were perennially anoxic while the upper water column circulated relatively freely. Wilson (1977) and Wilson and Barton (1996) both support a monomictic model for the lake (see Chapter 1). Because of the similarity in preservation of varves and fossils, the paleoecology of the H3 interval is likely similar to that of the H2 section. This study will provide more information specifically on the paleoecology of the H3 section.

By far the most common fish in the H3 deposits is *Amyzon aggregatum* (Cypriniformes: Catostomidae), which accounts for about 95% of all fish fossils recovered. To avoid any potential problems of inter-specific variations in taphonomy, all other species from the H3 interval have been omitted from comparisons of preservational patterns, although their temporal distributions are discussed.

Methods.--A total of 698 specimens from the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) and Royal British Columbia Museum (RBCM) collections were used in this study (see Appendix). All of these specimens were collected by University of Alberta field crews in the past 20 years (with the vast majority collected in 1996), with some specimens subsequently donated to the RBCM. Specimens were first assigned to the varve in which they are preserved (and therefore their relative year of death) as described in Wilson and Bogen (1994) and in Chapter 1. All references to year for the

remainder of this paper refer to the relative year on the stratigraphic column. Occasionally, when a specimen is situated on a slab so that a thin part of the fish (*e.g.* ends of the fins) is visible in cross-section, I could assign it to the pale or dark portion of the couplet. If no cross-section is visible, assigning pale or dark portion of the couplet cannot be done with any confidence.

Specimens of *Amyzon* and other genera from the H3 section (*Eohiodon, Priscacara*; see Chapter 1, Wilson 1977b) were plotted against relative year of death.

Whenever possible, standard lengths of specimens of *Amyzon* were measured. These data were then plotted as a frequency distribution for the entire section combined, and split by millennium of death. Temporal trends in standard length were also examined by plotting standard length against relative year of death. Size per millennium was compared using an ANOVA test. Comparisons of large numbers of values such as this have a high probability of type I errors (Sokal and Rohlf 1981) in which the null hypothesis (in this case, no significant correlation) is true, but is rejected nonetheless. To correct for this problem, I used the sequential Bonferroni method (Holm 1979; see also Rice 1989) to test for significance at the $p<0.05$ level.

Specimens from the H3 interval tend to fall into one of two distinct patterns of disarticulation: either centered around the skull (as described in Wilson and Barton 1996) or around the abdominal cavity and mid-body musculature. Patterns of disarticulation in these two regions were therefore used in temporal analyses. Disarticulation of fins, which can indicate something about the amount of time that a specimen remained unburied on the sediment, was also recorded. Each of these three regions was assessed for degree of disarticulation independently on each specimen with a relative scale representing the major stages of disarticulation. Nominal values were used for this scale because of the absence of a reliable, relatively easy method for quantifying scatter. Fairly standard examples of each level of disarticulation for each body region were chosen before the analysis as references with which to compare other specimens (in an attempt to standardize levels). Although disarticulation was recorded on a nominal scale, data were generally treated as continuous, thus decreasing the importance of ensuring that individuals are assigned to their precise level of disarticulation, and increasing the emphasis on trends. As many data were

gathered from each specimen as possible, but because many of the specimens were not complete, there were numerous missing data. This conservative approach has the advantage that any trends that are seen are almost certainly real, but also has the disadvantage that it might miss trends.

The fins were the first body region to be examined for signs of disarticulation. There were three categories of disarticulation of fins and one for specimens that were not disarticulated. If one or two of the fins had slight lepidotrichial disarticulation they were counted as slightly disarticulated. If most fins had fairly major lepidotrichial damage they were counted as largely disarticulated. If all fins had many lepidotrichia highly disarticulated, they were counted as completely disarticulated.

The skull (and pectoral series) was the next body region to be examined for signs of disarticulation. There are very few skulls of *Amyzon* that are preserved completely intact, but much of the damage is caused by compaction of the sediment. This type of damage is easy to recognize (crushing of bones with no scatter) and was not included in the analyses as skull disarticulation because it is not related to environmental change. Three nominal levels of disarticulation of the skull (plus a fourth category for no disarticulation) were used. If only one or a few of the skull or pectoral bones were disarticulated and scattered around the specimen, the specimen was counted as slightly disarticulated. If there were several to many bones scattered, the specimen was counted as largely disarticulated. Although scatter can be high in these specimens, they generally retain the overall shape of the skull. Finally, if the skull and pectoral series were completely scattered around the carcass with little to no retention of skull shape, the specimen was counted as completely disarticulated.

The abdominal (and mid-body) area was the next region of the body to be assessed for disarticulation. For disarticulation to be counted as abdominal, it had to be clear that the source of disarticulation was the mid-body region (and not the skull). For example, if only the anterior half of the body is disarticulated along with the skull, but the posterior half the the body is articulated, it would not be included as abdominal disarticulation. This situation was not very common: it was usually easy to determine when disarticulation of abdominal elements was an extension of skull disarticulation, and when it was independent of skull

disarticulation. There was one category for no abdominal disarticulation, and two categories for increasing amounts of disarticulation. Specimens were counted as slightly disarticulated if there were one or a few ribs or vertebrae out of place. This category includes many specimens with a single break in the vertebral column. Specimens with ribs and vertebrae scattered around the body were counted as largely disarticulated. These specimens probably correspond to what other authors have described as "gas explosion" (Schäfer 1962; Elder 1985).

In an attempt to isolate only those specimens whose patterns of disarticulation could have been caused by partial flotation, I also excluded all specimens with any skull disarticulation from the trends of disarticulation of abdomen and analyzed these data separately. This analysis also avoids some of the arbitrariness of the decision of where skull disarticulation ends and abdominal disarticulation begins.

I also recorded the relative amount of tetany displayed by each specimen. Tetany was estimated primarily by fins. Except for three specimens with almost no tetany of fins, nearly every specimen is preserved with its mouth open. Tetany was recorded on a scale of 1 to 5 in which "1" indicates no tetany of fins (all pressed against body) and mouth either open or closed, "2" indicates slight tetany (one or more fins slightly splayed), "3" indicates moderate tetany (one or more fins moderately splayed and raised from the body), "4" indicates high tetany (dorsal, anal, and caudal fin are all largely stretched with clear separation between rays), and "5" indicates extreme tetany (all fins, usually including paired fins, highly stretched). Obviously tetany could be scored on only those specimens whose fins were not completely disarticulated.

Figures 2-4 through 2-6 illustrate several specimens from the H3 interval, and the different categories of disarticulation to which they were assigned.

Analyses.--Temporal trends in disarticulation of each of the body regions were then examined by graphing the preservational scores of various factors against relative year of death. Smoothing functions were used to compare temporal trends because they are powerful and effective tools for data exploration without any of the assumptions of regressions (linearity or uni-directionality) (Velleman 1992). Smoothing functions, however, are still exploratory, and no tests of significance have yet been developed. The

A

B

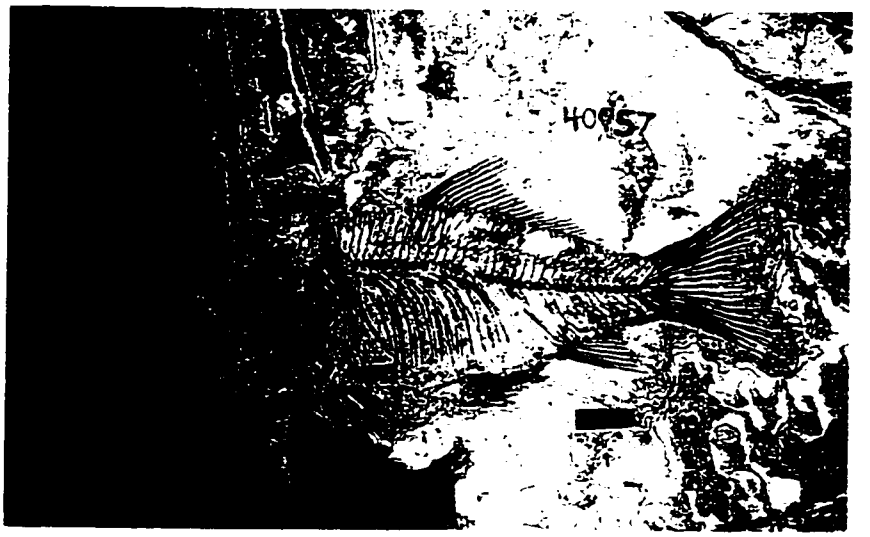


Figure 2-4: Examples of well-preserved specimens of *Amyzon aggregatum* from the H3 interval of the Horsefly locality, British Columbia showing little disarticulation. A, UALVP 31113, showing no disarticulation of skull, abdomen or fins (fins were slightly damaged in preparation), and slight tetany of fins. B, UALVP 40957 showing high tetany of fins, but no disarticulation of skull, abdomen or fins.

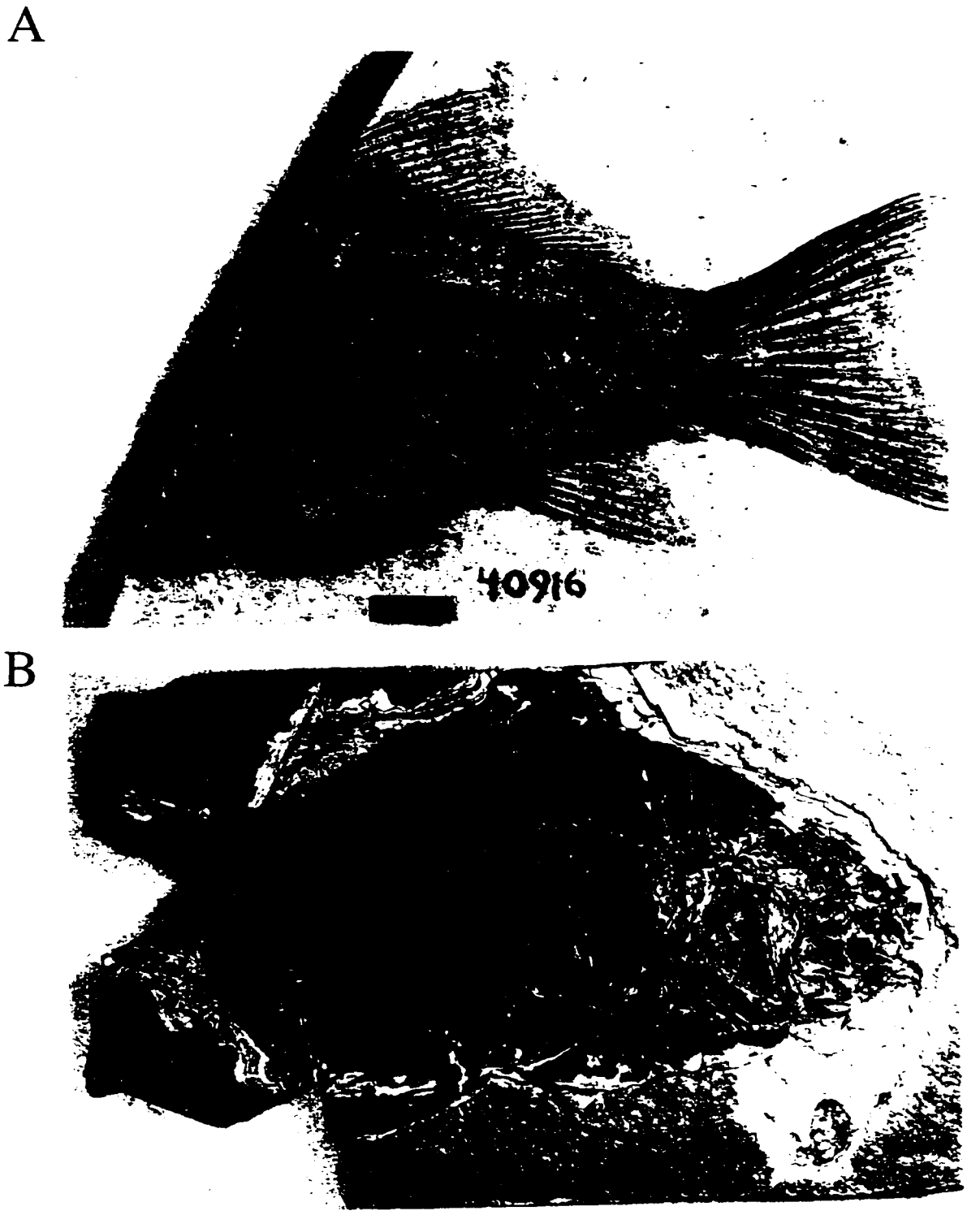
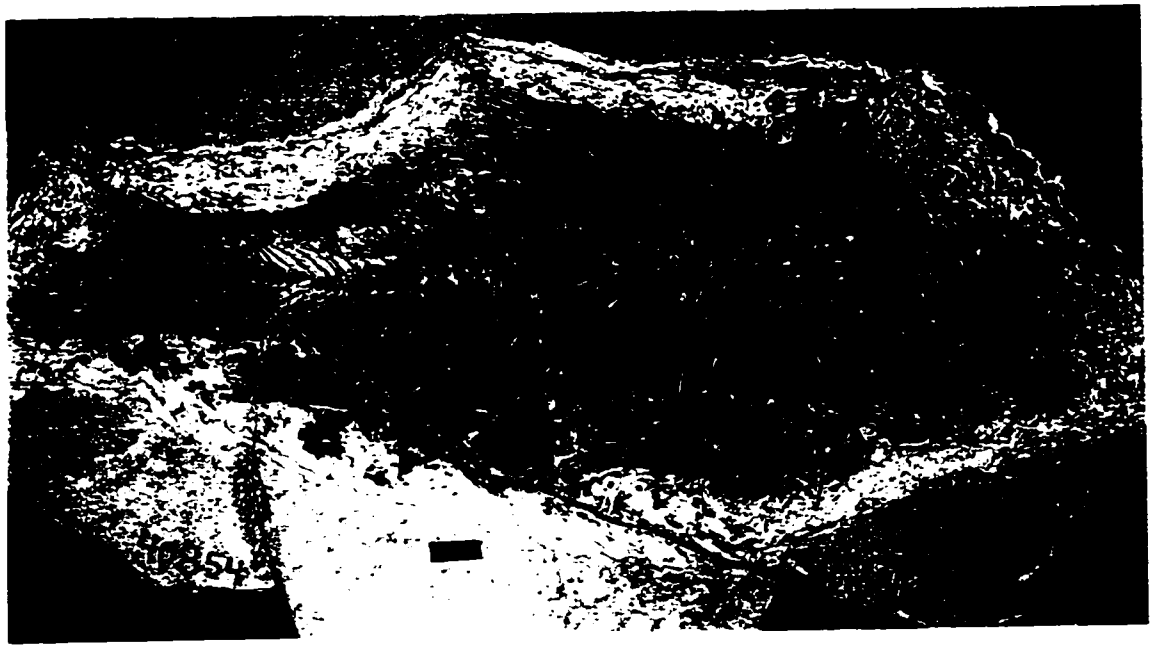


Figure 2-5: Examples of specimens of *Amyzon aggregatum* from the H3 interval of the Horsefly locality, British Columbia, showing patterns of disarticulation that can be attributed to partial flotation. A, UALVP 40916, showing slight abdominal disarticulation (notice breaks in vertebral column), no disarticulation of fins, and high tetany (skull could not be recorded). B, UALVP 41218, showing no disarticulation of skull, slight disarticulation of fins, slight abdominal disarticulation, and low tetany.

A



B

Figure 2-6: Examples of specimens of *Amyzon aggregatum* from the H3 interval of the Horsefly locality, British Columbia, showing patterns of disarticulation that can be attributed to scavenging. A, UALVP 40854, showing moderate disarticulation of skull, moderate disarticulation of fins, and moderate abdominal disarticulation. B, UALVP 40974 showing severe disarticulation of skull.

smoothing function used for all of the temporal analyses here was LOWESS (Locally weighted regression scatterplot smoothing) with a span of 20% of the data (Cleveland 1979). The LOWESS smoothing function was chosen because it emphasizes "grand-scale patterns" in the data (Velleman 1992: p. 33/11), and is less affected by minor fluctuations (that might be caused by chance).

In order to test for trends over a much higher resolution (on a scale of centuries instead of millennia), I isolated the 715-year interval with the greatest density of specimens. A section of 715 years was chosen because it represents the exact amount of time represented by the H2 section examined for taphonomic variation by Wilson and Barton (1996). Results of these tests were not analyzed in any detail other than to provide an idea of temporal trends occurring within the longer term variation through the entire section.

Finally, I tested for any relationships between disarticulation of skull and tetany because both of these factors can indicate something about oxygen levels in the lake. A contingency table analysis and a visual comparison of temporal trends were used.

Results

General

There are approximately six intervals in the H3 section in which specimens of *Amyzon* are most common (Fig. 2-7). The 715-year interval with the highest density of specimens occurs between the years 3800--4515. Specimens are more common in the middle of this interval than at either end. The two other genera from the site have different distributions, with *Priscacara* concentrated at the end of the section, and *Eohiodon* distributed throughout, but more common than *Amyzon* in certain intervals, especially at the end of the section.

Size distribution.--Standard length of fishes from the H3 section ranges from less than 50 mm to almost 250 mm (Fig. 2-8). There appears to be some polymodality in the size

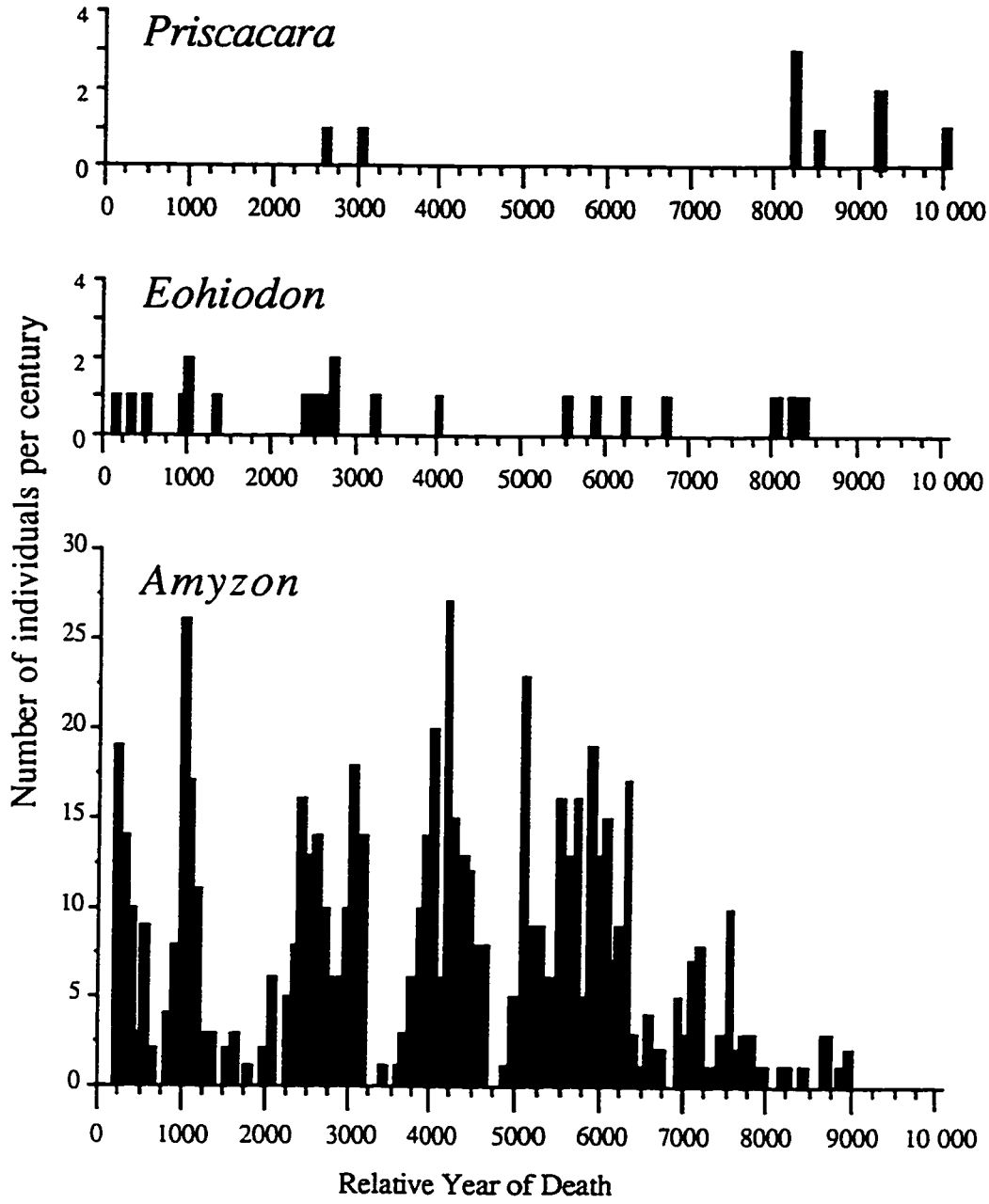


Figure 2-7: Distribution of specimens of *Amyzon*, *Eohiodon* and *Priscacara* through the 10 000 years represented by the H3 section of the Horsefly locality, British Columbia. Polymodality of distribution of *Amyzon* can likely be explained by sampling biases (see text), but such biases cannot explain the different distributions of the three genera through time.

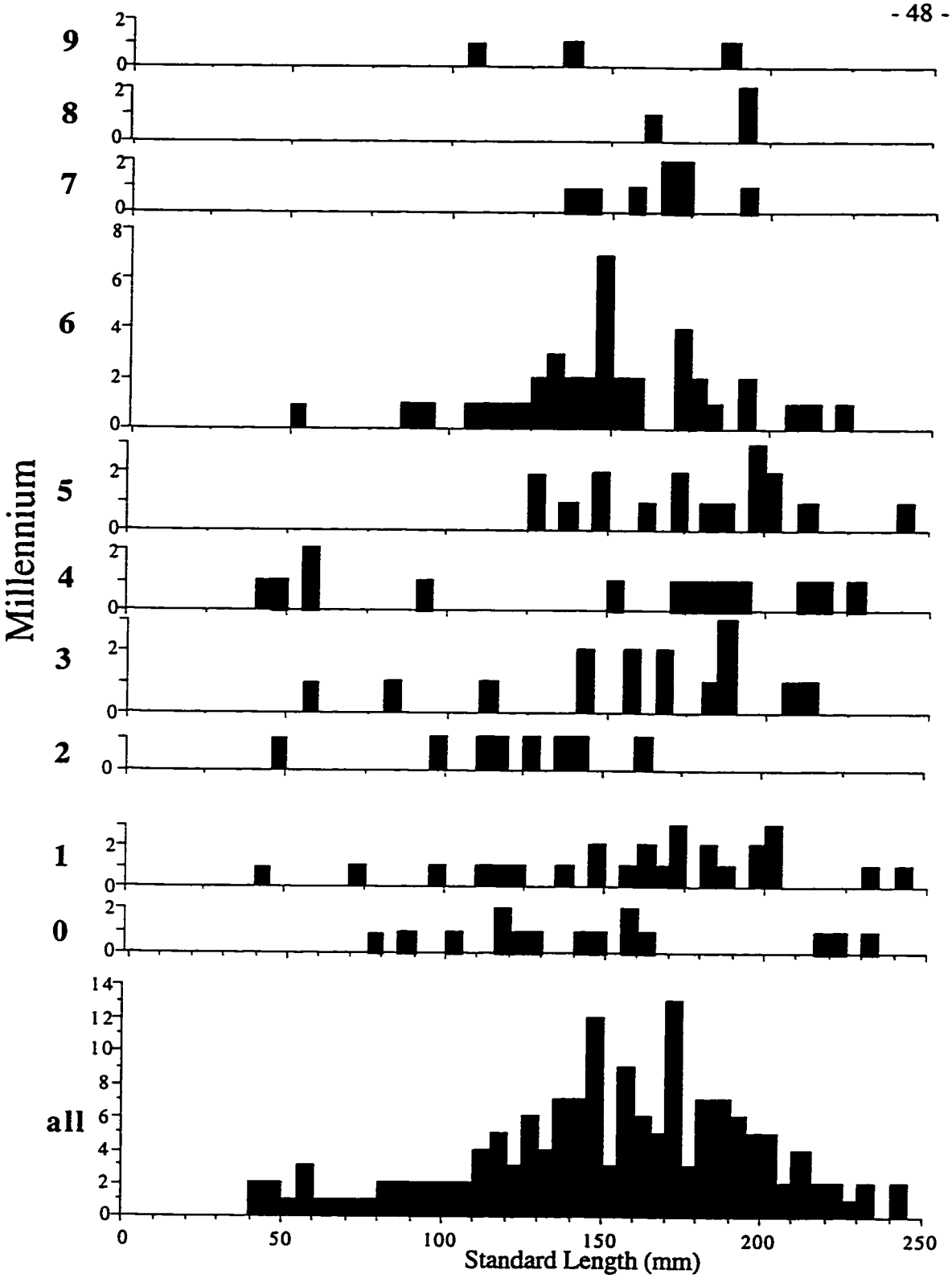


Figure 2-8: Size-frequency distribution of specimens of *Amyzon aggregatum* from the H3 section for the entire section (bottom) and by millennium of death (0 to 9; millennium 0 represents relative years 0–1000).

distribution, but peaks are not distinct. Only millennium six (years 5000--6000), with a peak around the 150 mm size, has enough specimens to be able to identify any peaks in size distribution within a millennium. Mean standard length of specimens varies through the H3 section (Fig. 2-9). Mean standard length was significantly lower in the third millennium than in the sixth and eighth millennia. Mean standard length of the seventh millennium was significantly lower than the sixth millennium.

Pale/dark.--Only 184 specimens could be assigned with confidence to either the pale or dark portion of a varve. Only one of these specimens was clearly preserved in the pale portion of the varve; the rest (183) were preserved either within the dark portion of the varve or between the dark portion and the previous pale layer.

Variation in preservation

General.--There is variation in preservation of all body regions over the millennia (Fig. 2-10). A more detailed description of the variation in each preservational feature is presented below. Some features (*e.g.* disarticulation of fins) are relatively invariant over the interval, whereas others (*e.g.* disarticulation of the skull) vary dramatically.

There is also variation in preservation over the 715-year interval (Fig. 2-11). Preservational patterns of these regions appear as smooth lines in the longer interval, but when this fossil-rich section is examined in detail, a higher resolution of variability is seen.

There are very few isolated bones from the H3 interval, accounting for just 2.8% (11/392) of all specimens from the interval.

Fins.--Some 57% (398/698) of the specimens are complete enough to assess the disarticulation of fins. Of these specimens, 58% show no disarticulation of fin elements, 30% show only slight disarticulation, 10% show severe disarticulation and only one specimen showed complete disarticulation of the fins.

Disarticulation of fins decreases slightly until the year 2000, increases slightly for about 1000 years, decreases to a minimum around the year 6000, and then increases to the end of the section (Fig. 2-10).

Skull and Pectoral series.--Some 55% (386/698) of the specimens are complete enough

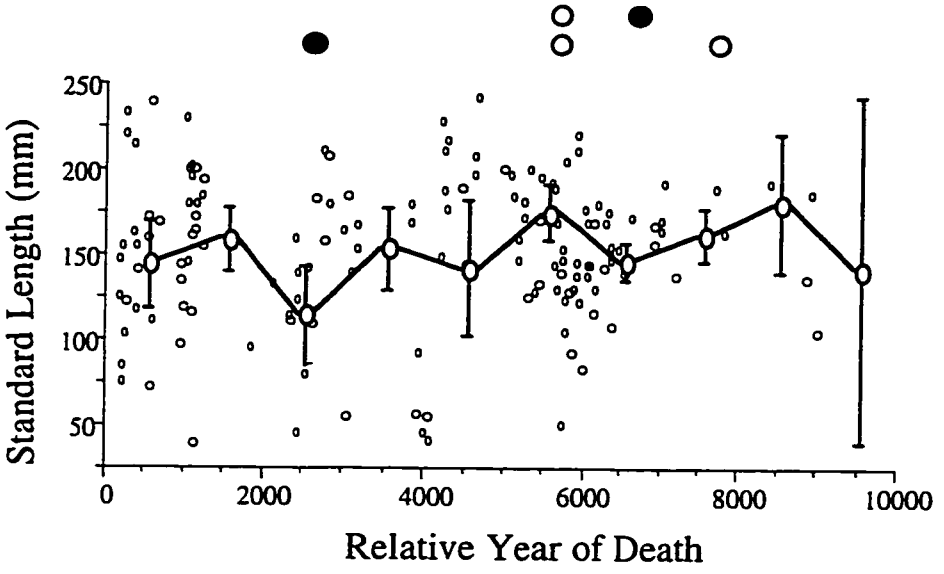


Figure 2-9: Temporal trends in size distribution of *Amyzon* from the H3 interval Small circles indicate actual data points. Larger circles and error bars represent means per millennium and 95% confidence intervals associated with those means. Millennia with significantly different means (ANOVA, with sequential Bonferroni correction) are indicated with circles at the top of the figure. Shaded circles indicate millennia with standard length significantly lower than open circles on the same line (thus millennium 3 is significantly smaller than both of millennia 6 and 8 and millennium 7 is significantly smaller than only millennium 6).

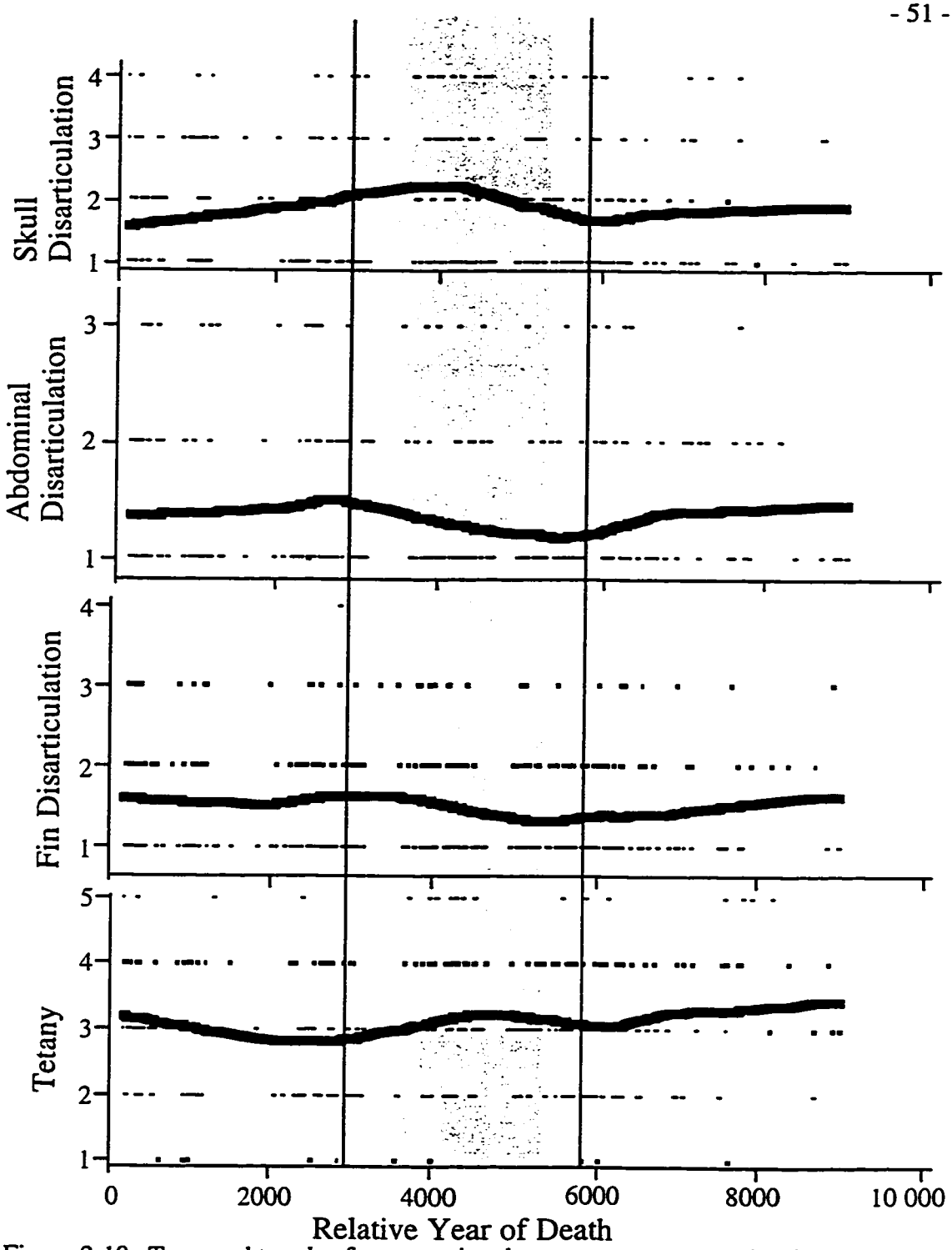


Figure 2-10: Temporal trends of preservational patterns vary on a scale of millennia through the H3 section. All lines shown are LOWESS smoothing functions of the temporal data with a span of 20% of the data. Disarticulation increases towards the top of the page, with increasing number in each cateogory indicating increased disarticulation ("1" indicates no disarticulation). Shaded area is shown in more detail in Figure 2-11. Vertical lines delineate major intervals of change as described in the text.

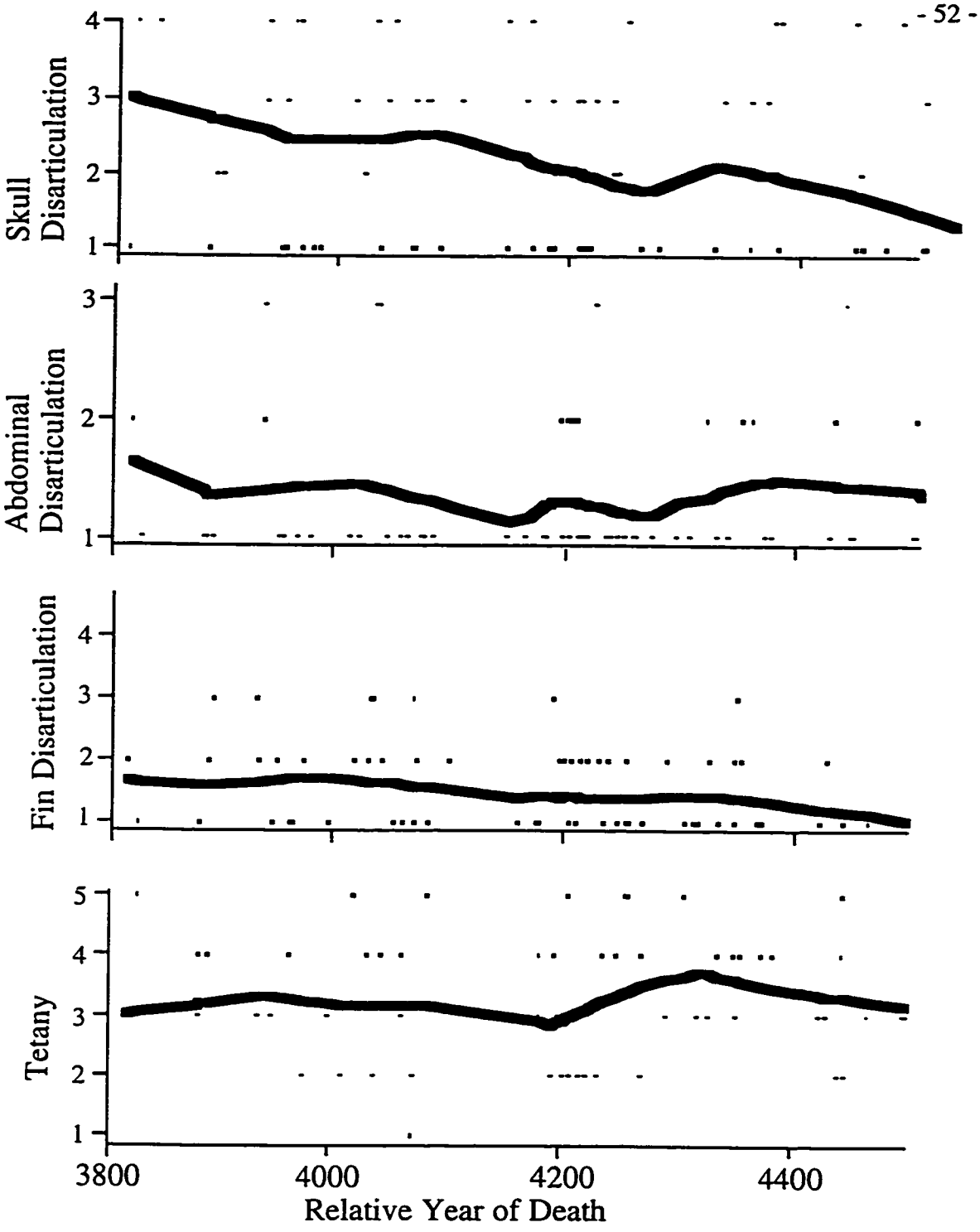


Figure 2-11: Temporal trends of preservational patterns vary on a scale of centuries through the H3 section. All lines shown are LOWESS smoothing functions of the temporal data with a span of 20% of the data. Disarticulation increases towards the top of the page, with increasing number in each cateogory indicating increased disarticulation ("1" indicates no disarticulation).

to assess the degree of disarticulation of the skull and pectoral series. Exactly half of these show no disarticulation at all (other than that caused by compaction), 18% show slight disarticulation, 22% show a large amount of disarticulation, and 10% are completely disarticulated.

There is a high amount of temporal variation in the amount of disarticulation of the skull through the H3 section. Disarticulation increases until about the year 4000, decreases until about the year 6000, and then increases slowly to the end of the section (Fig. 2-10).

Abdomen.--Some 54% (381/698) of the specimens are complete enough to assess the degree of disarticulation of the abdominal area. Of these specimens, 64% show no disarticulation of the abdominal area, 20% show slight disarticulation, and 16% show high disarticulation. After specimens with skull disarticulation are excluded from the analysis of abdominal variation, 72% of specimens show no abdominal disarticulation, 19% show slight disarticulation, and only 8% show high abdominal disarticulation.

Temporal trends of abdominal disarticulation with skull disarticulation excluded are almost identical to temporal trends with skull disarticulation included; temporal trends with skull disarticulation excluded are illustrated in Figure 2-10. Variation in abdominal disarticulation is high across the entire section. There is an increase in disarticulation through the first 3000 years, followed by a steady decrease until about the year 6000, followed by an increase to the end of the section.

Tetany.--Some 51% (356/698) of the specimens are complete enough to assess the amount of tetany. The highest proportion of specimens show moderate amounts of tetany (33% at level 3). Only 6% of the specimens show complete tetany of the fins and mouth, and only 3% of the specimens show no tetany at all.

The proportions of specimens with high tetany decreases until about the year 3000, increases until about the year 5000, decreases until about the year 6000, and then increases through the end of the section (Fig. 2-10).

Tetany-Scavenging correlation.--A contingency table analysis between disarticulation of skull and tetany indicates a highly significant relationship (chi square=49.4, d.f.=16, $p<0.0001$). Comparing the observed and expected values shows that specimens with high tetany have lower skull disarticulation than would be expected under the null hypothesis,

and vice versa. A comparison of temporal trends shows the same relationship: when tetany increases, disarticulation of skull tends to decrease.

Discussion

Results of these taphonomic studies can help to address paleoenvironmental questions on two different levels: yearly cycles in the lake, and longer-term environmental changes in and around the lake basin. I will discuss results pertaining to each of these categories separately.

Seasonal Changes/Yearly Cycle

Results of both size distribution of fish and preservation in the pale or dark portions of varves can contribute information about yearly cycles in the lake represented by the H3 section.

Dark/pale varves.--Nearly every specimen that is preserved (or prepared) so that a thin part of the specimen is visible in cross-section (*e.g.* the end of a fin) is within the dark portion of the varve, indicating that the vast majority of specimens were preserved in the winter. The proportion of specimens in the dark portion of the varves of the H3 section (183/184) is even greater than that reported for the H2 section (89/97, Wilson 1977a). Two possible explanations for the predominance of fishes in the dark layers are that nearly all fish are dying in winter, or that fishes dying in the summer are not being preserved in the same sediments. Information presented below indicates that it is likely a combination of these factors.

Size distribution.--Elder (1985) noted that especially large and small individuals tend to be less predictable in their taphonomic responses to different environmental changes. Size difference is not a major concern in this study because extremes in size are rare in the H3 section (Fig. 2-8).

Although there appears to be some polymodality in the size frequency of the fishes from the H3 section, it is certainly not as distinct as the polymodality of specimens from the H2 section (Wilson 1984, 1993). Wilson attributed the polymodality of the H2 *Amyzon* specimens to a seasonal kill of fish during the fall or winter, as a result of either overturn-induced anoxia (caused by oxygen depletion when hydrogen-sulphide rich waters from the hypolimnion mix with the epilimnion) or starvation in the winter months.

Because of the greater proportion of specimens in the dark portion of the varves in the H3 interval, we might expect an even greater size polymodality than in the H2 interval. This, however, is not the case. The less distinct polymodality of the H3 section might be explained by several factors. The H3 interval spans a much longer interval of time than does the H2 section, so it is possible that the growth rate of fish is gradually changing through time, resulting in a smearing of year-class peaks in the size distribution. Wilson (1984, 1993) found no such temporal trend over the centuries reported in the H2 section, although the number of specimens per century might have been too low to detect such a trend. Within the H3 section, there are too few specimens to be able to detect any trends through the millennia (Fig. 2-8). A second possible explanation for the lack of polymodality is that there was more natural variability in the lake (*e.g.* year-to-year variation in temperature), and therefore size classes are more variable from year to year. This would result in size classes (even within millennia) becoming temporally averaged. Finally, the lack of polymodality in the size of specimens of the H3 section might be explained by the relatively larger size of individuals as compared to the H2 section. Polymodality in the H2 section is most obvious for small specimens, and much less clear for larger individuals (as environmental effects on body size accumulate over time) (Wilson 1984, 1993). Because there are few small individuals from the H3 section, peaks representing the smallest age classes (and therefore the most distinct peaks) are not distinct.

Although these results cannot provide direct information about yearly cycles in lakes, they can supplement information available from other sources. Several yearly cycles are possible for the H2 section (see Methods), but Wilson (1977) and Wilson and Barton (1996) favour a monomictic model. The presence and preservation of varves, however, is a clear indication that the sediments are inaccessible to bioturbation for most of the year (see

Chapter 1). It is unlikely that the bottom sediments in a lake that remains mixed for a significant part of the year (as monomictic lakes are), would be isolated from all bioturbation. I believe, therefore, that the most likely lake model (for the H3 section, at least) is meromictic, in which bottom waters are permanently anoxic, separated from the rest of the water column by a chemical gradient (usually salt) (chemocline). The vast majority of modern varved sediments are formed in meromictic lakes (Anderson *et al.* 1985). The exclusion of oxygen from sediments precludes bioturbation, and limits the activity of scavengers, therefore allowing the preservation of microlaminations. The presence of a chemocline ensures that the delicate consistency of the sediment is not affected during an overturn event. The water column above a chemocline in meromictic lakes (the monimolimnion) can have properties of non-meromicitic lakes. In other words, the monimolimnion can circulate freely as with any other lake. Although I cannot find any modern analogues, a meromictic lake in which the monimolimnion overturns in the fall or winter could explain all the preservational features of the H3 (and H2) section. In such a lake, an overturn event (especially if it includes the top of the mixolimnion [chemically stratified layer]) would result in seasonal kill of specimens by anoxia, therefore accounting for the polymodality of specimens, the preservation of specimens in the dark portions of the varves, and the predominance of specimens preserved with tetany (indicating death in anoxia). This model can also account for the excellent preservation of varves as the bottom is isolated from mixing and bioturbation. I cannot think of any other model that can equally well explain all of the preservational features of specimens from the H3 interval.

This scenario is consistent with several modern lakes in warm temperate climates. The warm-temperate climate that has been proposed for the Eocene localities of British Columbia is likely somewhat warmer and more moist than current conditions in the area (Hopkins *et al.* 1972; Wilson 1977, 1980), despite a higher paleolattitude (Jurdy and Van der Voo 1975). The North American distribution of modern meromictic lakes and lakes in which sediments are preserved in microlaminations is scattered throughout the continent, although there is a concentration around the Canada-United States border (Anderson *et al.* 1985: Fig. 10). There are varved and meromictic lakes as far south as Guatemala and Panama (Anderson *et al.* 1985). In addition, Wetzel (1983: p. 87) points out that "nearly

all of the extremely deep lakes of the equatorial tropics are meromictic". Although the Horsefly locality is clearly not equatorial, this observation does indicate that meromixis can occur in very warm climates. Finally, many geological studies on the Green River Formation have pointed towards a saline environment (*e.g.* Buchheim and Surdam 1981) even though the biota strongly indicates a freshwater environment (*e.g.* Grande 1984, 1994). This disconcordance might be explained by meromixis in the lake, which would give the sediments the appearance of marine deposits, while freshwater fishes (and amphibians) could live in the surface waters. The Green River Formation was likely deposited in somewhat warmer conditions than Horsefly based on a more tropical flora including palm fronds (Grande 1984). Many meromictic lakes, in addition to being chemically stratified, can also be thermally stratified (see, for example, Anderson *et al.* 1985: Fig. 9) as I have suggested for the H3 interval.

There are many specimens from the H3 interval which are associated with framboids pyrite (*e.g.* filling vertebrae). A meromictic lake can account for this as well, because pyrite is formed only under reducing conditions (see, for example, Dean 1991; Wilkin *et al.* 1997). There are many other analyses that could test some of these hypotheses (see, for example, Tracey *et al.* 1996), but these are beyond the scope of this thesis.

Environmental Change

Preservational patterns of fossil fishes can also provide information about longer-term environmental changes in and around the lake in which they are preserved. The extremely high temporal resolution provided by the varved sediments in the H3 interval allow such a reconstruction on a time scale of thousands, and even hundreds, of years. Paleoenvironmental reconstructions on time scales such as these (although not based on taphonomy of fishes) are common for Holocene deposits (*e.g.* Dean 1997; Campbell 1998), but it is rare such a high resolution is possible in sediments dating beyond the Holocene. I will first present relevant results from this study individually, followed by a hypothesis of paleoenvironmental changes in and around the lake based on changes in preservation of fishes. The other relevant results will then be used as a preliminary test for

these hypotheses.

Temporal distribution of specimens.--The unequal distribution of specimens through the H3 section (Fig. 2-7) can be attributed to several factors. Sampling bias is surely an important cause for at least some of the variations in temporal distribution. Some parts of the section were only exposed in deep and fast waters of the Horsefly River, whereas others parts were exposed in shallow slow-moving waters where collection is much easier. The somewhat polymodal distribution of specimens (on a scale of about 1000--2000 years) can likely be attributed to such sampling biases. Layers that could be removed in large slabs from the river were more likely to be sampled, and specimens in the middle of these slabs are less likely to be lost while slabs are being removed from the river. I therefore believe that the polymodality of *Amyzon* through time (Fig. 2-7) is an artifact of sampling methods. This could easily be tested in further studies on the site (see below). Based on my collecting experiences, however, there does appear to be some heterogeneity of specimens through the entire H3 section (gradual changes in biota, not peaks and crashes in populations as might be suggested by Fig. 2-7). The top 3000 years of the section were sampled exclusively for about three days with only about five fish recovered. In contrast, collecting around the year 4000 produces about one fish per collector hour. The different distributions of different species (which cannot be explained by sampling biases) also suggests a true temporal heterogeneity of fossils in the H3 section. Specimens of *Eohiodon* are more common than might be expected in certain intervals, and specimens of *Priscacara* are only found in two parts of the H3 section: around the year 3000 and at the end of the section (Fig. 2-7). Temporal distribution of specimens and of species has many important implications for the paleoecology of the site (Wilson 1980, 1988b) (see below).

Gaps between specimens in this study are not large in relation to the entire section (up to 200 years with no fishes) and should therefore not affect study of temporal trends over millennia. There are few specimens near the top of the section (above the year 8000) compared to the rest of the section, therefore any trends in this part of the section are more likely to have been caused by chance.

Size distribution per millennium.--There are differences in standard lengths of specimens of *Amyzon* through the H3 section (Fig. 2-9). Several millennia are

characterized by only large or small individuals. Larger fish might be expected to be more common further away from shore, in which case changes in the average size of fish is likely related to changes in the relative depth (or distance-from-shore, see Wilson 1980, 1988b) of the site in the lake deposit (see below).

Preservational patterns.--There are clearly two distinct patterns of preservation of specimens of *Amyzon* from the H3 section, with disarticulation centered around either the anterior end (skull, pectoral series) (Fig. 2-6) or around the abdominal cavity (Fig. 2-5). The pattern of preservation of a particular individual is a product of the taphonomic process to which it was subjected, which, in turn, is a product of the environment in which the fish died (Fig. 2-2). For each diagnostic pattern of disarticulation, we can identify the taphonomic process that was the most likely cause, and the environmental conditions that produced these processes. Each of the three body regions that I examined in this study (abdomen, skull and fins) have distinct causes of disarticulation that can provide specific information about different aspects of the environment of the fish. Each of these will be addressed below.

Abdomen.--The most obvious cause of abdominal disarticulation is the escape of decay gas from a carcass on the bottom of a lake. This release of decay gas is most common at or near threshold temperatures (Fig. 2-2). Below these temperatures, buildup and release of decay gas is not sufficient to cause disarticulation; and above these temperatures, decay gas causes the specimens to float to the surface. Abdominal disarticulation can also be caused by scavengers, but the results presented here suggest that (at least in the H3 section) partial flotation is the most common cause. When specimens showing any sign of disarticulation of the skull (presumably caused by scavengers, see below) are removed from the analysis, there is little change in the total numbers and proportions of specimens in each of the categories of abdominal disarticulation. By excluding specimens with skull disarticulation, I am attempting to ensure that no specimens that were scavenged are included in the abdominal disarticulation category (which I will use to infer partial flotation). This assumes that scavengers do not specifically target only the abdominal cavity. Based on the patterns of preservation described here, however, this seems like a safe assumption. Most of the disarticulation that was counted as minor abdominal disarticulation involved only

minor displacement of vertebrae or breaks in the vertebral column (Fig. 2-5). Such patterns of disarticulation were rarely accompanied by any other damage (*e.g.* scattering of scales, etc.) that would be expected if they were caused by macroscavengers. "Gas explosion" (highly disarticulated abdominal cavity) is a well-documented product of the release of decay gas under high pressure as at the bottom of lakes (Schäfer 1962; Elder 1985). Such "gas explosion" (especially if it is particularly violent) might also result in disarticulation of skull elements; therefore, the number of such specimens is likely underrepresented when I exclude specimens also displaying disarticulation of the skull. Environmental implications of scavenging and partial flotation (at least at the bottom of deep lakes) are similar (see below); therefore, even if scavengers did cause the occasional abdominal disarticulation in the absence of skull disarticulation, paleoenvironmental reconstruction should not be adversely affected.

Presence of abdominal disarticulation has several environmental implications. Inasmuch as it can be attributed to partial flotation, its presence indicates that temperatures were warmer on the bottom than during its absence. Above the threshold temperature, specimens float to the surface; therefore, placing an upper limit on temperatures represented by partially floated specimens (Fig. 2-2). Although it has not been shown in actualistic studies, decay at the upper end of threshold temperatures should result in more gas accumulation (and therefore more violent expulsion when integument ruptures) than at the lower end of threshold temperatures. The degree of abdominal disarticulation, therefore, is likely a reflection of increased temperature within the range of threshold temperatures.

Wilson (1977) noted little "gas rupture" of specimens from the H2 section. This "gas rupture", however, probably corresponds only to the highest level of abdominal disarticulation used here. A brief qualitative analysis of some specimens from the H2 section revealed several specimens with minor abdominal displacement that can be likely be attributed to partial flotation.

Skull and pectoral series.--Macroscavengers, which tend to cause a multi-directional scatter of elements on the bedding plane, are the most likely cause of skull disarticulation (Fig. 2-6). Disarticulation of the skull and pectoral series was occasionally accompanied by abdominal disarticulation, but usually this involved only the most anterior regions.

More often than not, it was just elements of the skull (and sometimes fins, see below) that were disarticulated. The fact that the skull and pectoral series were often the only part of the body to be scavenged suggests that scavengers were preferentially feeding on the anterior parts of carcasses. This seems almost counter-intuitive; scavengers should feed on the meatiest parts of carcasses. These findings, however, are consistent with studies by Elder (1985), who found that many of the skull, fin and pectoral elements of fish carcasses were scavenged before the mid-body musculature. This is also consistent with the pattern of disarticulation that Wilson and Barton (1996) reported for the H2 section, with the skull being almost completely disarticulated before there was even minor disarticulation of the rest of the body (including fins).

The identity of the scavenging organism or organisms from the H3 interval is not immediately obvious. Not a single fossil of a benthic invertebrate has been found from the entire H3 section. There are some lines on the sediment that might suggest invertebrate traces, but given the excellent preservation of flying insects from the H3 sediments (see references in Chapter 1), body fossils of benthic invetebrates living in the same interval should also be preserved. The excellent preservation of varves also strongly suggests that there was no life in or on the sediment. Aquatic invertebrates, because they tend to be less mobile than fish, are unlikely to venture quickly into the hypolimnion to feed. Fish, therefore, seem the most likely scavengers of specimens in the H3 interval. *Amyzon* was likely a planktivore; some specimens appear to be preserved with the remains of diatoms in their stomach areas. None of the other fish that have been reported from the Horsefly deposits (*Eohiodon*, *Priscacara*, and *Amia*) are known to have been scavengers, but little is known about the feeding habits of each of these species. In the H3 section, *Eohiodon* and *Priscacara* are only known from a handful of (complete and articulated) specimens each, and *Amia* is known only from scales. More specimens might reveal some stomach contents and help to identify the most likely scavenger from the site.

The presence of scavenging in this site is also a little unusual in that it might be expected to disrupt the preservation of varves. There is no evidence of decreased lamination of the sediment around scavenged specimens. The presence of scavenging, therefore, suggests that the sediment was slightly more solid than a gel.

Barton and Wilson (1997) previously compared trends in the proportion of specimens that shows any sign of skull disarticulation per millennium with the intensity of disarticulation (smoothing trend of only those specimens that do show any sign of disarticulation) of specimens from the H3 interval (Fig. 2-12). These two independent indications of scavenging show almost identical temporal patterns, supporting the trends presented here. In other words, in intervals in which the skull is more frequently disarticulated, the skull is also more heavily disarticulated. Although it was not reported, preservation of the abdominal cavity shows a similar relationship.

Increased disarticulation of the skull, which most likely indicates increased scavenging, can be attributed to several possible causes. In past studies, lack of scavenging of carcasses has been used as an indication of lack of oxygen. Lack of scavenging, however, is only an indirect effect of low oxygen, and could be caused by many other factors (such as absence of scavengers in the lake). However, scavenging can clearly be limited by oxygen levels. In high oxygen, scavenging of carcasses is not limited to the number of individuals who venture into the hypolimnion, nor is it limited by the amount of time these individuals can spend in low oxygen. In lakes with a normally anoxic bottom (as in the H3 interval), scavengers reach carcasses either during periods of mixing following overturn, or by swimming into the anoxic hypolimnion. Increased scavenging could therefore result from either an increased length of time that the lake remains mixed following overturn, or from a thinner hypolimnion that is easier for scavengers to penetrate. Tetany, which is a more direct indication of oxygen levels, will be discussed below.

Fins.--Disarticulation of fins can be attributed to a number of possible causes. For example, fins can easily be disarticulated during heavy scavenging, especially if the carcass is largely decomposed. The soft tissue supporting the lepidotrichia can break down relatively rapidly (depending on temperature), and therefore disturbance to carcasses can result in disarticulation of these elements as well. Because disarticulation of fins in the absence of other types of disarticulation is related to the amount of time that a specimen lies unburied on the sediment, it is informative to isolate specimens that show only disarticulation of fins. There were only 42 specimens for which the fins were the only part of the body disarticulated: 35 specimens with slight fin disarticulation, and seven with

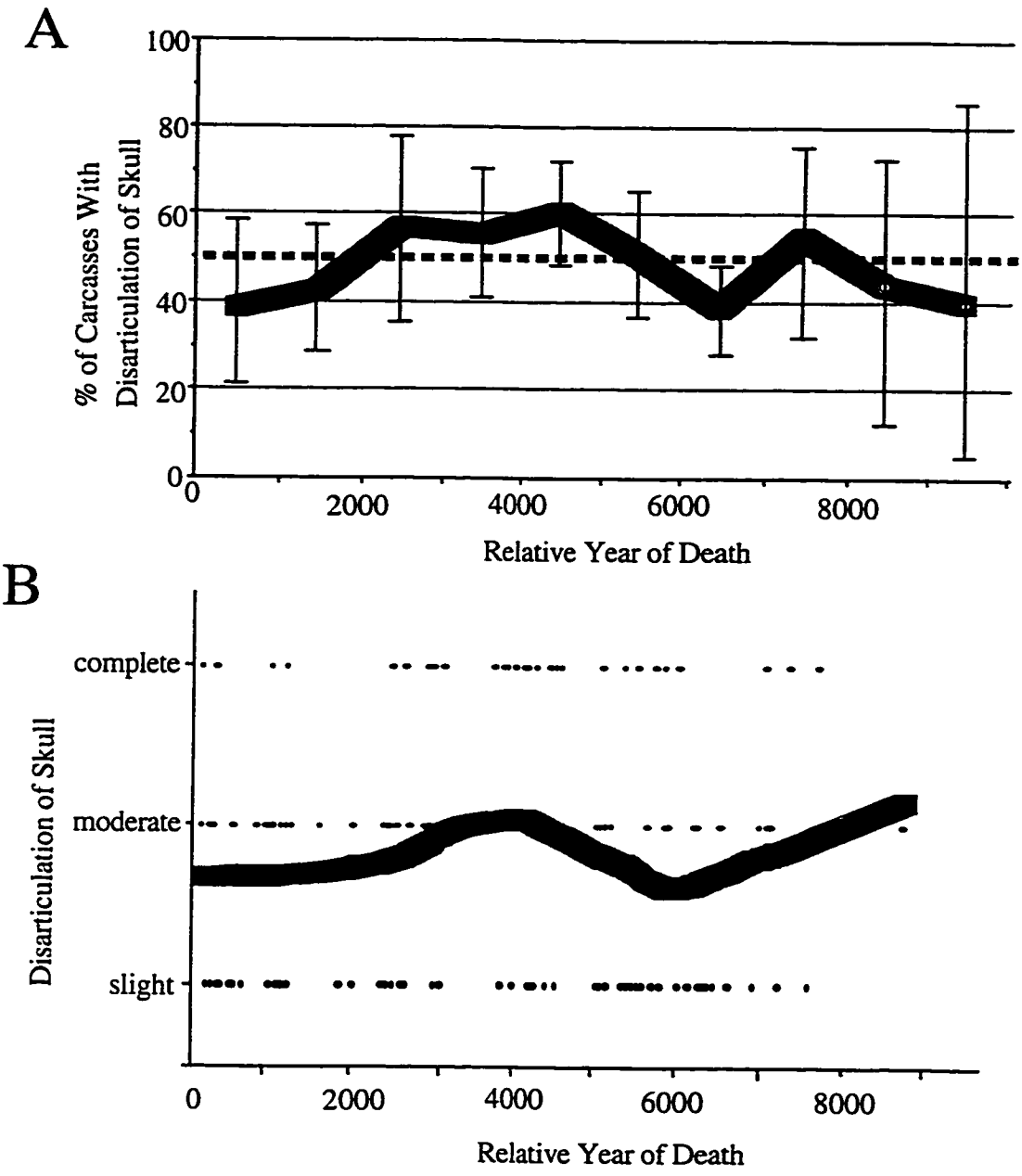


Figure 2-12: Comparison of temporal trends in percentage of specimens with disarticulation of skull and degree of disarticulation of skull. A) Percentage of any carcasses showing any sign of skull disarticulation per millennium. Open circles indicate millennia with fewer than 20 specimens. B) LOWESS smoothing function of degree of disarticulation of skull over the H3 interval. Specimens with no skull disarticulation have been excluded from this graph. The similarity of these two figures indicates that when specimens are more likely to show skull disarticulation, it is also more likely to be more severe; in other words, there is no threshold above which skull disarticulation can occur, it is not an all-or-nothing occurrence.

severe fin disarticulation. Temporal trends of these specimens (not shown) show slight increases in disarticulation of fins at either ends of the section, possibly suggesting that specimens remained unburied for longer periods of time at the start and end of the H3 interval. Because of the low sample size, the lack of a clear trend, and the absence of any vital information that disarticulation of fins can contribute to paleoenvironmental reconstruction, the trends will not be included in paleoenvironmental reconstructions presented below.

Tetany.--Tetany of fossil fish is a clear indication of death in low oxygen (Elder 1985). Elder (1985) does not mention any variation in degree of tetany; however, in the H3 interval, there is a clear spectrum of tetany ranging from none to severe. Increased tetany likely indicates lower levels of oxygen, although this relationship has not been proven in actualistic studies.

Both tetany (Smith and Elder 1985; Ferber and Wells 1995; Wilson and Barton 1996) and lack of scavenging of carcasses (McGrew 1975; Wilson and Barton 1996) have been used to indicate low levels of oxygen in a fossil lake. Both of these patterns, however, can provide more precise information. Tetany is a direct indication of the conditions at the moment and place of death (and therefore might not indicate usual conditions in the lake). For example, if fish are killed in an overturn event in which oxygen is depleted from water (as Wilson [1977] has proposed for the H2 section), fish carcasses will show tetany, even if oxygen levels are quickly restored in the lake. Because scavengers are often limited by oxygen, trends in scavenging can provide (indirect) information about overall (longer-term) conditions at the bottom of lakes.

The high correlation between anoxia and lack of scavenging in this study suggests that oxygen is a limiting factor in the lake. Fishes are likely killed in conditions of low oxygen (in an overturn, for example), and are preserved in (usually) anoxic or hypoxic waters at the bottom of the lake. Scavengers could occasionally gain access to carcasses, most likely by swimming into hypoxic waters. Periods when tetany decreases and amount of scavenging increases represent periods in which the bottom waters were more oxygenated.

Other taphonomic processes.--Several additional taphonomic observations should be mentioned here.

There are two layers in the H3 section that have large accumulations of disarticulated bones (bone beds). There are few articulated elements so the causes of disarticulation and sources of these bone beds cannot be determined. I did not prepare these beds (they are covered with a few millimeters of sediment), but each bed seems to represent more than one individual. Future study could involve an analysis of the causes and significance of these beds.

Nine isolated skull or pectoral bones (with no other bones in the near vicinity) have been recovered from the H3 interval, only a fraction of the number of complete or nearly complete specimens. One of the most likely sources of these isolated bones is floating carcasses. There are also two specimens with no skull and pectoral bones (or fins) that can be attributed to floating carcasses that lost all their decay gas and subsequently sank to the bottom. At most, therefore, there are 11 specimens (of a possible 698) whose patterns of preservation could have been caused by flotation. Floating carcasses are pushed by surface winds towards shore (Neumann 1959). Because the H3 deposit represents the deep part of a stratified lake, it is also likely far from shore. The paucity of specimens attributed to floating specimens, therefore, is probably due to the relative position of the deposit in the middle of a lake. This also helps to explains the lack of specimens preserved in the pale portions of the varves: during summer months, specimens are much more likely to float, and therefore are less likely to be preserved in this interval. Unfortunately none of the eleven specimens that might represent floated specimens can be positioned in the pale or dark portion of the varve.

Time scale of variability.--Patterns and degree of disarticulation vary quite dramatically through the roughly 10 000 years represented by the H3 section (Fig. 2-10). Because there are many fewer data points in the 715-year section (Fig. 2-11), trends are not as reliable as those across the entire section. In fact, trends of the shorter interval would have shown up in the longer interval had I chosen a shorter span for the smoothing function. The short interval with the most specimens also happens to be the interval of greatest change in preservation of all features; therefore, trends in this interval might be exaggerated compared to other intervals of similar lengths.

There is a high amount of temporal variation in the 715-year section that is not visible at

the resolution that was used for the complete interval. Wilson and Barton (1996) also found variation in preservational patterns on a scale of centuries in the H2 section. The number of specimens in the short interval of this study is similar to the number of specimens examined by Wilson and Barton (1996), and the magnitude of the trends appears to be similar. Different temporal scales of variation are known in other sedimentary features (*e.g.* Dean 1997), but have not been demonstrated for patterns of preservation of fossils. The considerable temporal variation in preservational patterns and degree of disarticulation on two different time scales over this interval suggest that sediments with lower temporal resolution will almost certainly be subject to temporal averaging of preservational patterns.

Variation of preservational patterns through time.--Preservational patterns and their most likely taphonomic causes can provide information about particular aspects of the environment. A combined analysis of all these changes can indicate major overall environmental changes in or around the lake. Because of the methods and the conservative approach used in this study, the paleoenvironmental reconstructions presented below are quite robust. Changes in preservation of the two main body regions (skull and abdomen) can be attributed to different taphonomic processes (scavenging and partial flotation). Changes in these taphonomic processes, although they each indicate specific environmental changes, are both caused by similar general environmental change (at least in the H3 section). Increased partial flotation is a direct result of increased temperatures at the bottom of the lake. Increased benthic temperatures, however, are almost always associated with increased accessibility of specimens to scavengers; if bottom waters are warmer they are more likely to be oxygenated (see Wetzel 1983). Some overlap between patterns of preservation attributed to scavenging or partial flotation, therefore, will not greatly affect paleoenvironmental reconstruction.

The first major interval of change in preservational features occurs from the bottom of the section to about the year 3000 (Fig. 2-10). During this interval, disarticulation of the abdomen, and especially skull, increases rather dramatically, and tetany decreases. Increased skull disarticulation suggests that carcasses are more accessible to scavengers. Increased abdominal disarticulation suggests increased partial flotation of specimens on the

bottom and therefore increased benthic temperatures. Decreased tetany suggests increasing levels of oxygen.

The simplest explanations for these coincident changes involve relative changes in the lake affecting the depth of the H3 deposit (or at least the relative position of the thermocline/chemocline): a shallowing of the entire lake, a change in the morphology of the lake such that the H3 section is more shallow (a relative shallowing of the H3 section), or a deeper thermocline (or chemocline) (Fig. 2-13). Each of these changes will result in the deposit being closer to the thermocline (or chemocline), which can account for increased scavenging (less anoxic distance for scavengers to cross), decreased tetany (less anoxic waters to mix if whole lake is shallower, or less anoxic water between the chemocline and the bottom in which specimens can die) and increased partial flotation (increased benthic temperatures at shallower depths). For the rest of this section, because each of these changes is associated with a shallowing of the deposit (either absolute, relative to the rest of the lake, or relative to the thermocline/chemocline), they will all be referred to as a shallowing event (and the reverse a deepening trend).

The interval of greatest change in preservational patterns in the entire section occurs between the years 3000 and 6000. Disarticulation of the abdomen decreases through this interval. Disarticulation of the skull increases slightly for 1000 years, and then drops dramatically to the year 6000. Tetany increases slightly to the year 5000. Again, if changes in taphonomic processes can be inferred from these features, through this interval there is a decrease in partial flotation, a decrease in scavenging (with a slight increase at the start of the section), and an increase in death in anoxic water. The simplest explanation for all of these coincident changes is a deepening trend. All else being equal, this would result in a thicker anoxic zone, decreasing the chance of scavengers feeding on the bottom. A deeper position of the deposit would also likely be associated with lower benthic temperatures. Increased death in anoxic waters could be due to either a more toxic overturn, or to an increase of fishes dying in the (relatively larger) hypolimnion (or mixolimnion).

The third and final major interval of change in preservational features occurs from the year 6000 to the end of the section. Disarticulation of skull and abdomen both increase to

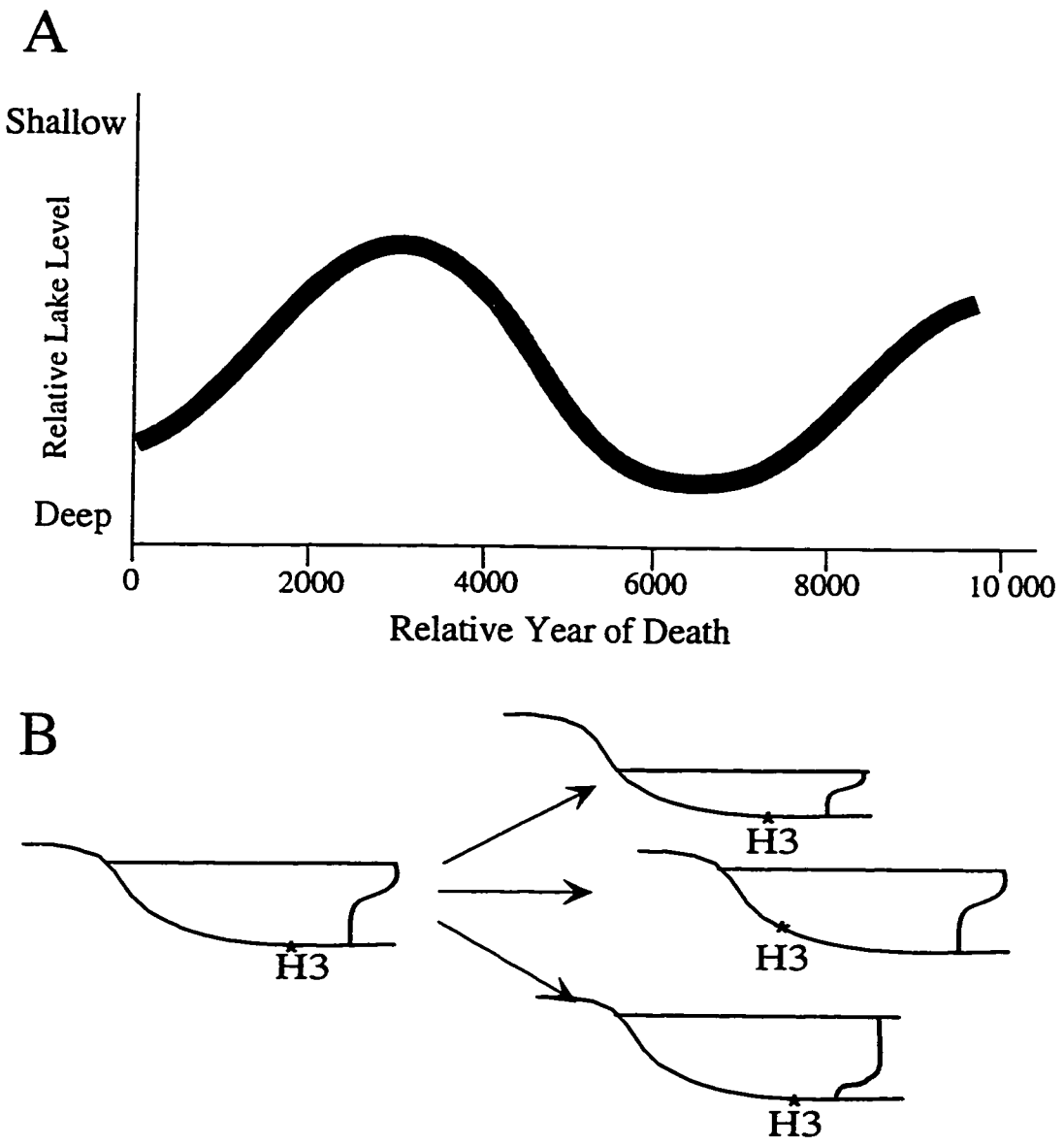


Figure 2-13: Relative changes in lake levels as reconstructed from changes in preservational patterns of fossil fish. A: Reconstructed relative lake level changes through the 10 000 year section represented by the H3 interval. B: Three different ways that the H3 section can become shallower. The position of the H3 deposit is indicated by the asterix, and the thermocline (and/or chemocline) by the gray line on the right. The entire lake can shallow (top), the lake can shift so that the position of the H3 section is more shallow (middle), or the thermocline can drop (bottom). All of these situations have the same results on preservation of fishes.

the end of the section, suggesting increased scavenging and partial flotation. These combined trends suggest a shallowing trend, resulting in specimens being more accessible to scavengers, and bottom waters being warmer. Tetany is also increasing during this interval, suggesting that more fishes are dying in anoxic waters, which seems to contradict the other trends for this section. Throughout the entire section, there is a gradual increase in the amount of tetany (with some fluctuations; Fig. 2-10) which might be explained by a gradual increase in the amounts of dissolved salts (or other chemicals) accumulating at the bottom of the lake, creating a thicker chemocline and therefore more anoxic waters. More data would be required to support this hypothesis, but it seems likely that if this were a meromictic lake, such an accumulation would occur, especially if the lake were draining from above the chemocline.

Ten thousand years is a significant period of time in the history of a lake, and will likely be associated with some significant changes in the shape and depth of the lake. As mentioned before, the simplest explanations to account for all these trends involve changes in the lake that affect the relative depth of the H3 section (Fig. 2-13). Other explanations to account for all of these trends would involve combinations of simultaneous changes in different environmental variables.

We can now compare these reconstructed trends to other results (distribution of specimens and size distribution of fishes) that relate to environmental changes in and around the lake.

The end of the H3 interval is associated with a dramatic change in fauna. From about the year 6000, *Priscacara* and *Eohiodon* become much more common, while proportions of *Amyzon* decrease. According to Wilson's (1980) depth/distance-to-shore model (based on Eocene lakes), deposits representing deeper parts of lakes tend to have lower fish diversity (and, for Eocene lakes of British Columbia, are usually dominated by *Amyzon*) than intermediate or near-shore assemblages. Wilson's model also indicates that flying insects and plants should be much more common in shallower deposits than in deeper ones. Although no quantitative data were collected in this study, insects seemed to be more common near the end of the H3 section (in fact, the end of the present H3 section was once informally called "bug varves" before a detailed analysis of the H3 varved interval). Other

features such as sedimentology can also provide information about paleoenvironmental changes in the lake. Grain size of the sediments increases near the end of the section, and microlaminations become less and less distinct as the varved interval grades into a laminated sandstone. All of these results strongly support the shallowing trend as reconstructed based on preservational patterns. They also seem to rule out the possibility that the thermocline in the lake is dropping, because such a change would not be associated with either changes in sedimentation or changes in the fauna of the deposits. Changes in size of fishes might help to distinguish between absolute shallowing of the lake and a relative shallowing of only the H3 interval, but there are too few individuals for which standard length data can be obtained in this interval to be able to see any such changes.

Because varves are formed only in deep waters, the start and end of varved intervals will be associated with predictable changes in depth of the lake. Just as the end of the varved interval is associated with a shallowing trend, the onset of varve formation should be associated with a deepening trend. Unfortunately, the bottom of the H3 exposure is limited by exposure, so this cannot be tested.

The lowest interval of the varved sediments (0--3000) that is currently exposed was reconstructed as a shallowing trend. This interval also coincides with changes in other taphonomic features (although not as clearly as the end of the section). There is a concentration of specimens of *Eohiodon* and *Priscacara* around the year 3000, when the lake was reconstructed as being shallowest. In fact, specimens of *Priscacara* are only found in the two intervals that were reconstructed as being shallowest (around 3000, and after 8000). There also seemed to be more insect and plant specimens from the layers around the year 3000, but this should be verified with more data. The millennium with the smallest specimens of *Amyzon* in the entire section is between the years 2000 and 3000. Although it is possible that fish were not growing as large in this interval, it is more likely that the larger fish are simply not represented. This suggests that it is only the relative position of the H3 deposit that is changing (closer to shore, and therefore, shallower) and that large fishes are not represented in the deposit because (at least during the winter) they are out in the deeper waters. Changes in the lithology during this interval also suggest a shallowing trend. Just above the year 3500 (which is just above the shallowest point in the

reconstruction), the sediment is less microlaminated, and grain size is quite large (Fig. 2-3).

Finally, the interval from the years 3000 to 6000 was interpreted as a deepening trend. This interval is characterized by an increasing size of specimens of *Amyzon*, and a lower diversity of fishes. Information about other fossils from this interval (insects and plants) is not available. Again, because of the increasing size of *Amyzon*, it is likely that the changes are such that the H3 section is in a deeper (or at least further from shore) part of the lake.

There appears to be some cyclicity to each of the preservational patterns (and therefore environmental change) in this interval, with a period of approximately 8000 years. This is only represented by one cycle in the currently exposed H3 section, a further exposure of the bottom of the interval could test this hypothesis. Cyclicity has been reported for much longer periods in other lakes (with lower temporal resolution) (Olsen 1986; McCune 1987) and has been attributed to variations in the earth's orbit (Milankovitch cycles). Cyclicity over longer periods might be shown by the entire Horsefly section (see Chapter 1), but a more detailed stratigraphic study would be needed. Such environmental variability over time has implications for studies of current climate change: it is important to know the scale and magnitude of past environmental changes before we can decide whether current climate changes are anything more than natural cycles.

The reconstructions of lake level changes based on preservation of fishes presented here are quite speculative and are based on a number of assumptions, but they are strongly supported by the other results presented here. These reconstructions, however, remain hypotheses, and should be further tested with other paleoenvironmental studies. A more detailed study of the deposits of the H3 exposure would provide a direct indication of changes in material being deposited in the lake through time. In some deposits for which sedimentology is much better understood (such as the Green River Formation), general preservational patterns of fishes over long stratigraphic intervals have been associated with particular lithologies, and changes in these factors indicate broad environmental changes (Wells *et al.* 1993; Ferber and Wells 1995). The present study is an extension of those concepts, but on a much finer scale, with minor changes in preservation likely accompanied by minor changes in sediment (grain size, etc) which indicate subtle changes in or around

the lake. A detailed study of changes in diatoms through time could also provide further paleoenvironmental data. Diatoms have proven to be powerful indicators of environmental change in modern lake systems (*e.g.* Smol *et al.* 1991; Dixit *et al.* 1992; Hui 1996; Pan *et al.* 1996; Vyverman *et al.* 1996); they could certainly provide some indication of directions of environmental change in the H3 section. Even if the diatoms are too damaged to be able to identify precisely (M. V. H. Wilson personal communication 1996), relative changes in abundances of certain groups could indicate (at least) relative timing of environmental changes in the lake. Increased exposure of the site (both laterally and vertically) could help to identify the size of the lake. An increased lateral exposure might allow testing of some of these hypotheses for geographic continuity, while an increased vertical exposure would allow access to the bottom of the varved interval represented by H3, which should represent a deepening trend (just as the end of the varved section indicates a shallowing trend). Finally, even though I compared distribution of different fossil groups through time, these observations were merely qualitative. A quantitative analysis of different fossils groups (including insects and plants) through time would be extremely interesting for such paleoenvironmental reconstructions.

Conclusions

The study of taphonomy has progressed much beyond a basic comparison of articulated and disarticulated specimens. Increasing numbers of actualistic studies have created a better understanding of processes associated with death and decay under different environmental conditions in different taxa. A knowledge of these processes has allowed taphonomists to look for causes of disarticulation in the fossil record, and to make hypotheses about what these causes of disarticulation indicate about paleoenvironmental changes. Some specific conclusion from this study:

1) Different taphonomic features vary through time, and on different time scales. In the Horsefly section, not only is there variation on the scale of centuries (Wilson and

Barton 1996 and this study), but there is also variation on the scale of millennia.

2) Preservational features can help to reconstruct yearly cycles in lakes. Distribution of specimens in the dark portions of varves and the size frequency distribution of fishes from the H3 deposits suggests that surface waters were likely thermally stratified and monomictic, and fishes were killed in winter. The preservation of varves suggests that the bottom waters in the lake were isolated from bioturbation and perhaps even mixing, suggesting that the lake was also meromictic.

3) Preservational patterns can also help to reconstruct environmental changes in and around the lake. Coincident changes in preservational patterns of different body regions (indicating different taphonomic processes) and other features (such as standard length of individuals), suggest changes in the relative depth of the H3 deposit through time.

Literature Cited

Abel, O. 1912. Grundzüge der Palaeobiologie der Wirbeltiere. E Schweizerbartsche Verlagsbuchnandlung Nagele, Stuttgart.

Anderson, R. Y., and W. E. Dean. 1988. Lacustrine varve formation through time. Palaeogeography, Palaeoclimatology, Palaeoecology 62:215-235.

Anderson, R. Y., W. E. Dean, J. P. Bradbury, and D. Love. 1985. Meromictic lakes and varved lake sediments in North America. U.S. Geological Survey Bulletin 1607:1-19.

Barton, D. G., and M. V. H. Wilson. 1997. Variation in frequency and intensity of scavenging of fish carcasses over a 10 000 year interval. Journal of Vertebrate Paleontology 17(supplement to Number 3):31A.

Behrensmeyer, A. K., and S. K. Kidwell. 1985. Taphonomy's contributions to paleobiology. Paleobiology 11:105-119.

Bell, M. A., M. S. Sadagursky, and J. V. Baumgartner. 1987. Utility of lacustrine deposits for the study of variation within fossil samples. Palaios 2:455-466.

Blob, R. W. 1997. Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates. Palaios 12:151-164.

Brett, C. E., and G. C. Baird. 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. Palaios 1:207-227.

Buchheim, H. P. and R. C. Surdam. 1981. Paleoenvironments and fossil fishes of the Laney Member, Green River Formation, Wyoming. Pp. 415-452 *in* J. Gray, A. J.

Boucot and W. B. N. Berry, eds. Communities of the past. Hutchinson Ross Publishing Co., Stroudsburg, Pennsylvania.

Burrow, C. J. 1996. Taphonomy of acanthodians from the Devonian Bunga Beds (late Givetian/early Frasnian) of New South Wales. Historical Biology 11:213-228.

Campbell, C. 1998. Late Holocene lake sedimentology and climate change in southern Alberta, Canada. Quaternary Research 49:96-101.

Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. Journal of the American Statistical Association 74:829-836.

Davis, P. G., and D. E. G. Briggs. 1998. The impact of decay and disarticulation on the preservation of fossil birds. Palaios 13:3-13.

Dean, W. E. 1991. Carbonate minerals and organic matter in sediments of modern north temperate hard-water lakes. Pp. 213-231 *in* G. Ethridge and R. M. Flores, eds. Recent and ancient nonmarine depositional environments: models for exploration. Society of Economic Paleontologists and Mineralogists Special Publication 31.

——— 1997. Rates, timing and cyclicity of Holocene eolian activity in north-central United States: Evidence from varved lake sediments. Geology 25:331-334.

Dixit, S. S., J. P. Smol, J. C. Kingston, and D. F. Charles. 1992. Diatoms: Powerful indicators of environmental change. Environmental Science and Technology 26:23-33.

Efremov, J. A. 1940. Taphonomy: new branch of paleontology. Pan-American Geologist 74:81-93.

——— 1950. Taphonomy and the geological record. Trudy Paleontologicheskogo Instituta 24:1-177.

Elder, R. L. 1985. Principles of aquatic taphonomy with examples from the fossil record. Ph.D. Thesis, University of Michigan.

Elder, R. L., and G. R. Smith. 1984. Fish taphonomy and paleoecology. Geobios Mémoire Spéciale 8:287-291.

——— 1988. Fish taphonomy and environmental inference in paleolimnology. Palaeogeography, Palaeoclimatology, Palaeoecology 62:577-592.

Fagerstrom, J. A. 1964. Fossil communities in paleoecology: their recognition and significance. Geological Society of America Bulletin 75:1197-1216.

Ferber, C. T., and N. A. Wells. 1995. Paleolimnology and taphonomy of some fish deposits in "Fossil" and "Uinta" Lakes of the Eocene Green River Formation, Utah and Wyoming. Palaeogeography, Palaeoclimatology, Palaeoecology 117:185-210.

Frickhinger, K. A. 1985. Fossil atlas fishes. (R.P.S. Jefferies, translation) Mergus, Melle, Germany.

Gaudant, J. 1983. L'ichthyofaune des milieux confinés: intérêt pour l'étude paléolimnologique. Sciences Géologiques, Bulletin 36:231-238.

Grande, L. 1984. Paleontology of the Green River Formation with a review of the fish fauna (second edition). Geological Survey of Wyoming Bulletin 63:1-333.

——— 1994. Studies of paleoenvironments and historical biogeography in the Fossil Butte and Laney members of the Green River Formation. University of Wyoming Contributions to Geology 30:15-32.

Hills, L. V., and H. Baadsgaard. 1967. Potassium-Argon dating of some Lower Tertiary strata in British Columbia. Bulletin of Canadian Petroleum Geology 15:138-149.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandanavian Journal of Statistics 6:65-70.

Hopkins, W. S., N. W. Rutter, and G. E. Rouse. Geology, paleoecology and palynology of some Oligocene rocks in the Rocky Mountain Trench of British Columbia. Canadian Journal of Earth Sciences 21:1132-1144.

Hui, J. 1996. Diatoms from the surface sediments of the Skagerrak and the Kattegat and their relationship to the spatial changes of environmental variables. Journal of Biogeography 23:129-137.

Johnson, R. G. 1960. Models and methods for analysis of the mode of formation of fossil assemblages. Geological Society of America Bulletin 71:1075-1086.

Jurdy, D. M. and R. Van Der Voo. 1975. True polar wanderer since the Early Cretaceous. Science 188:1193-1196.

Kemp, R. A., and D. M. Unwin. 1997. The skeletal taphonomy of *Archaeopteryx*: a quantitative approach. Lethaia 30:229-238.

Mathews, W. H. 1964. Potassium-argon age determination of Cenozoic volcanic rocks from British Columbia. University of British Columbia Department of Geology Report 2.

McGrew, P. O. 1975. Taphonomy of Eocene fish from Fossil Basin, Wyoming. Fieldiana Geology 33:257-270.

Mörs, T. 1993. Taphonomische Beobachtungen an den Clupeiden (Teleostei, Pisces) aus den Plattenkalken von Schernfeld (Unteres Untertithon, Südliche Frankenalb, Deutschland). Neues Jahrbuch für Geologie und Palaeontologie (Abhandlugen) 188:345-362.

Neumann, J. 1959. Maximum depth and average depth of lakes. Journal of the Fisheries Resource Board of Canada 16:923-927.

Olsen, P. E. 1986. A 40-million-year lake record of early Mesozoic orbital climate forcing. Science 234:842-848.

Pan, Y., R. J. Stevenson, B. H. Hill, A. T. Herlihy, and G. B. Collins. 1996. Using diatoms as indicators of ecological conditions in lotic systems: A regional assessment. Journal of the North American Benthological Society 15:481-495.

Rahel, F. J., and J. W. Nutzman. 1994. Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. Ecology 75:1246-1253.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Richter, R. 1928. Aktuopaläeontologie und Paläeobiologie, eine Abgrenzung. Senckenbergiana 10:285-292.

Rouse, G. E., and W. H. Mathews. 1961. Radioactive dating of Tertiary plant-bearing deposits. Science 133:1079-1080.

Rouse, G. E., W. S. Hopkins, and K. M. Piel. 1971. Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. Geological Society of America Special Paper 127:213-246.

Schäfer, W. 1962. Ecology and Paleoecology of Marine Environments. (I. Oertel, translation, 1972). University of Chicago Press, Chicago.

Seilacher, A., and A. Labarbera. 1995. Ammonites as Cartesian Divers. Palaios 10:493-506.

Smith, G. R., and R. L. Elder. 1985. Environmental interpretation of burial and preservation of Clarkia fishes. Pp. 85-93 *in* C. J. Smiley, ed. Late Cenozoic history of the Pacific Northwest. Pacific Division, American Association for the Advancement of Science and California Academy of Sciences, San Fransisco.

Smol, J. P., I. R. Walker, and P. R. Leavitt. 1991. Paleolimnology and hindcasting climatic trends. Verhandlugen der Internationalen Vereingung für Theortetische und Angewadte Limnologie 24:1242-1246.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry (second edition). W.H. Freeman and Co., San Fransisco.

Symons, D. T. A., and M. R. Wellings. 1989. Paleomagnetism of the Eocene Kamloops Group and the cratonization of Terraine I of the Canadian Cordillera. Canadian Journal of Earth Sciences 26:821-828.

Tracey, B., N. Lee and V. Card. 1996. Sediment indicators of meromixis: comparison of laminations, diatoms, and sediment chemistry in Brownie Lake, Minneapolis, USA. Journal of Paleolimnology 15:129-132.

Valentine, J. W. 1973. Evolutionary paleoecology of the marine biosphere. Prentice Hall Inc., Englewood Cliffs, New Jersey.

Velleman, P. F. 1992. Data Desk Statistics Guide. Data Description, Inc. Ithica, New York.

Vyverman, W., R. Vyverman, V. S. Rajendran, and P. Tyler. 1996. Distribution of

benthic diatom assemblages in Tasmanian highland lakes and their possible use as indicators of environmental changes. Canadian Journal of Fisheries and Aquatic Sciences 53:493-508.

Walther, J. 1894. Einleitung in die Geologie als historische Wissenschaft. Fisher Verlag, Jena.

Wells, N. A., C. T. Ferber, and J. C. Ohman. 1993. Discriminant analysis of fish-bearing deposits in the Eocene Green River Formation of Utah and Wyoming. Palaios 8:81-100.

Wetzel, R.G. 1983. Limnology (second edition). Saunders College Publishing, Fort Worth.

Wilkin, R. T, M. A. Arthur, and W. E. Dean. 1997. History of water-column anoxia in the Black Sea indicated by pyrite framboid size distributions. Earth and Planetary Science Letters 148:517-525.

Wilson, M. V. H. 1977a. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. Canadian Journal of Earth Sciences 14:953-962.

——— 1977b. Middle Eocene freshwater fishes from British Columbia. Life Sciences Contributions, Royal Ontario Museum 113:1-61.

——— 1980. Eocene lake environments: depth and distance-from-shore variation in fish, insect, and plant assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology 32:21-44.

——— 1984. Year classes and sexual dimorphism in the Eocene catostomid fish *Amyzon aggregatum*. Journal of Vertebrate Paleontology 3:137-142.

——— 1988a. Paleoscene #9: Taphonomic processes: information loss and information gain. Geoscience Canada 15:131-148.

——— 1988b. Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 62:609-623.

——— 1993. Calibration of Eocene varves at Horsefly, British Columbia, Canada, and temporal distribution of specimens of the Eocene fish *Amyzon aggregatum* Wilson. Kaupia: Darmstädter Beiträge zur Naturgeschichte 2:27-38.

Wilson, M. V. H., and D. G. Barton. 1996. Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. Paleobiology 22:535-542.

Wilson, M. V. H., and A. Bogen. 1994. Tests of the annual hypothesis and temporal calibration of a 6375-varve fish-bearing interval, Eocene Horsefly Beds, British Columbia, Canada. Historical Biology 7:325-339.

Zangerl, R., and E. S. Richardson Jr. 1963. The palaeoecological history of two Pennsylvanian black shales. Fieldiana Geology Memoir 4:1-352.

CHAPTER 3:

PHENOTYPIC CHANGE IN *AMYZON* THROUGH THE H3 INTERVAL

"The capacity of the fossil record to test any theory regarding the patterns and processes of evolution depends on the accuracy of measuring the rates of evolution. This in turn depends on both the completeness of the fossil record and the ability to date the fossils accurately and over short time intervals" (Carroll 1997: p. 61).

Introduction

Microevolutionary studies

Patterns and rates of phenotypic change.--One of the most active areas of research in evolutionary biology over the past few decades has been in attempting to reconstruct patterns and processes of evolution (see Carroll [1997] for a recent review). The traditional thinking, ever since the end of the 19th century, was that evolution of species and populations is a gradual process, with a slow accumulation of changes resulting in distinct populations (that could be considered a new species) (Carroll 1997). This view of evolution formed the foundations of phyletic gradualism, the theory that phenotypic change within a lineage is unidirectional, and gradually (but continuously) changing through time (see, for example, Gingerich 1976). According to this model, speciation occurs as a gradual divergence of two genetic lineages. In 1972, Eldredge and Gould championed an alternative theory, which they called punctuated equilibrium, to account for large morphological gaps seen between taxa in the fossil record (later refined in Gould 1982, 1995; Gould and Eldredge 1977, 1993). This theory states that the evolutionary history of a lineage is characterized by long periods of stasis in phenotypic characters, with short periods of rapid phenotypic change associated with speciation. Both phyletic gradualism and punctuated equilibrium make hypotheses about what patterns should be observed in

natural populations and in the fossil record (see Fig. 3-1, see also Vrba [1980] for a more complete contrast of patterns and processes associated with phyletic gradualism and punctuated equilibrium). According to the phyletic gradualism model, phenotypic change is slow and gradual (and not necessarily associated with speciation), whereas in the punctuated equilibrium model, phenotypic change is low or absent except during periods of speciation. According to the phyletic gradualism model, phenotypic change within a species is directional, whereas in the punctuated equilibrium model it oscillates around a stable mean.

The debate as to whether evolution occurs by phyletic gradualism or punctuated equilibrium has continued in the literature for several decades, but these two theories of evolutionary change merely represent alternative ends of a spectrum. It is now generally agreed that the true patterns of evolution do not lie on either of these extremes, but fall somewhere in the middle (*e.g.* Carroll 1997). One of the most important results of this debate, however, is that it has stimulated a great interest in, and established protocol for, examining patterns of phenotypic change in the fossil record. The models predict distinct patterns of phenotypic change, which paleontologists can look for in the fossil record; namely the prevalence of either stasis (including fluctuations about a stable mean) or gradual change in phenotypic characters through time. Unfortunately, there are several major barriers to these studies of patterns and tempos of evolution in the fossil record. Some of these problems are a lack of taxonomic completeness, a lack of an accurate way of determining the absolute time represented by a stratigraphic section, and temporal averaging and lack of stratigraphic completeness.

Barriers to microevolutionary study.--The fossil record is notoriously incomplete taxonomically, and heavily biased towards certain groups (Raup 1987; Maxwell and Benton 1990). In order to understand general trends in evolution, however, a large number of taxa from different lineages, each represented by (ideally) hundreds of specimens should be examined. Raup (1987) estimates that only a half a percent of the species that have ever lived are represented at all in the fossil record. Of the groups that are represented, it is only a small percentage that are represented by a large number of specimens (*e.g.* Durham 1967; Smith and Patterson 1989; Koch 1991). As a result, there

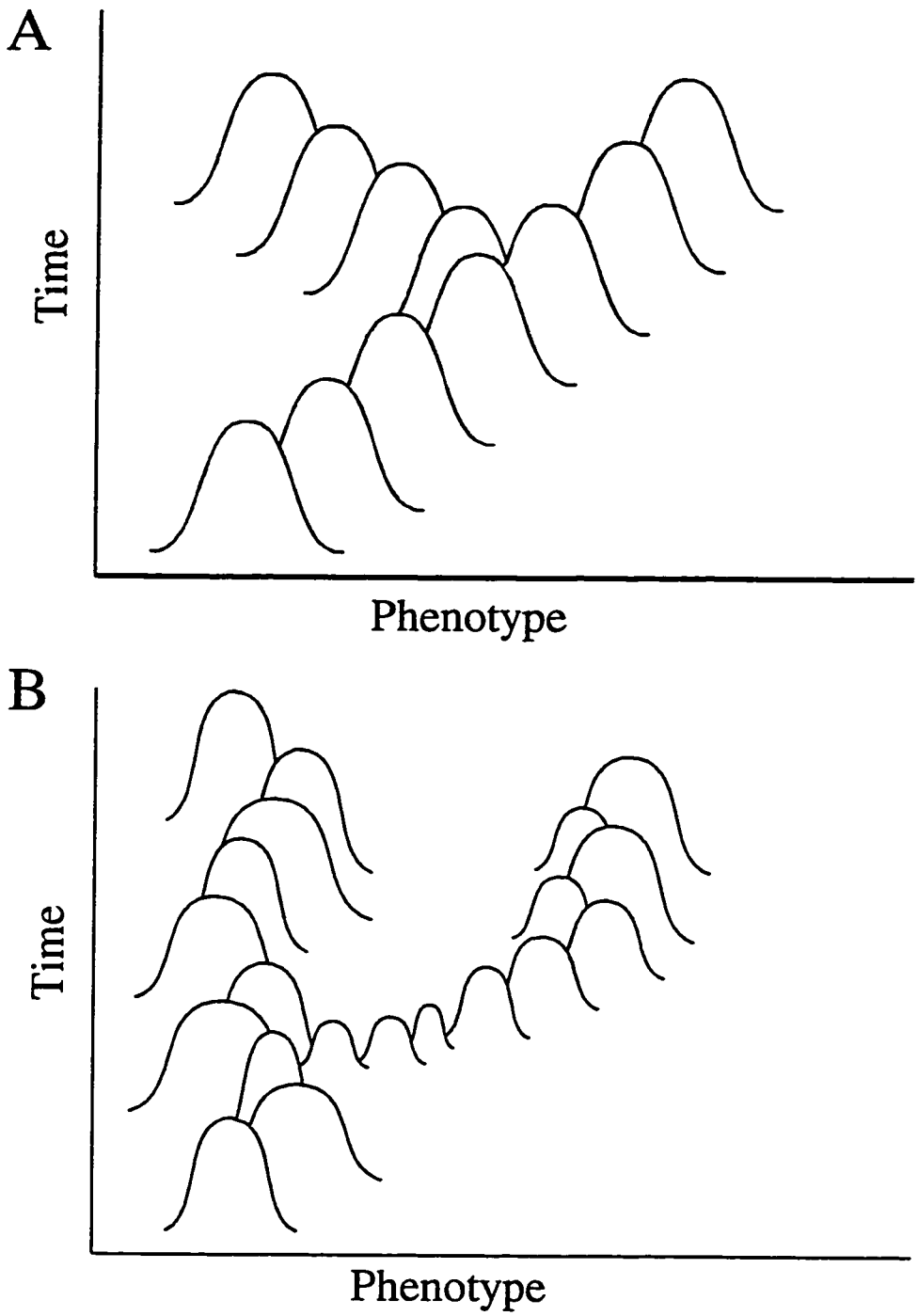


Figure 3-1: Comparison of patterns of phenotypic change associated with phyletic gradualism (A) and punctuated equilibrium (B). Adapted from Vrba (1980)

is a limit on the number and diversity of species that can be used to study evolutionary patterns in the fossil record.

Determining the absolute time represented by fossil sequences is often a difficult problem facing paleontologists hoping to observe patterns and rates of evolution. Even if the stratigraphic record were continuous and rates of deposition were constant through time (but see below), it would be difficult to calibrate it to an absolute time scale. Radiometric dating methods can be useful for obtaining absolute dates, but these methods have some limitations in evolutionary study. A stratigraphic unit needs to contain at least two layers that can be radiometrically dated (*e.g.* volcanics), preferably at either end of the interval of interest for the duration of the deposit to be determined. Even if these layers are preserved, however, the margin of error associated with radiometric dates is generally too high to be of use in studies of evolution of all but the most general patterns. Schindel (1980, 1982) developed a method to estimate the total time represented by different depositional environments based on a series of regression lines. Although these methods can be useful in that they give an approximate amount of time represented by a stratigraphic unit, they can quite easily be off by a factor of ten, so their usefulness, especially in microevolutionary studies, is somewhat limited.

A final, and perhaps most serious, set of problems facing paleontologists hoping to observe patterns and processes of evolution in the fossil record are those relating to temporal averaging and stratigraphic completeness (Dingus and Sadler 1982; Gingerich 1983; Sheldon 1990; MacLeod 1991; Kidwell and Behrensmeyer 1993a; Carroll 1997). As Schindel (1980: p. 408) points out, "the fossil record is too incomplete in most places to allow sampling on the short time scale over which [ecological and microevolutionary] processes occur". Problems of stratigraphic completeness and temporal averaging are closely related: they both limit the confidence that we can have in the stratigraphic record. The two major problems associated with stratigraphic completeness are gaps in the stratigraphic record, and changes in the rates of sedimentation through time; while the two major problems associated with temporal averaging are short generation times relative to sedimentation rates, and mixing of sediments. These two sets of problems will be examined separately.

Stratigraphic records are often not complete enough to study microevolutionary change (Durham 1967; Schindel 1980, 1982; Anders *et al.* 1987; Carroll 1997). A stratigraphic record is not complete when it contains gaps in sedimentation, as a result of either a cessation of deposition or erosion. Although gaps in the stratigraphic record are usually easy to recognize by sedimentological features, the amount of time that is represented by the gap is difficult, if not impossible, to determine. One solution to this problem is to avoid gaps by concentrating studies on complete intervals (Schindel 1980). However, even if a stratigraphic interval is complete, changes in sedimentation rates through time can cause serious problems in inferring time from stratigraphic distance. Changes in sedimentation rates are a more serious problem than gaps because they are much more difficult to identify. Algeo (1993) developed a method to quantify completeness of longer stratigraphic sections based on paleomagnetic data, which might also be applied to detecting changes in rate of sedimentation. These methods, however, depend on the preservation of a magnetic history and are also useful only for stratigraphic sections long enough to preserve a number of magnetic reversals.

Temporal averaging, whereby organic material from different time periods is preserved in the same strata (Kidwell and Behrensmeyer 1993a), is another major barrier to studies of evolution in the fossil record. Most organisms have generation times of only a year or two. An extremely high sedimentation rate would therefore be needed to distinguish phenotypic change between generations, or even hundreds of generations in the fossil record of these species. A second major problem associated with temporal averaging is actual physical (or biological) mixing of sediments, which disrupts the precise temporal sequence of fossils.

Much progress has been made in the past few decades in our understanding of both stratigraphic completeness and consistency (Schindel 1980, 1982; Anders *et al.*, 1987) and temporal averaging (Behrensmeyer 1982; Martin and Wright 1988; Flessa *et al.* 1993; Graham 1993). In fact, "Taphonomic approaches to time resolution in fossil assemblages" was the subject of a symposium at a recent annual meeting of the Geological Society of America (Kidwell and Behrensmeyer 1993b). Despite these advances, temporal averaging and incomplete knowledge of the stratigraphic record remain the most important barrier to studies of phenotypic change in the fossil record.

These stratigraphic problems have several results on the appearance of patterns of phenotypic change in the fossil record. Gaps in sedimentation can make gradual patterns of phenotypic change appear punctuated. Changes in sedimentation rates can have the same effect; decreases in sedimentation rate give the appearance of an increased rate of phenotypic change (Fig. 3-2; see also Wilson 1988a). This, in turn, has implications on which patterns of evolution are easiest to demonstrate in the fossil record. Proof of punctuational change requires knowledge sedimentation through time, and proof of gradualism requires a large number of specimens spaced through time. Differentiating between gradual and punctuational patterns of phenotypic change, therefore depends entirely on stratigraphic consistency.

Problems caused by an incomplete knowledge of the rate and consistency of sedimentation can be illustrated best by an example. Malmgren and coworkers (Malmgren *et al.*1983, 1984) reported a punctuational pattern ("punctuational anagenesis") in a sequence of foraminifera through time. MacLeod (1991) later re-examined the depositional history of the same sequence, and found that the punctuation event reported by Malmgren *et al.* (1983) occurred in an interval of temporally-condensed sediment, and in fact, the phenotypic pattern is not punctuated at all, but gradual.

Previous studies of patterns of phenotypic change have avoided some of these problems by focusing on long stratigraphic intervals. The longer the stratigraphic interval, the lower the impacts of such processes as temporal averaging and changes in rates of sedimentation will have on the observed patterns of phenotypic change. Longer intervals will be associated with more beds that can be radiometrically dated, and the errors associated with these dates will be less important in overall rates of change. Longer intervals are also more likely to be better dated by other methods such as stratigraphic correlation. For example, much of what is currently known about evolutionary patterns in the vertebrate fossil record is based on Tertiary mammals, for which a long sequence of biostratigraphic land mammal ages has been developed. Methods for examining, and even quantifying, evolutionary change across such long intervals is now well established in the literature (*e.g.* Gingerich and Gunnell 1995). A review of some of these studies can be found in Carroll (1997). Few studies, however, have been able to examine patterns of

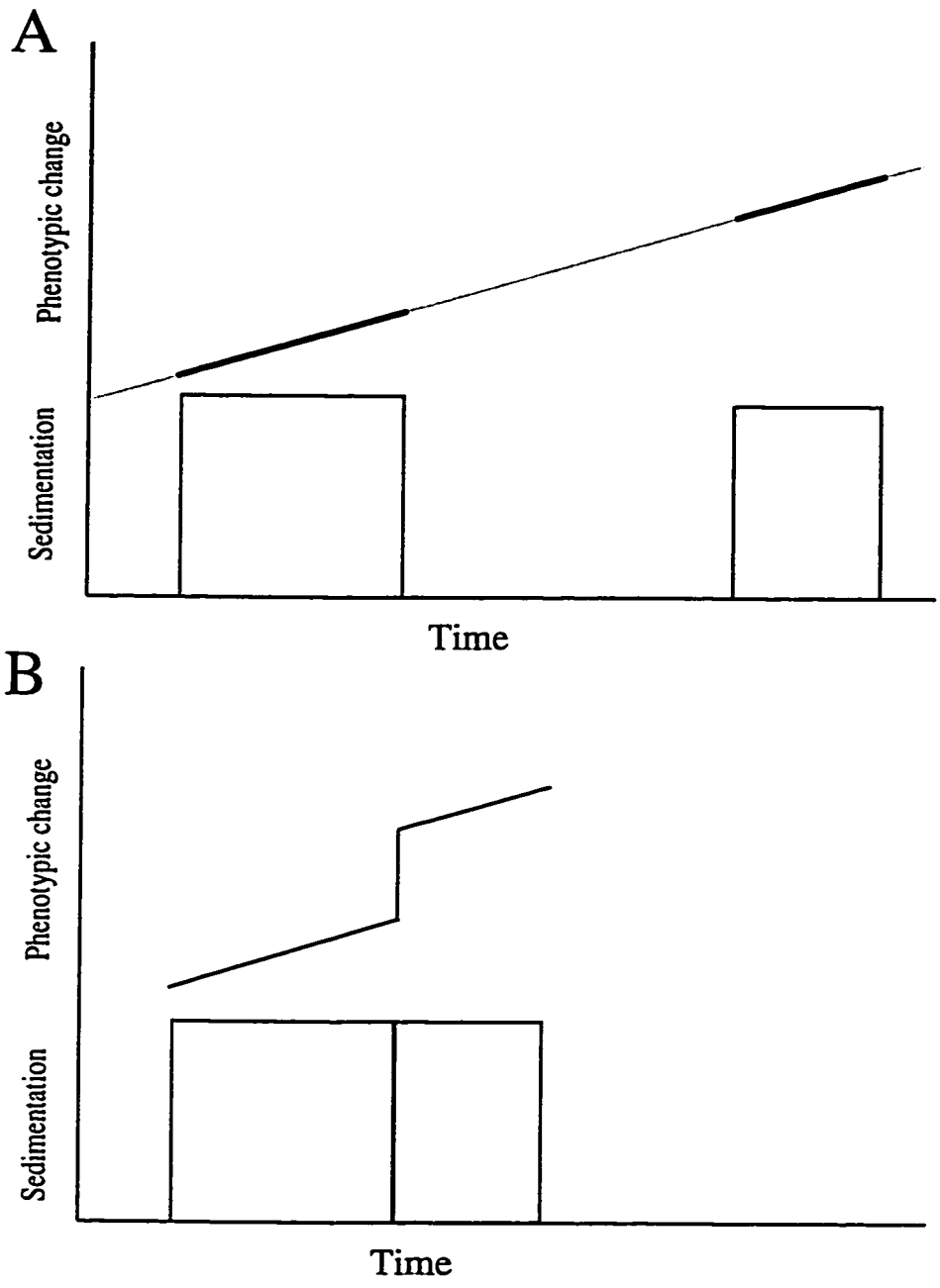


Figure 3-2: Gaps in sedimentation can give the false appearance of punctuational change. A, True pattern of sedimentation and gradual phenotypic change through time. B, Perceived patterns of phenotypic change are altered drastically by gaps in sedimentation. A gradual pattern of change appears to show relative stasis, followed by a period of rapid phenotypic change, followed by another period of relative stasis.

phenotypic change at a much higher time resolution, on a scale of generations instead of thousands of generations (the sampling interval in Gingerich and Gunnell [1995], for example, is about 2700 years). Studies of phenotypic change on a scale of generations or dozens of generations are needed because they can allow an estimation of the amount of variation that occurs within the sampling intervals of longer studies. Such intergenerational variation also forms the basis of broader patterns of variation, and a knowledge of these processes is important to our understanding of longer-term patterns of evolutionary change.

Ideal situation for microstratigraphic study.--Based on the limitations outlined above, the ideal stratigraphic sequence in which to study fine-scale evolutionary change will have the following features: an abundance of well-preserved fossils within one lineage, a complete stratigraphic history with rates of deposition clear and easy to interpret, and a method of easily determining absolute time separating specimens.

The varved lacustrine sediments at Horsefly, British Columbia are such stratigraphic sequences. The site contains abundant, well-preserved (see Chapter 2) fossils of an early catostomid, *Amyzon aggregatum* (Osteichthyes: Cypriniformes). Lakes are among the most continuous sites of sedimentation (Schindel 1980), making them ideal for microstratigraphic studies. There are several intervals in the Horsefly locality which are preserved in varves, or yearly laminations. H3, the longest of these intervals (representing 10 176 years), is the focus of this study. The presence of varves provides even more stratigraphic control, to the point that it is almost unmatched in the fossil record (Bell *et al.* 1987; Wilson and Barton 1996; see also Anderson and Dean 1988 for a discussion of varve formation). There is no need to make any "patently absurd" assumptions of constant sedimentation rates (Raup and Crick 1981: p. 203): there is a continuous stratigraphic record with evidence of constant and consistent sedimentation incorporated right into the sediment. There is also no need to make any assumptions about total time represented by the section (as proposed by Schindel 1980) because the total time can be directly determined by counting varves.

Previous microstratigraphic studies on fish.--The present study follows two previous sets of studies that have examined changes in fish populations in lacustrine deposits. M. A. Bell and his colleagues (Bell 1973, 1988; Bell and Haglund 1982; Bell *et al.* 1985; Bell

and Legendre 1987; Bell *et al.* 1987) studied sticklebacks from the Miocene, and A. R. McCune and her colleagues (McCune 1987a, 1987b, 1990, 1996; McCune *et al.* 1994) studied semionotids from the Triassic and Jurassic. A brief review of these studies will be presented here.

McCune's studies are based on a series of Triassic and Jurassic lakes within several depositional basins in northeastern United States. Within these basins, *Semionotus* exhibits a high richness of different phenotypic forms that have been interpreted as species. McCune compares this richness to that of species flocks of cichlids in the Great Lakes of Africa (*e.g.* 1987b, 1990). McCune examined short-term patterns of phenotypic change within one lake preserved in microlaminations (probably varves) (1990, 1996). Phenotypic anomalies tend to be concentrated in the early stages of a lake's history, which McCune attributes to decreased selection pressure (1990). Speciation rates in these lakes were rapid, as short as 5000 to 8000 years (McCune 1990). Nearly all of the variation in these fishes, however, is considered to be inter-specific; there is no evidence of phenotypic change within one lineage through time.

The studies most similar to the present one are those by M. A. Bell and his colleagues on the Miocene stickleback *Gasterosteus doryssus* (Bell 1973, 1988; Bell and Haglund 1982; Bell *et al.* 1985, 1987; Bell and Legendre 1987). These fish are preserved in a diatomaceous varved lacustrine sediment. Bell and Haglund (1982) first compared phenotypes of fish from different samples, each sample approximately 1500 - 3900 years, and each separated by anywhere from 4000 - 50 000 years. The authors found (possibly) significant changes in the structure of the pelvis and a dramatic increase in the number of specimens with one dorsal spine on a time scale of tens of thousands of years (Bell and Haglund 1982). There was also some variation within samples, on a scale of centuries, but this variation is not discussed in any detail (Bell and Haglund 1982).

In a later study, Bell and his colleagues (Bell *et al.* 1985, Bell and Legendre 1987) examined samples over a much shorter time interval, with each sample composed of approximately 1300 years, and each separated by approximately 5000 years. Number of dorsal fin rays, number of dorsal spines, number of anal fin rays, pelvic structure, standard length and number of predorsal pterygiophores were examined for temporal trends.

Almost all of these characters were correlated with each other, even after the authors attempted to correct for temporal trends. Most of the phenotypic change in these characters had a "stepped pattern" with phenotypic change occurring in fairly short intervals (Bell *et al.* 1985). Near the end of the section, all characters change rather dramatically. The authors attribute this sudden change (estimated to be over about 30 years) to migration of new populations into the basin (Bell and Legendre 1987).

McCune and Bell's studies both take advantage of the high temporal resolution provided by lacustrine sediments, and especially by microlaminations in these sediments. The present study, however, differs from those of both Bell and McCune in several important ways. The total time represented by the section studied in this paper is much shorter than that of Bell (about 1/10 the time) and that of McCune (about 1/2 the time represented by individual lakes, and only a tiny fraction of the entire basin). This shorter time span allows study at a much higher resolution, and observation of changes occurring on a time scale within the time represented by individual samples of Bell and McCune. McCune examined rates of speciation and patterns of selection, but she could not address the major focus of this paper, variation in one lineage through time. Bell and his colleagues examined variation within one lineage, but because of the length of their stratigraphic section, they grouped their specimens within samples, each of which they treated as separate data points. Bell recognizes that there is temporal variation within samples (see Bell and Haglund 1982: Fig. 5) but when the data are pooled, this variation becomes temporally averaged.

The present study is an attempt to use the same high temporal resolution provided by lacustrine sediments to examine patterns of phenotypic change within a single lineage through time at a high temporal resolution.

Meristic Variation

Ecophenotypic responses of meristics.--There is little to no variation in osteological features of *Amyzon aggregatum* through the H3 section. This study, therefore, focuses on variation in meristic series (serially repeating structures such as vertebrae and fin rays).

The number of meristic features within a series can vary on much shorter time scales than do osteological features (*e.g.* Svärdson 1945; Kirpichnikov 1979). The number of meristic elements in a series, however, is a product of not only genotype, but also environmental conditions during development (ecophenotypic effects). In contrast to morphometric features (*e.g.* relative body proportions) that continue to change throughout life, meristics are fixed early in development. A brief review of our knowledge of the relative contributions of genetic and environmental contributions to meristic counts is presented here. For a more comprehensive review, see Lindsey (1988). Environmental variables, therefore, can have two different effects on meristic series: either directly during development (ecophenotypic), or as a result of selective pressures for certain meristic counts in particular environments.

Environmental influence on number of meristic features has been recognized for many years (*e.g.* Hubbs 1922; Barlow 1961) and has been the focus of a large number of studies in the past 20 years (see references in Lindsey 1988). Unfortunately, the effects of environmental variation on meristic counts are not easy to predict. According to Lindsey (1988: p. 205) a similar change in environment can have different effects on different meristic series:

> "1. In different species the same meristic series may have different response patterns [to similar changes in environment]
> 2. Different meristic series of the same species may have different response patterns.
> 3. Different genotypes of one species may have response curves with similar shapes but with absolute values of the meristic character widely displaced.
> 4. Different genotypes of one species may even have response curves of different shapes."

Fortunately, not all responses are so unpredictable and some generalizations can be made.

Temperature is the best-studied environmental variable that can affect meristic series. Effects of all environmental variables are determined by taking eggs of a particular individual, rearing them in two different environments, and then comparing meristic counts. The most common response of both number of vertebrae and number of fin rays to increased temperature in many different species is negative (lower meristics at higher

temperatures) (references in Lindsey 1988). Positive responses (increased meristics at increased temperature) are rare in vertebrae, and relatively rare in fin rays. V-shaped responses (highest number of meristic at both extremes of temperature) are common in vertebrae but rare in fin rays. Arched responses (highest meristics at some intermediate temperature) are rare in vertebrae but reasonably common in fin rays. The carp and the rainbow trout are two well-studied species that can illustrate how different meristic series can be affected differently by similar environmental changes.

In the common carp, *Cyprinius carpio*, increased temperature during development has different effects on nearly every meristic series (Tartarko 1968). Total number of vertebrae and number of dorsal fin rays both decrease with increased temperature. Number of anal fin rays is highest at some intermediate temperature. Number of pectoral fin rays is highest at the highest temperature of development.

The relationship between temperature and meristics, however, is not always as complex as that seen in the carp. In the rainbow trout, *Onchorhynchus mykiss*, number of vertebrae, number of dorsal fin rays, number of anal fin rays, number of caudal fin rays, number of pelvic fin rays, number of scales, and number of branchiostegal rays all show a negative correlation with temperature (lower meristic counts at higher temperature); only number of pectoral fin rays and number of gill rakers show a positive trend (Orska 1963; MacGregor and MacCrimmon 1977; Lindsey *et al.* 1984; Lindsey 1988).

The range of phenotypic variability due to environmental change in vertebrae and fin rays is also variable: between 0.1% and 1.0% per degree Celsius for vertebrae and between 0.3% and 3.0% per degree Celsius for fin rays.

Although temperature is the best-known environmental influence, other factors can also influence meristic counts. Responses of both vertebrae and fin ray counts to increased oxygen are almost always negative. Increased salinity usually also has negative effects on meristic counts, but relationships are not as predictable. Similarly, the effects of increased radiation are almost always negative, but can also be positive or arched.

Meristic counts are fixed early in development of fishes; therefore, in order to understand the implications of environmental variations in these counts, the embryology of fishes has to be considered (refer to Lindsey 1988 or Dunn 1983 for a complete review; I

will only discuss meristic series that I counted in this study). The sequence of appearance and ossification of each meristic series has implications on how such series will be affected by environmental change. There is some inter-specific variability in embryogenesis of meristic series, but several generalities can be made.

The first meristic elements to appear in a fish embryo are the somites, which eventually determine the spacing of vertebrae. Development of vertebrae generally proceeds from anterior to posterior (usually with the exception of the most posterior few vertebrae which appear early in development) (Itazawa 1963; Nagiec 1977; Grande and Bemis 1998).

Development of fin rays is more complex, because they are composed of three distinct elements: the rays themselves, pterygiophores and muscles, each with its own developmental pathway. Development of median fins begins early in embryogenesis, before much of the vertebral column is ossified (Nagiec 1977). The ossification of the last fin rays, however, can be very late in development (Lindsey *et al.* 1984). For most of the fin there is a one-to-one relationship between rays and pterygiophores. This relationship, however, breaks down at either end of the fin: several small rudimentary rays can develop at the anterior end of the fin, and the posterior-most ray is usually double (with two distinct rays from the same base).

Development of paired fins is the least regimented of all meristic series. There are no internal supports associated with each ray in paired fins. The full complement of paired fin elements is fixed late (possibly the last meristic series to ossify) in development (Nagiec 1977; Lindsey *et al.* 1984; Beacham and Murray 1986).

Meristic series that are the last to fix also tend to be the most phenotypically plastic. Lindsey (1988) mentions that pectoral fins are particularly good for meristic studies because the full complement of rays is usually the last series to appear. Although he does not specifically mention a relationship between time to development and relative plasticity, there seems to be a fairly strong positive correlation between these factors. We can arrange meristic series in order of earliest to latest to become fixed: vertebrae, median fins, and paired fins. If the elements that are latest to become fixed are also the most plastic, this should also be the order of relative plasticity.

Lindsey and Arnason (1981; see also Lindsey *et al.* 1984; Swain and Lindsey 1986;

and Lindsey 1988) developed a model to attempt to explain how similar environmental changes can affect meristic series in different ways. Their model, which they named the atroposic model, combines embryological studies with information from actualistic studies. The atroposic model depends on two distinct processes in development, each with its own regulatory control: growth and differentiation. A detailed description of the model is beyond the scope of this paper, but see Lindsey and Arnason (1981) for further details. The model still needs to be rigorously tested, but it appears to be a good first step towards our understanding of the development of meristic series.

Heredity of meristics.--Although environmental contributions to meristic variation are quite clear, heredity can also play an important role in determining the number of elements in a particular meristic series. This aspect of meristic variation has been neglected in the scientific literature during the past several decades. The most recent complete review of genetic contributions to meristic variation can be found in Kirpichnikov (1979: especially chapter 4).

Heritability of number of vertebrae is generally high: 0.59 in *Etmopterus spinax* (Tave 1984), 0.66 in *Onchorhynchus mykiss* (Orska 1963), and 0.9 in *Cyprinius carpio* and *Salmo trutta* (Nenashev 1966; Schmidt 1919a). Some studies, however, have found little to no heritability of number of vertebrae (Ferguson and Liskauskas 1995).

Number of elements in median fins tend to have much higher heritabilities than do numbers of elements in paired fins (Kirpichnikov 1979). Dorsal (soft) fin ray heritability is high: 0.57 to 0.63 in *Cyprinius carpio* (Kirpichnikov 1979; Nenashev 1966), 0.59 in *Poecilia reticulata* (Schmidt, 1919b), and 0.79 in *Zoarces viviparus* (Schmidt 1917). Heritability of anal fin rays is also high: 0.60 in *Z. viviparus* (Schmidt 1917). Heritability of pectoral fin rays is somewhat lower: 0.54 in *Z. viviparus* (Smith 1921). Finally, heritability of caudal fin rays is very high: 0.80-1.00 in *P. reticulata* (Beardmore and Shami 1976).

Many of these heritability studies, however, are old and are based on only one or two species. Future study should attempt to better understand the role that heredity can play in the determination of meristic counts.

According Lindsey and Arnason's (1981) atroposic model, genetics plays only an

indirect role in the determination of meristic counts. Genes provide a framework, or a set of bounds within which environmental variation can occur, or in the words of Lindsey (1988: p. 256), "genes [...] control meristic number only indirectly via changes in the parameters of the curves of growth and of differentiation; indeed their influence would likely be still more remote since the forms of these curves are the results of many interacting processes". Environment, on the other hand, directly influences meristic counts by changing either the rate of growth or the rate of differentiation. There is no doubt, however, that genetics does play a role in meristic development, and, according to heritability studies, that role can be quite important.

As Lindsey (1988: p. 202) points out, "the effects of heredity and of the environment are hard to disentangle in nature"; they are even more difficult to disentangle when environment cannot be measured directly, but has to be inferred from other factors (the situation that is presented in the fossil record). Fortunately, the paleoenvironment of the Horsefly section has been studied in some detail. In the previous chapter, I reconstructed paleoenvironmental changes based on changes in the preservation of fishes through a 10 000 year interval in the Horsefly section. In this study, I identify changes in meristic features through the same interval. These changes are then compared to paleoenvironmental changes in an attempt to explain causes and the significance of meristic variation through the H3 section.

Materials and Methods

Locality

The Horsefly locality is exposed along the banks of the Horsefly River in central British Columbia (see Chapter 1). The site is biostratigraphically correlated, based on both palynological (Rouse *et al.* 1971) and paleoichthyological (*e.g.* Wilson 1977a) studies with other freshwater sites of western North America. Some of these other sites, in turn, have been dated as middle Eocene using both radiometric (Rouse and Mathews 1961; Mathews

1964; Hills and Baadsgaard 1967) and paleomagnetic (Symons and Wellings 1989) methods.

The entire Horsefly locality is composed of about 100 stratigraphic meters of lacustrine sediments. Several parts of the section are preserved in microlaminations consisting of couplets of pale and dark layers. Two of these intervals, informally named H2 and H3, have been demonstrated to be varved, or preserved in yearly laminations (Wilson 1993; Wilson and Bogen 1994). The H3 section, the focus of this paper, is the longer of these intervals, composed of approximately 10 000 varves. The pale lamina of the varves are composed almost entirely of diatom tests, whereas the dark layers are rich in clays (Wilson and Bogen 1994).

The H3 section has been extended by about 4000 laminations since it was first described by Wilson and Bogen (1994) thanks to the discovery of a more complete exposure on the west bank of the river (Fig 3-3). The new layers are continuous with the old section, and their colour, thickness and overall composition cannot be differentiated from the original 6000 varves. Although they have not been subject to the same rigorous testing as the original 6000 layers, there is no reason to believe that they do not also represent varves (see Chapter 1). For the remainder of this paper, the entire H3 section will be assumed to be varved.

The paleoecology of the Horsefly locality has been studied extensively (Wilson 1977b, 1980, 1984, 1988b, 1993; Wilson and Barton 1996). There are four species of fish from the H3 section, but 95% of all specimens are *Amyzon aggregatum*. This species, especially in the H2 section, is preserved in distinct size classes, probably the result of a seasonal kill during the fall or winter overturn (Wilson 1977a, 1984, 1993; see Chapter 2). The vast majority of fishes from the H3 section are preserved in the dark portion of the varves (see Chapter 2), likely indicating death in the winter months.

Methods

A total of 698 specimens from the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) and Royal British Columbia Museum (RBCM) collections were

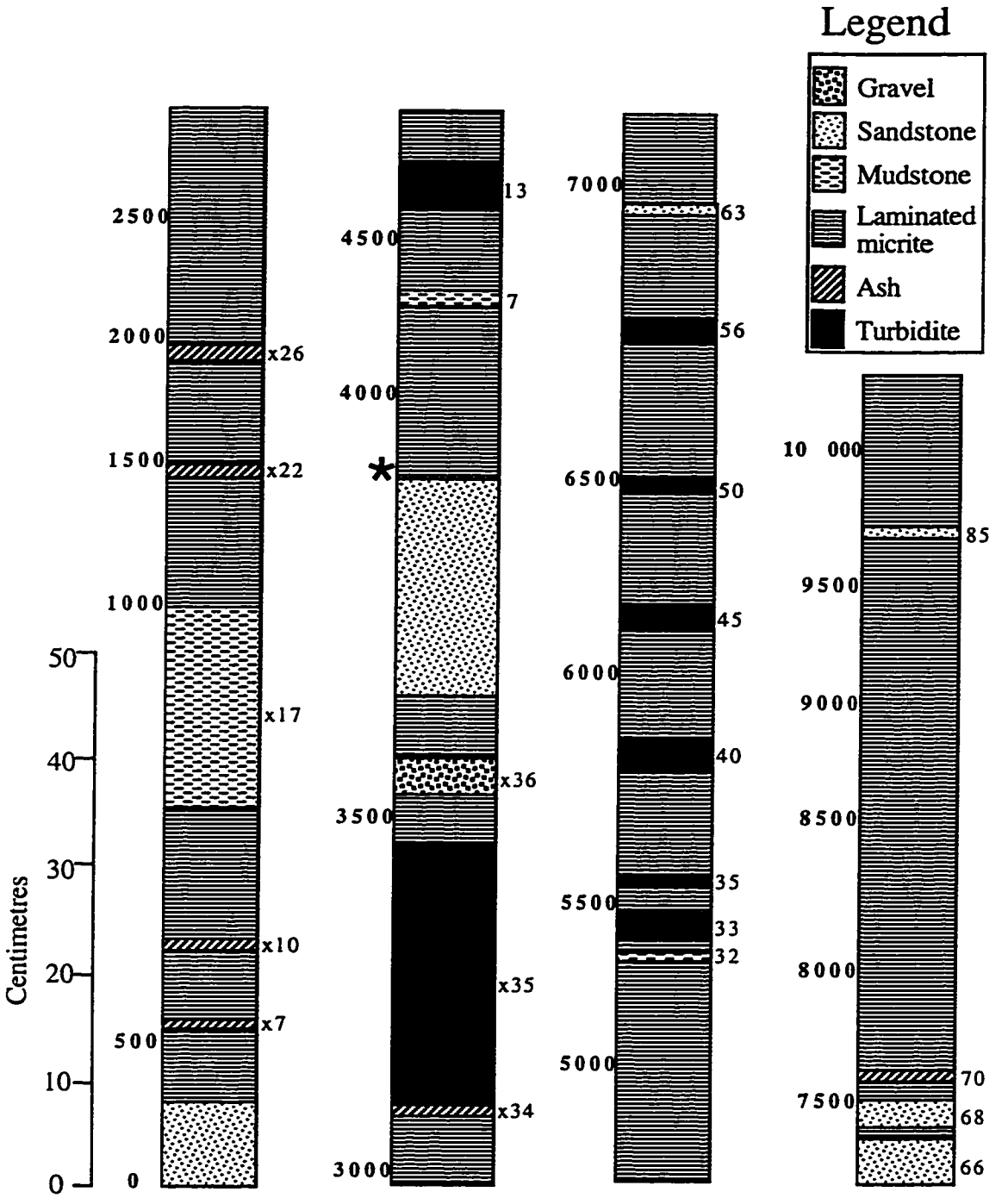


Figure 3-3: Detailed stratigraphic section of the H3 section of the Horsefly locality. Lithologies are not usually distinct, but tend to grade into each other (with the exception of ash and turbidites which are interpreted as event layers). Laminated micrite layers are interpreted as annually laminated (varved). Asterix indicates the bottom of the old H3 section (Wilson and Bogen 1994). Numbers along left side of section indicate relative year (as described in the text). Breaks between parts of the section here are arbitrary.

used in this study (see Appendix). All of these specimens were collected by University of Alberta field crews in the past 20 years (with the vast majority collected in 1996), with some specimens subsequently donated to the RBCM. A typical specimen from the H3 locality is illustrated in Figure 3-4. Specimens were first assigned to the varve in which they are preserved (and therefore their relative year of death) as described in Wilson and Bogen (1994) and in Chapter 1. All references to year for the remainder of this paper refer to the relative year on the stratigraphic column.

Fossils were prepared sufficiently to allow counting of all the meristic characters used in this study (see list of characters used below). As much data were gathered from each specimen as was possible based on completeness and articulation. Patterns of disarticulation are predictable (see Chapter 2); therefore, it was easy to identify any character that might be missing any elements because of incomplete preservation. Many of the specimens were incomplete, and therefore only yielded one or two characters, whereas others specimens were complete and all characters were able to be counted or measured.

To avoid any problems of inter-observer differences, I personally counted all meristics reported in this study. Because this study includes a comparison with previous descriptions of the species, I conferred with M. V. H. Wilson to ensure that we were using the same criteria for counting meristic series. I counted each meristic series on each specimen at least twice; once from the anterior end and once from the posterior end. If the counts differed, I counted again until I was satisfied with the result.

Meristic counts and measurements are based on the methods outlined in Hubbs and Lagler (1964) except where noted below. I counted or measured the following characters:

Predorsal fin rays (pDFR): The number of incomplete (rudimentary) dorsal fin rays preceeding the first complete (principal) dorsal fin ray.

Dorsal fin rays (DFR): Number of complete (principal) dorsal fin rays. The first principal dorsal fin ray is unbranched; the rest are branched. The last dorsal fin ray is double, and is only counted as one.

Anal fin rays (AFR): Number of complete (principal) anal fin rays. As with dorsal fin, the first ray is unbranched, and the last anal fin ray is double and only counted as one.

Anal fin pterygiophores (AP): Number of anal fin pterygiophores. The first anal

Figure 3-4: Representative specimen of *Amyzon aggregatum* (UALVP 31113) from the H3 section of the Horsefly locality.

pterygiophore is expanded as a short plate.

Lower caudal fin rays (lCFR): Number of complete (principal) caudal fin rays that originate on the lower half of the tail. The first complete ray is unbranched.

Upper caudal fin rays (uCFR): Number of complete (principal) caudal fin rays that originate on the upper half of the tail. The first complete ray is unbranched.

Total caudal fin rays (CFR): Total number of complete caudal fin rays (=lower caudal rays+upper caudal rays).

Pectoral fin rays (PFR): Number of pectoral fin rays. The number of pectoral fin rays in fish can be bilaterally asymmetrical (*e.g.* Valentine *et al.* 1973; Beacham 1991; Hubert and Alexander 1995; Campbell *et al.* 1998), but fossils are usually preserved with one side better exposed than the other. I included only the side that was easier to count.

Pelvic fin rays (VFR): Number of complete pelvic fin rays. As with pectoral fin rays, I included only the side that was easier to count..

Predorsal vertebrae (PDV): Number of vertebrae posterior to the Weberian apparatus but anterior to the first dorsal fin pterygiophore. Following Wilson (1977a), the four vertebrae incorporated into the Weberian apparatus are not included in any of the vertebral counts.

Dorsal vertebrae (DV): Number of vertebrae posterior to the first dorsal pterygiophore but anterior to the first caudal vertebra (defined as the first vertebrae with a haemal spine).

Pre-caudal vertebrae (PCV): Predorsal vertebrae + dorsal vertebrae. Note that some specimens might be included here that were not included in the previous counts if the position of the first dorsal pterygiophore is not clear, or if there was evidence that the dorsal fin shifted post-mortem.

Caudal vertebrae (CV): Number of vertebrae from the first caudal vertebra (first vertebra with a haemal spine) to the most posterior vertebrae supporting the hypurals (inclusive).

Post-anal vertebrae (PAV): Number of vertebrae posterior to the first anal pterygiophore. This category is included to correct for any errors produced by an incomplete development of the first haemal spine that occurs in some specimens. Occasionally it is difficult to assess whether the first haemal spine is complete or not.

Total vertebrae (TV): Total number of vertebrae (exclusive of the Weberian apparatus).

Hypurals (hyp): Number of hypurals.

Standard length (SL): Length from the anterior end of the maxilla to the posterior end of the hypurals. Note that the premaxilla was not used as a landmark because many specimens have a high degree of tetany in which the premaxilla is shifted upwards. The maxilla is a more stable landmark in this situation.

Body depth: Measured as a perpendicular from the level of the base of the dorsal fin (insertion of the first predorsal fin ray) to level of the center of the pelvic girdle. The body is often preserved deeper than this measurement, but some of this depth might be a taphonomic artifact. I chose these landmarks because they are more stable than the soft tissue that would be measured in a traditional body depth measurement.

Many of the vertebral counts are not independent of each other, but instead reflect relative positions of other landmarks in relation to the vertebral column. For example, dividing precaudal vertebrae into predorsal and dorsal vertebrae can indicate which portion of the vertebral column is more plastic (associated with changes in total vertebrae), and it can indicate changes in the relative position of the division between the caudal and precaudal regions. Similarly, the dorsal vertebrae and predorsal vertebrae counts, because they are associated with the origin of the dorsal fin, can indicate whether changes in the number of dorsal fin rays occurs at the front or back of the dorsal fin. The information that can be obtained by comparing these counts is somewhat analogous to that obtained by morphometric studies. Unlike morphometrics, however, these positions are fixed early in development, and do not change through the life of the fish.

Analyses and Statistics

Repeatability.--In order to test the confidence that I can have in the precision of the counts, I recounted the meristic series of 30 specimens one year after the initial count. These specimens were chosen haphazardly from among the original 698 specimens and counted using the same criteria as I used in the original counts.

Summary statistics.--I compiled all of the meristic counts into a summary table to report

the ranges, means and standard deviations of all series. I then compared these counts with the original description of *A. aggregatum* (Wilson 1977a) and a more recent review of the genus (Bruner, 1991) to examine variability of meristic characters across the range of the species, and to address any systematic problems within the genus that my counts might bring to light.

Correlations.--I then assembled a correlation matrix to identify all pairs of characters that were correlated (Statview 4.5, Correlation analysis, pairwise deletions). I tested these correlations for significance using Fisher's r to z transformation. As Rice (1989: p. 223) mentions, this kind of test judges far too many tests to be significant, and "appropriate probability values must adjust for the number of simultaneous tests". I used the sequential Bonferroni method (Holm 1979; see also Rice 1989) to retest for significance at the $p<0.05$ level.

Lindsey (1975) reported positive correlations between standard length and number of vertebrae (and negative correlations between total vertebrae and body depth) at several different levels of classification [between closely related species, populations within species, and in one case, sexes within populations], which he termed pleomerism. Reimchen and Nelson (1987) found similar trends within populations of *Gasterosteus aculeatus*, but also found correlations with microhabitat, warning that sampling biases can affect such studies. I tested for correlations between standard length and total number of vertebrae, and body depth and total number of vertebrae in the specimens from this study.

Temporal trends.--I then plotted the meristic counts against relative year of death of the specimen to examine temporal trends.

In order to see whether there were any significant changes in any meristic value across the entire H3 section, I ran a simple regression on each character. This regression tests only whether the character changes directionally over the total section. A character can change dramatically through time, but if the values at the start and end of the section are similar, it will show no significant regression.

Next, I applied a smoothing function to the data. Smoothing functions have the benefit that they do not pool data into artificial groups; and none of the temporal data are lost. Smoothing functions are powerful and effective tools to explore trends in data without any

of the assumptions of regressions (linearity and uni-directionality) (Velleman 1992). However, smoothing functions are still exploratory, and no tests of significance have yet been developed. The LOWESS (Locally Weighted Scatterplot Smoothing) smoothing function (Cleveland, 1979) was chosen because it emphasizes "grand-scale patterns" (Velleman 1992: p. 33/11) in the data, and is less affected by minor fluctuations (that might be caused by chance). For this same reason, a relatively robust span (20% of the data) was chosen. One problem with this smoothing function is that it tends to exaggerate trends at the ends of the intervals; therefore, these will be treated with caution.

Finally, because there is no way of testing for significance with smoothing functions, I divided the specimens into millennium of death. For each meristic character, I plotted the mean and 95% confidence intervals per millennium on a scatterplot. I tested mean values per millennium for significant differences using the sequential Bonferroni technique to correct for the number of tests per character.

In order to attempt to identify further correlations and trends that were not evident by examining individual meristic counts, I subjected the meristic counts to several principal components analyses (PCA). Ideally, a PCA could be run on all counts simultaneously. Unfortunately, the large amount of missing data in this study precludes such an analysis. The four counts with the highest sample sizes, dorsal fin rays, anal fin rays, number of dorsal vertebrae and number of caudal vertebrae, were combined for a PCA. A second PCA was run on dorsal fin rays, number of dorsal vertebrae, number of predorsal vertebrae and total number of vertebrae. Factor scores for these PCAs were plotted against time to identify any temporal variations in these factors.

Finally, I isolated the 715-year interval with the greatest density of specimens in order to test for trends over a much higher resolution (on the scale of centuries instead of millennia). A span of 715 years was chosen because it represents the exact amount of time represented by the H2 section. I plotted the meristic counts against time and analyzed the smoothing functions of the data. These results will be compared with those of meristic counts of the H2 section in a later paper, and are therefore not discussed in any detail here. They are mentioned, however, to compare different scales of temporal variation in meristic features across the H3 section.

Results

Repeatability.--Repeatability (defined as the proportion of specimens for which two counts were identical) of meristic counts varied considerably among characters (Table 3-1). Nine out of ten of the differing counts differed by only one element. Lowest repeatability was recorded for pectoral fin rays and pelvic fin rays (53% and 67% respectively). Repeatability of dorsal fin, anal fin and caudal fin ray counts are high (84%, 84% and 100% respectively). Repeatability of vertebral counts varied from 75% for caudal vertebrae to 92% for post-anal vertebrae.

Summary Statistics.--Summary statistics of meristic characters are presented in Table 3-2. The range of meristic counts through the H3 section was high, comparable to the range of counts across the entire geographic range of the species (Wilson 1977a; Bruner 1991). Several characters had some values outside of the published range of the species (Wilson 1974, 1977a and Bruner 1991): dorsal fin rays (18-26; published range (p.r.) 21-27); anal fin rays (7-12; p.r. 7-11); upper caudal fin rays (8-10; p.r. 9-10); total caudal fin rays (16-20; p.r. 17-19); pectoral fin rays (8-16; p.r. 12-20); total vertebrae (30-35; p.r. 32-37); precaudal vertebrae (15-20; p.r. 16-19); and predorsal vertebrae (4-8; p.r. 5-9).

Correlations.--The correlation matrix of all meristic variables involved 120 total tests (Table 3-3). After the initial Fisher's r to z transformation, 23 of those correlations are significant to (at least) the $p<0.05$ level; 17 are significant to the $p<0.01$ level and 14 are significant to the $p<0.0001$ level. After the sequential Bonferroni correction, only 15 correlations are significant (to the $p<0.05$ level). Only these 15 correlations will be considered to be significant.

Most of the significant relationships (11 of 15) are between vertebral characters. Total number of vertebrae is significantly positively correlated with all vertebral subcounts except predorsal vertebrae (positively correlated but not significantly). Number of caudal vertebrae is negatively correlated with number of dorsal vertebrae and precaudal vertebrae, but positively correlated with number of post-anal vertebrae. Number of post-anal vertebrae is also negatively correlated with number of dorsal vertebrae and number of

Table 3-1: Intra-observer repeatabilities of meristic counts of *Amyzon aggregatum* from the H3 section of the Horsefly locality, British Columbia. Approximately 30 specimens were chosen haphazardly one year after the initial counts, and recounted using the same methods as with the original counts. Indented characters indicate subcounts. Repeatability is counted as the proportion of specimens for which the two counts were exactly the same.

Character	Repeatability
Principal dorsal fin rays	21/25 (84%)
Anal fin rays	22/26 (84%)
Anal fin pterygiophores	20/22 (91%)
Total caudal fin rays	19/19 (100%)
Upper caudal fin rays	21/22 (95%)
Lower caudal fin rays	20/20 (100%)
Pectoral fin rays	7/13 (53%)
Pelvic fin rays	8/12 (67%)
Total vertebrae (+4 Weberian)	19/22 (86%)
Precaudal vertebrae (+4)	15/20 (75%)
Pre-dorsal vertebrae (+4)	21/22 (95%)
Dorsal vertebrae	15/19 (79%)
Caudal vertebrae	18/24 (75%)
Post-anal vertebrae	22/24 (92%)
Hypurals	18/20 (90%)

Table 3-2: Summary statistics of meristic counts of *Amyzon aggregatum* from the H3 section of the Horsefly locality, British Columbia, with a comparison to previous studies of meristic counts of the species. Mean count ± standard error are given for each count, and in brackets, ranges and sample size for each count. The original complete description of the species (Wilson, 1977a) as well as counts from only the Horsefly locality (almost exclusively the H2 section) and those of "*A. gosiutensis*" from the Green River Formation are included for comparison. Ranges of meristics of *A. aggreagtum* from the H3 section are comparable to those of the whole species, and are generally higher than those of the H2 section. Extensions of previously published meristic counts are indicated in bold.

Character	This study (H3 only)	Wilson, 1977a (all localities)	Wilson, 1977a (Horsefly only)	Bruner, 1991* (Horsefly only)	Grande *et al.*, 1982 (Green River Formation)
Principal dorsal fin rays	22.46±.10 (**18-26**; n=226)	23.69±.14 (21-27; n=86)	23.74±.15 (21-27; n=76)	24.13±1.78 (21-27; n=15)	22.5±0.798 (22-25; n=12)
Anal fin rays	8.35±.04 (7-**12**; n=305)	8.65±.06 (7-11; n=107)	8.62±.06 (7-11; n=96)	9.4±1.98 (7-11; n=13)	7.90±0.316 (7-8; n=8)
Anal fin pterygiophores	8.61±.08 (7-10; n=110)	8.41±.07 (6-10; n=96)	8.43±.07 (6-10; n=84)	8.56±1.316 (7-10; n=16)	8.70±0.483 (8-9; n=10)
Total caudal fin rays	18.06±.04 (**16-20**; n=212)	18.05±.03 (18-19; n=75)	18.06±.03 (18-19; n=73)	18±0 (18; n=16)	18.2±0.422 (18-19; n=10)
Upper caudal fin rays	9.10±.03 (**8**-10; n=230)	9.04±.02 (9-10; n=79)	9.03±.02 (9-10; n=69)		
Lower caudal fin rays	8.95±.02 (8-10; n=234)	9.00±.02 (8-10; n=84)	9.02±.01 (9-10; n=73)		
Pectoral fin rays	12.45±.23 (**8**-16; n=91)	15.45±.21 (11-20; n=53)**	15.63±.32 (11-20; n=30)	15.15±1.88 (12-18; n=13)	16.0±0 (16; n=10)
Pelvic fin rays	9.83±.16 (7-15; n=88)	10.0±.17 (7-15; n=57)	10.32±.23 (8-12; n=19)	9.36±2.02 (8-14; n=14)	9.40±0.548 (9-10; n=5)
Total vertebrae†	33.36±.07 (**30**-35; n=177)	33.5±.14 (32-37; n=64)		33.44±.93 (32-35; n=15)	30.6±0.515 (30-31; n=12)
Precaudal vertebrae†	17.34±.06 (**15-20**; n=188)	17.46±.09 (16-19; n=70)	17.5±.09 (16-19; n=66)	17.8±1.05 (16-20; n=15)	16
Pre-dorsal vertebrae†	6.54±.04 (4-8; n=257)	6.72±.08 (5-8; n=71)	6.73±.08 (5-8; n=59)		
Dorsal vertebrae	10.76±.06 (9-13; n=215)	10.86±.11 (7-13; n=74)	10.84±.11 (7-13; n=63)		
Caudal vertebrae	16.14±.05 (14-18; n=251)	16.03±.07 (14-18; n=104)	16.11±.08 (14-18; n=92)	(14-18; n=15)***	14
Post-anal vertebrae	14.58±.05 (12-17; n=257)				
Hypurals	5.93±.03 (5-9; n=185)	5.79±.05 (5-7; n=95)	5.82±.05 (5-7; n=81)		

* - Bruner (1991) mistakenly reported standard deviations instead of standard errors. His original data are reported here; therefore, ± values are standard deviations.

** - range reported as 12-20 in Bruner, 1991. Wilson 1974 (on which Wilson, 1977a is based), however, includes one specimen with a pectoral fin ray count of 11.

*** - No mean value was reported by Bruner (1991) for number of caudal vertebrae.

† - All vertebral counts exclude the four vertebrae incorporated into the Weberian apparatus. Some of the vertebral counts that Bruner lists included the four Weberian vertebrae, others did not. All values reported on this table do not include the four vertebrae associated with the Weberian apparatus.

Table 3-3: Correlation matrix of meristic counts of *Amyzon aggregatum* from the H3 section of the Horsefly locality, British Columbia. Numbers below the diagonal are sample sizes for each correlation. Numbers above the diagonal are correlation coefficients. *p* values based on Fisher's r to z transformation are indicated with asterices (**p*<0.05, ***p*<0.01, ****p*<0.0001); correlations that are significant after the sequential Bonferroni transformation are listed in bold. See Methods for abbreviations.

Character	pDFR	DFR	AFR	AFP	uCFR	lCFR	tCFR	PFR	VFR	PDV	DV	CV	PAV	PCV	tV	hyp
pDFR	xxxx	.144	.017	.278*	-.207*	-.085	-.221*	.244	-.084	-.159*	.027	.002	.023	-.113	.002	.149
DFR	139	xxxx	**.271****	.204	.032	-.025	.041	.120	.069	-.088	-.030	.011	-.083	-.087	.026	.001
AFR	136	176	xxxx	**.620*****	.058	-.066	.003	-.049	-.041	-.092	.009	.095	.100	-.096	.039	.147
AFP	62	75	107	xxxx	-.141	-.083	-.197	.197	.062	0	.031	-.060	.051	-.018	-.117	.199
uCFR	110	145	193	85	xxxx	.007	**.796*****	-.004	.061	-.192*	.083	-.093	-.136	-.049	-.026	-.025
lCFR	112	146	200	85	210	xxxx	**.610*****	-.057	.027	.108	.060	-.150*	-.033	.144	-.027	-.037
tCFR	102	136	181	79	210	210	xxxx	-.027	.096	-.119	.084	-.144	-.117	.015	-.042	-.032
PFR	52	53	62	31	45	47	44	xxxx	.037	.062	-.048	-.023	.112	.017	.153	.281
VFR	46	50	64	32	45	47	41	34	xxxx	-.112	.070	-.066	-.101	-.089	-.056	.159
PDV	157	163	175	78	124	129	112	64	63	xxxx	**-.395*****	-.072	-.056	**.329*****	.237**	.138
DV	134	161	173	80	129	133	118	55	59	194	xxxx	**-.407*****	-.200**	**.743*****	**.323*****	-.169
CV	135	181	215	95	171	174	157	57	58	176	184	xxxx	**.699*****	**-.516*****	**.685*****	.154
PAV	127	172	225	100	170	175	157	58	56	167	172	223	xxxx	**-.336*****	**.400*****	.151
PCV	121	140	156	74	113	117	102	52	50	183	183	167	155	xxxx	**.494*****	-.109
TV	114	142	155	73	118	122	107	47	45	173	165	169	158	167	xxxx	.075
hyp	101	123	159	74	139	139	126	43	44	118	117	149	148	105	110	xxxx

precaudal vertebrae, but not as strongly as number of caudal vertebrae is.

Number of both upper and lower caudal fin rays are significantly correlated with total number of vertebrae. Number of anal fin rays and number of anal fin pterygiophores are also significantly positively correlated. Finally, there is a significant positive relationship between number of dorsal fin rays and number of anal fin rays.

There was no correlation between total number of vertebrae and standard length ($F=1.122$, $n=121$, $p=0.29$) across the entire section. There was also no correlation between body depth and number of vertebrae ($F=-0.084$, $n=151$, $p=0.30$).

Temporal trends.--Some of the meristic features vary considerably over the 10 000 years represented by the H3 section, while others hardly vary at all (Fig. 3-5). Those characters that do vary, do so at different times and in different directions. All temporal trends are illustrated in Figure 3-5. Test statistics for each meristic series per millennium are too numerous to report here. All relationships that are reported as significant in Fig. 3-5 are significant to at least the $p<0.05$ level after sequential Bonferroni correction.

Total number of vertebrae does not change significantly across the entire section, nor are there any millennia with mean number of vertebrae that significantly differed from any other millennia. The smoothing function does not show any temporal trends other than a slight increase around the 4th or 5th millennium. The total change over the entire section in total number of vertebrae is about half a count (~1.2%). When the vertebrae are divided into subcounts, however, more obvious trends are evident.

The two basic subcounts of total number of vertebrae (caudal and precaudal) show some trends through the H3 section. Over the entire section, the number of precaudal vertebrae increases, but not significantly ($F=2.466$, $n=178$, $p=0.118$) and the number of caudal vertebrae decreases, but again, not significantly ($F=3.58$, $n=242$, $p=0.059$). Smoothing functions of the two characters show more variation in number of caudal vertebrae than in the number of precaudal vertebrae. The number of precaudal vertebrae increases slightly the first two millennia while number of caudal vertebrae decreases. Both counts then increase to the year 4000, at which point the number of caudal vertebrae decreases while the number of precaudal vertebrae remains relatively stable. The mean number of precaudal vertebrae is significantly lower for the first millennium than the 7th

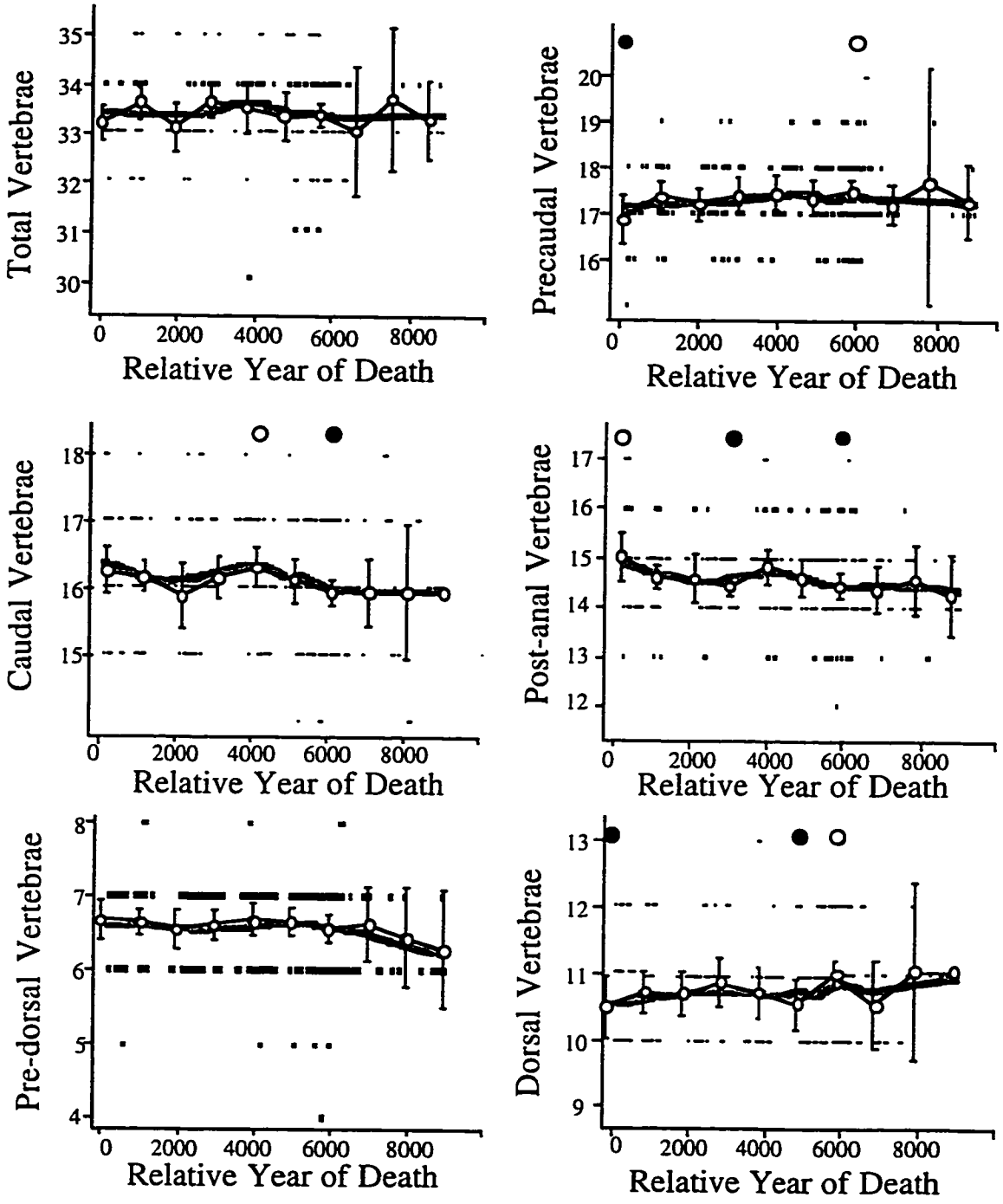
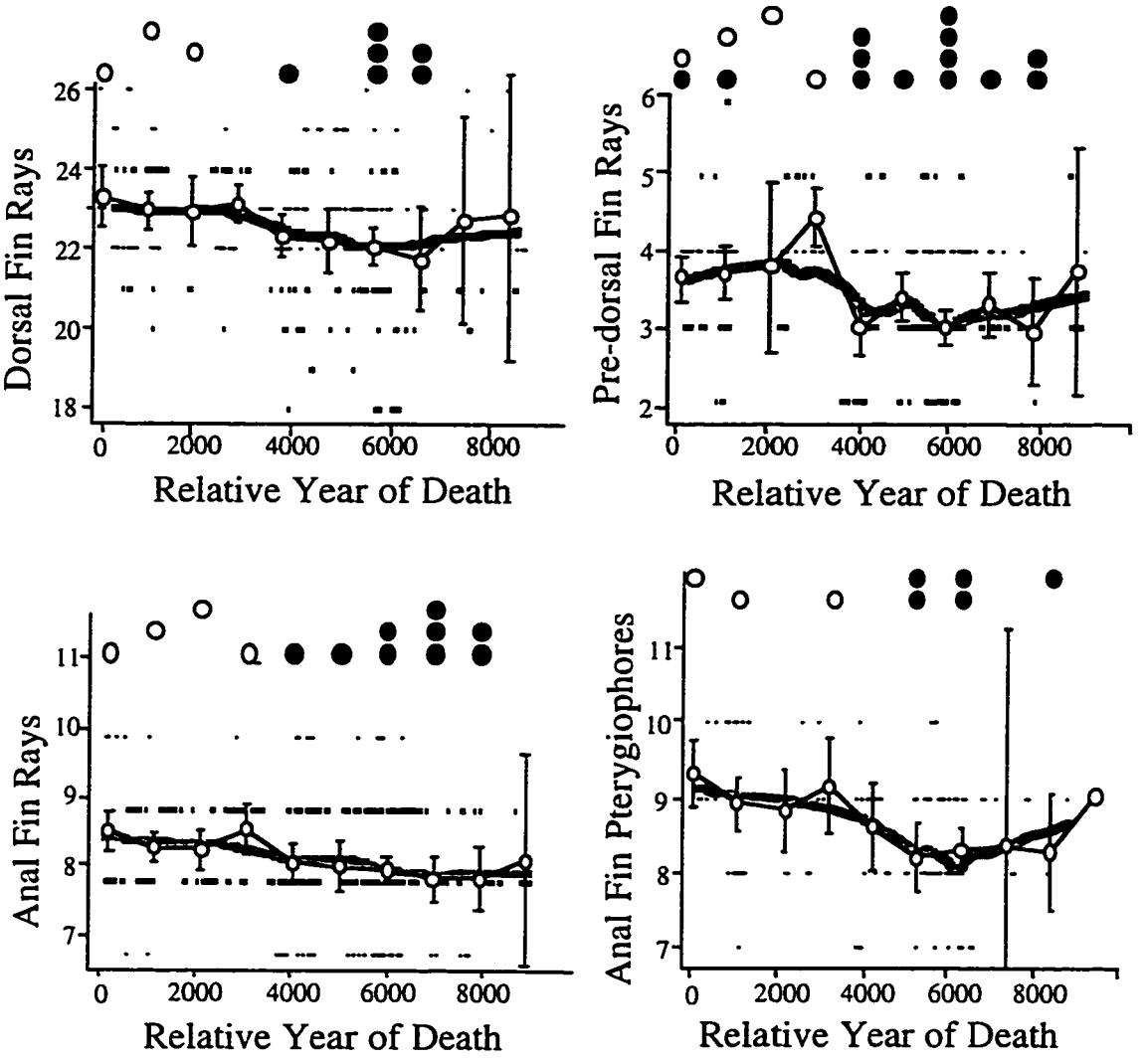


Figure 3-5: Temporal trends in meristic characters through the 10 000 years represented by the H3 section of the Horsefly locality, British Columbia. Individual points represent actual data points. Circles joined by lines represent mean values for each millennium with 95% confidence intervals indicated by bars. Millennia with significantly different means ($p<0.05$) are indicated by the black and white circles at the top of each plot; open circles represent millennia with significantly higher means than the black circles on the same line. Thick gray line represents the LOWESS smoothing function of the original data points (span 20%). Continued on following two pages.



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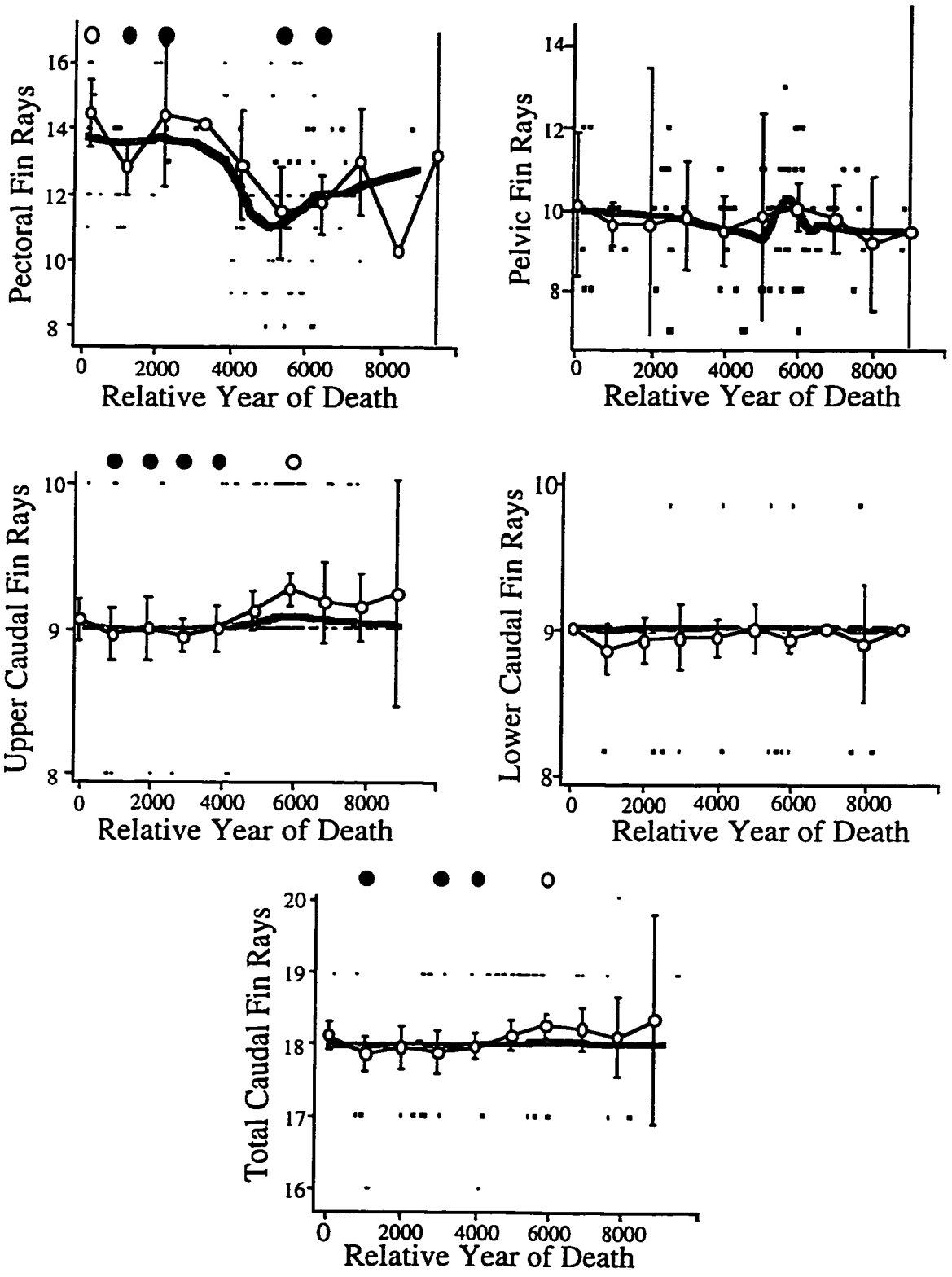


Figure 3-5 continued...

millennium, and the mean number of caudal vertebrae is significantly higher in the 5th millennium than in the 7th millennium. The amount of change in both subcounts is about 1/3 of a count (~2% each).

Number of post-anal vertebrae and number of caudal vertebrae, which both indicate changes in the caudal region, show very similar trends. However, only the number of post-anal vertebrae decreases significantly through the section (F=4.729, n=247, p=0.031). As with number of caudal vertebrae, number of post-anal vertebrae decreases until about the year 2000, increases to about the year 5000 and then decreases to the end of the section. Total change across the section is half a ray (~3.4%). Mean number of post-anal vertebrae in the first millennium is significantly higher than in the 4th and 7th millennia.

Number of precaudal vertebrae can be further subdivided into predorsal and dorsal vertebrae. There are no significant trends in either variable across the entire section (predorsal: F=0.608, n=242, p=0.436; dorsal: F=2.803, n=204, p=0.096). The smoothing functions, however, appears to show a decrease in number of predorsal vertebrae during the last three millennia, and an increase in the number of dorsal vertebrae during the last four millennia (the total change across the entire section is half a ray each: 7.6% and 4.8% respectively). Mean number of dorsal vertebrae in the seventh millennium is significantly higher than in the first and sixth millennia.

Number of dorsal fin rays decreases significantly across the entire section (F=10.89, n=212, p=0.001). The smoothing function shows that most of that decrease occurs between the 3rd and 7th millennia, and that there is a total change of about 1 count through the section (4.5%). The mean values for dorsal fin rays of the first three millennia are significantly different than the means of at least one (up to three) millennium between the 5th and the 8th millennia.

Number of predorsal fin rays also decreases significantly through the entire section (F=15.03, n=187, p<0.0001). LOWESS function shows that most of that decrease occurs between the years 3000 and 5000 (total change of 0.8 rays, or 23%). There are many significant differences between means for different millennia; in particular, the fifth through ninth millennia are significantly lower than some of the earlier millennia, and the fourth

millennium has a particularly high mean number of predorsal fin rays.

Number of anal fin rays also decreases significantly through time ($F=16.4$, $n=293$, $p<0.0001$). The smoothing function shows a general slow decrease through time. The total change over the entire section is about half a ray (6.2%). The first four millennia are significantly higher than at least one of the millennia between 5 and the end.

Number of anal fin pterygiophores (the only set of pterygiophores that I counted) was remarkably variable over time, especially compared to fin rays with which they are associated. Number of anal pterygiophores decreases significantly through time ($F=17.44$, $n=105$, $p<0.0001$). The smoothing function shows a gradual decrease until about the year 7000, followed by an increase to the end of the section. The total change over the section is one entire pterygiophore (12.5%). Millennia 1, 2 and 4 are each significantly higher than at least two of millennia 6, 7, and 9.

None of the counts for number of caudal fin rays (total, upper or lower) change significantly across the entire interval. Number of upper caudal fin rays is significantly higher in millennium 7 than in four other millennia; this is also reflected in total number of caudal fin rays, which is significantly higher in millennium 7 than in three other millennia. There appears to be a slight increase in number of caudal fin rays from the years 4000 to 6000, which is mirrored by an increase in number of upper caudal fin rays (total change of less than 1%). The number of lower caudal fin rays, however, is very stable through this interval.

Number of pectoral fin rays decreases significantly through the section ($F=11.69$, $n=85$, $p=0.001$). The smoothing function shows a dramatic decrease between the years 3000 and 5000, followed by a slight increase to the end of the section. The overall change across the section is two entire rays (17%). The first and third millennia have significantly higher mean numbers of pectoral fin rays than do the second, sixth and seventh millennia.

Number of pelvic fin rays does not significantly change from the start to the end of the section ($F=0.080$, $n=81$, $p=0.778$). The smoothing function shows a strong peak about the year 6000 (overall change of 1 entire ray, 10%, within one millennium), but otherwise little change through time. There is no millennium with a significantly different mean number of pelvic fin rays than any other millennium.

The two principal component analyses revealed some trends that were not evident by comparing individual meristic counts. Some 69% of the variation in number of dorsal fin rays, number of anal fin rays, number of dorsal vertebrae, and number of caudal vertebrae was explained by the first two principal components (Fig. 3-6). The first principal component, which accounts for 38% of the variation, is strongly positively weighted on number of caudal vertebrae and negatively weighted on number of dorsal vertebrae, and therefore is indicative of the relative division between the precaudal and caudal region. Temporal trends of this component show an increase until about the year 4000, followed by a decrease to the year 6000. The second principal component, which accounts for 31% of the variation, is strongly positively weighted on fin ray counts.

Some 68% of the variation in number of dorsal fin rays, number of dorsal vertebrae, number of predorsal vertebrae, and total number of vertebrae is explained by the first two principal components (Fig. 3-7). The first principal component, which accounts for 35% of the variation, is heavily weighted on predorsal vertebrae and negatively weighted on dorsal vertebrae, but with little weight on total vertebrae, likely indicates changes in the insertion of the dorsal fin. These changes are also likely associated with the length of the dorsal fin, as this is also fairly strongly correlated with these changes. Temporal trends of this component are stable to the year 3000, at which point they increase to the year 6000, and then decrease to the end of the section. The second principal component, which accounts for 33% of the variation, is strongly weighted on total number of vertebrae and positively weighted on both vertebral subcounts; therefore, it is likely indicative of changes in the total number of vertebrae.

715-year interval.--The 715-year interval with the greatest density of specimens occurs between the years 3800 and 4515 (Fig. 3-8). Meristic characters in this interval are highly variable (Fig. 3-8). This is partly due to the small number of data points. The span of smoothing functions is based on a percentage of the data (Velleman 1992); therefore, if there are fewer data points, the span will include fewer points. If there is much scatter in the data, false trends are more likely to appear if there are fewer data points from which to calculate the smoothing function. For these same reasons, temporal trends will tend to be exaggerated by the smoothing functions compared to those seen over the entire section.

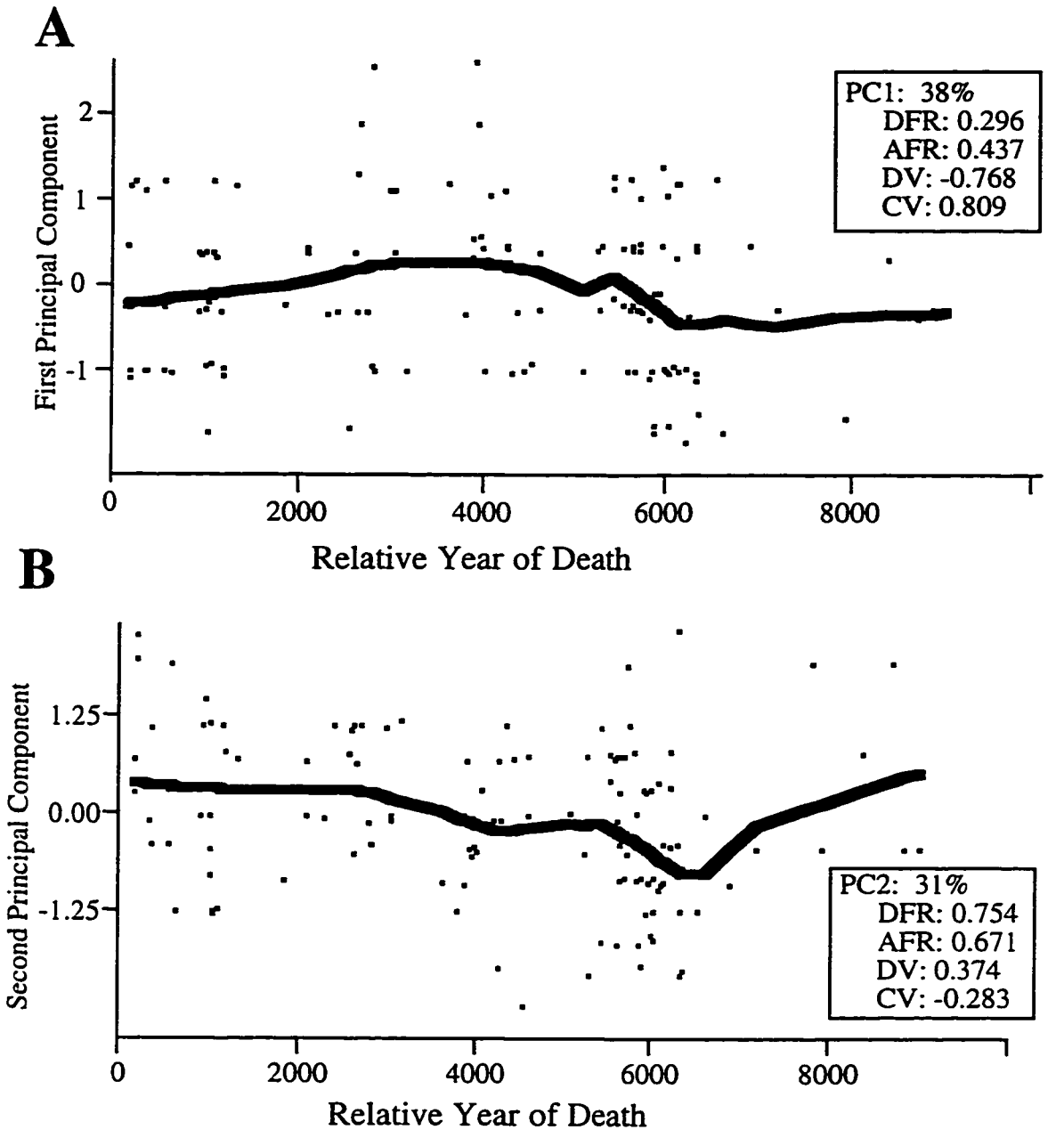


Figure 3-6: Results of a principal components analysis of meristic counts of dorsal fin rays, anal fin rays, dorsal vertebrae and caudal vertebrae plotted against relative year of death. The first prinicpal component (A) is strongly weighted on vertebral counts, and reflects the changing position of the division between precaudal and caudal vertebrae. The second principal component (B) is strongly weighted on fin ray counts, and might be indicative of ecophenotypic change (see text).

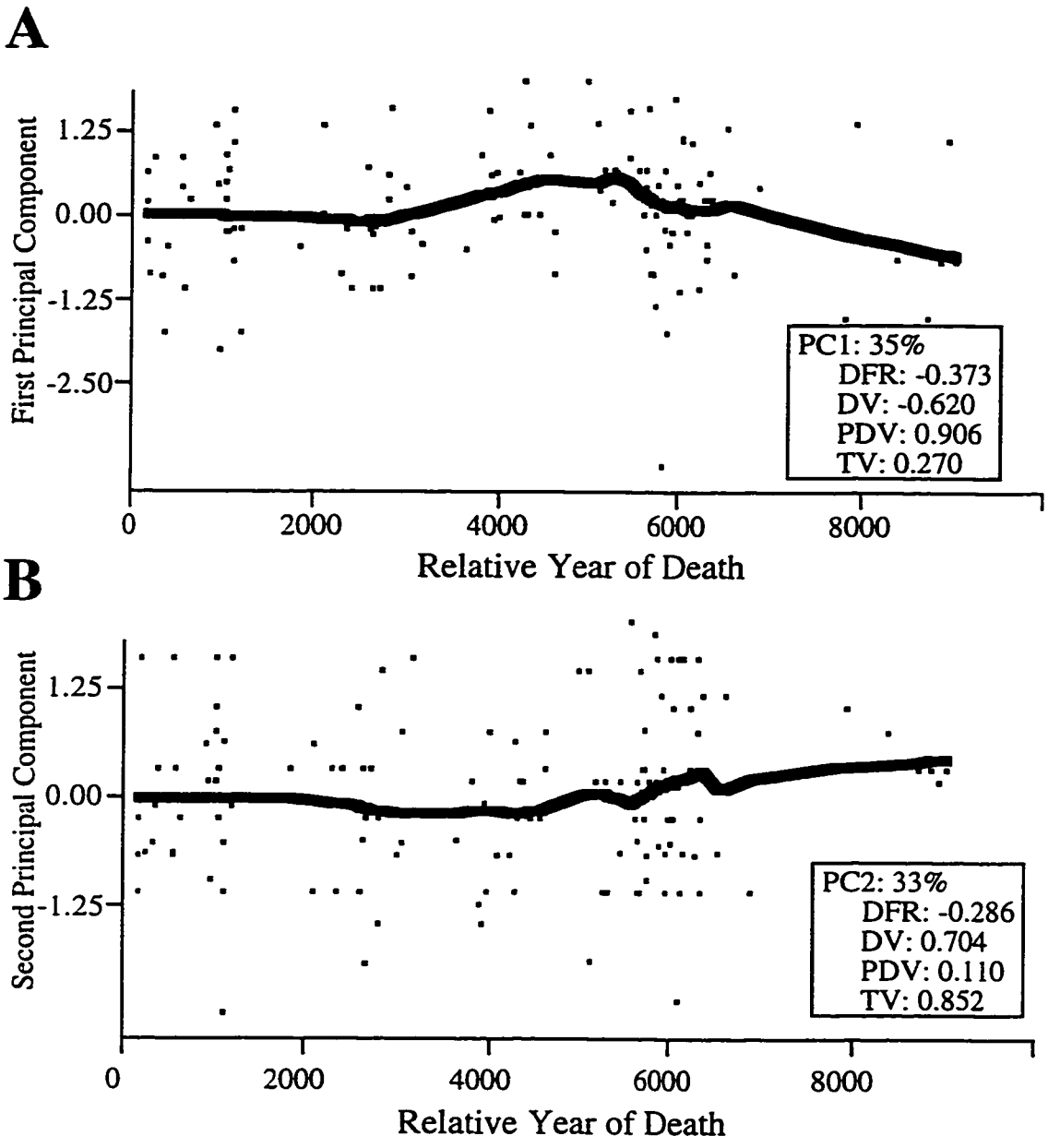


Figure 3-7: Results of a principal component analysis of meristic counts of dorsal fin rays, total vertebrae, dorsal vertebrae and predorsal vertebrae plotted against relative year of death. The first principal component (A), which explains 35% of the variance, is heavily weighted on dorsal and predorsal vertebrae, and therefore reflects the changing position of the insertion of the dorsal fin. Changes appear to be partly due to changes in the length of the dorsal fin, as this is positively correlated with dorsal vertebrae counts and negatively correlated with predorsal vertebrae counts. The second principal component (B), which explains 33% of the variance, is strongly weighted on total vertebrae, and therefore indicates changes in the total number of vertebrae (including subcounts).

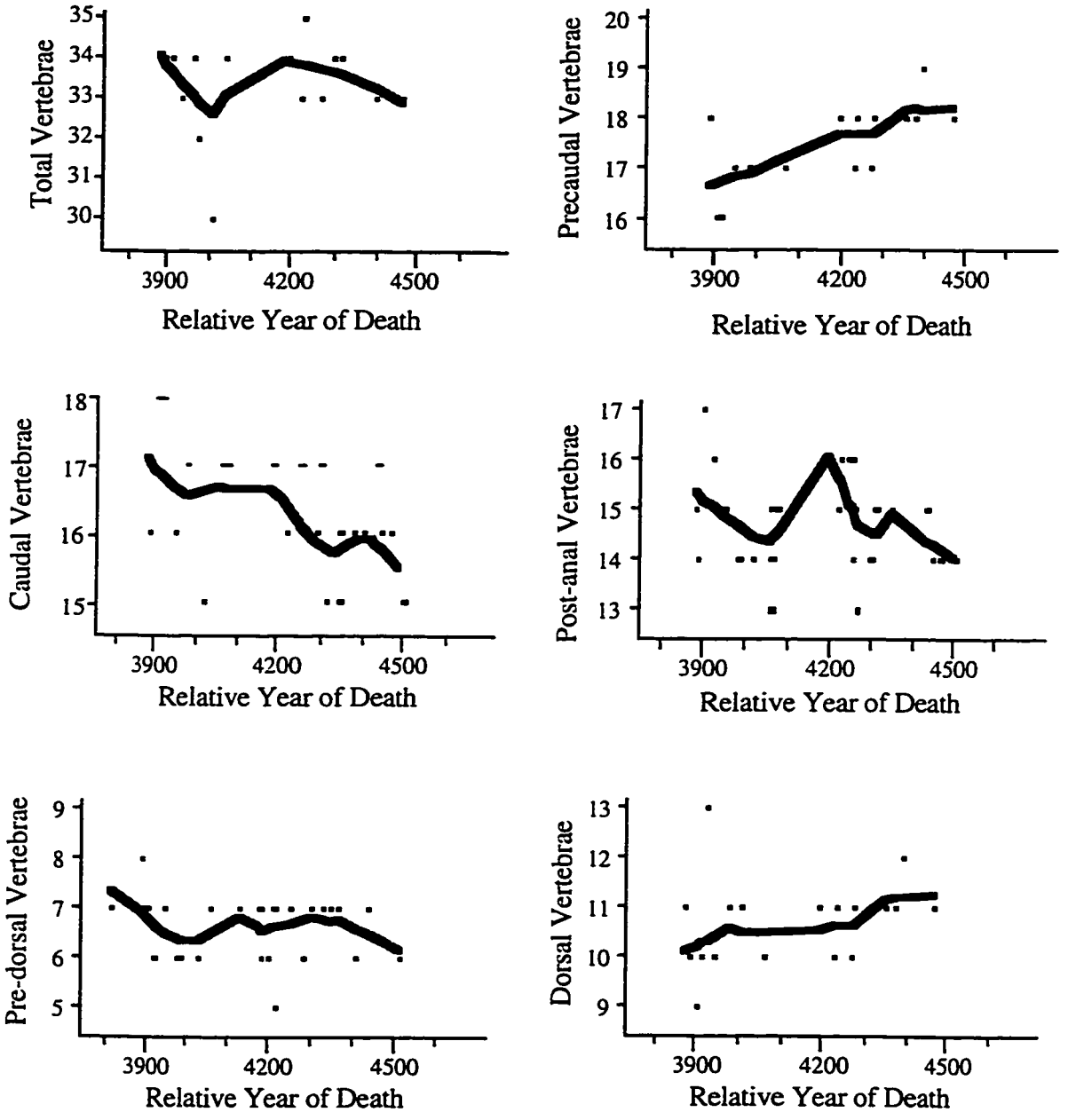


Figure 3-8: Temporal trends across a 715-year interval of the H3 section of the Horsefly locality, British Columbia. Lines indicate LOWESS smoothing function of the data points. Sample sizes are low so trends are exagerated relative to Fig. 3-5. Continued on next page.

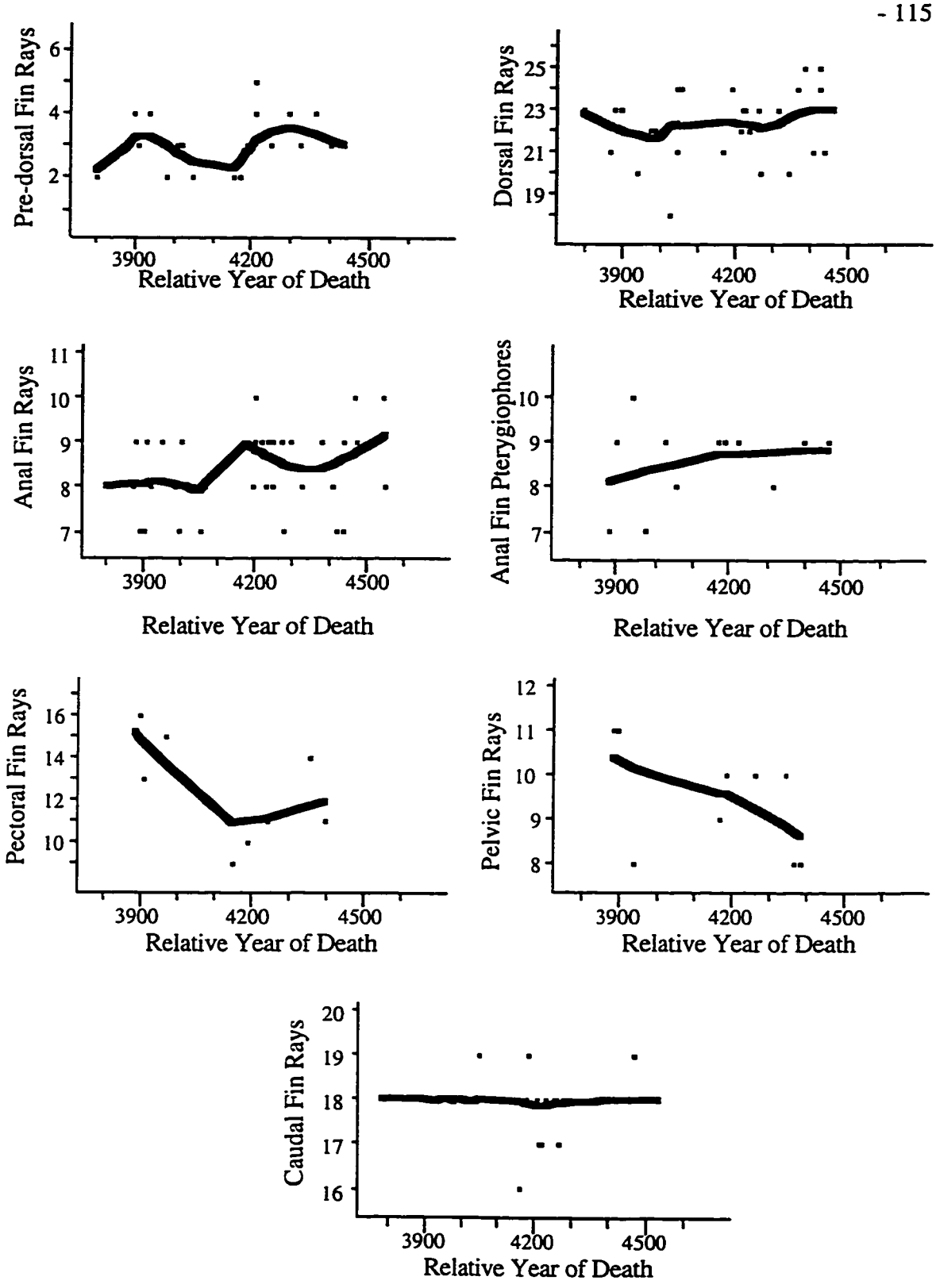


Figure 3-8: continued...

Despite these problems, there are some fairly clear temporal trends in the data. As with the longer interval, meristic characters change at different times, and in different directions.

Discussion

Repeatability

As Lee (1990: p. 31) points out, the "conclusions of literally thousands of ecological, evolutionary and, especially, systematic studies are based wholly or in part upon inferences drawn from the analysis of meristic characters", yet few authors have investigated the precision (repeatability) associated with these counts. Although there are standard methods of counting meristics, there is often some interpretation required on the part of the observer. Sometimes meristic elements within a series are incompletely developed, forcing the observer to judge whether such elements should be included in counts (Lindsey 1988). Previous studies of repeatability of meristic counts have been restricted to extant groups (Nisbet *et al.* 1970; Lee 1982, 1990; Hubert and Alexander 1995). Repeatabilities of meristic series on extant groups, however, should be higher than those of fossil groups for several reasons. Meristic series can be affected by processes of preservation (including compaction and disarticulation) in fossil groups, which will also decrease the confidence that we can have in such counts. Many fossil groups are known from only a few specimens, often resulting in less-than ideal counts being included in meristic studies on fossil groups. The repeatability of meristic counts of extant groups, therefore, cannot be used to estimate the repeatability that should be expected on fossil groups.

The effects of inter-observer variation on meristic counts of extant groups are well-known (Nisbet *et al.* 1970; Lee 1982, 1990; Hubert and Alexander 1995). A (sometimes) less severe (but just as common) problem that is rarely addressed is that of intra-observer variability (Hubert and Alexander 1995). In a study of extant fishes (Hubert and Alexander 1995), intra-observer repeatability ranged from 36% (for counts of mandibular pores) to 86% (for counts of pectoral fin rays). Counts of some observers had lower repeatabilities than others, but all of the observers were trained and experienced at counting meristics in

fishes. The authors of this study did not include counts of median fin rays and vertebrae, which might be expected to have higher repeatabilities.

Intra-observer repeatability in this study was higher than might be expected in other paleontological studies because I had the luxury of discarding counts that were somewhat ambiguous. Pectoral and pelvic fin ray counts had the lowest repeatabilities, likely because paired fins were often preserved with both sides superimposed. These were also the counts with the fewest data points, indicating that many specimens were excluded because of recognized ambiguity. Repeatabilities of median fins and vertebrae, which were generally easy to count, were high. Number of dorsal and number of caudal vertebrae had the lowest repeatabilities within the vertebral subcounts. This is probably a reflection of the difficulty in identifying the division between the caudal and precaudal regions. The first complete haemal spine is often difficult to identify, especially if there are also ribs associated with the same centrum.

Any study that depends on the accuracy of meristic counts should also include tests of repeatabilities of those counts as a gauge of the confidence that can be placed in the results. Such tests of repeatability, however, are rare in meristic studies. Results of these and other repeatability studies (Hubert and Alexander 1995) suggest that extreme care be used when using meristic data (for example, describing a new species based only on meristic counts, especially counts with particularly low repeatabilities such as pectoral fin rays).

In this study, intra-observer variability alone is not enough to account for the entire range of variation in meristic features through the H3 interval. Repeatabilities of only 15 to 25% of the counts are off by (usually) one element, yet temporal trends generally vary over at least half an element over the interval. Pectoral fin rays and pelvic fin rays were the only counts with repeatabilities less than 75%, however, temporal variation in these characters is much greater than the other characters (two and one entire ray, respectively). The magnitude of temporal trends across the H3 section is too large to be caused by variation due to intra-observer variability alone.

Summary Statistics

The range of variation in most meristic series of *A. aggregatum* from the H3 interval is as large as the range of these series across the entire geographic range of the species. This is probably partly due to the large number of specimens used in this study (relative to the number of specimens that have been included in previous studies). Much of this range, however, is due to phenotypic change in these characters through the H3 interval.

Many of the counts reported here extend the published ranges of meristic series of *A. aggregatum* (Wilson 1974, 1977a; Bruner 1991) (see Table 3-2). The counts and means reported here raise some interesting observations and questions about relationships of species within the genus. A full revision of the genus is beyond the scope of this chapter, but I will highlight some of the areas of concern that should be addressed in any future work.

A. gosiutensis.--My results support Bruner's (1991) synonomyzation of *A. gosiutensis* Grande *et al.* (1982) from the Green River Formation of the west-central United States with *A. aggregatum*. Bruner (1991) points out that many of the differences between the two species were due to a misquoting of the original ranges of meristic counts of *A. aggregatum* by Grande *et al.* (1982). Bruner (1991) then reanalyzed the data and found only three characters to be significantly different between *A. gosiutensis* and *A. aggregatum*: number of principal anal fin rays, caudal peduncle length/standard length ratio, and total number of vertebrae. I will re-examine each of these differences here, including a specific comparison to specimens of the H3 section.

The range of number of anal fin rays of *A. gosiutensis* is completely within the range originally reported for *A. aggregatum*, but mean values are significantly different. Specimens of the H3 section, however, have higher numbers of anal fin rays than those in the original description of the species, and are therefore closer to those of *"A. gosiutensis"*. Sample variances of "*A. gosiutensis*" and *A. aggregatum* from the H3 section are not significantly different ($F=1.30$, $p>0.05$); therefore, the *t*-test is an appropriate comparative test. Mean number of anal fin rays of "*A. gosiutensis*" and *A. aggregatum* specimens from this study are not significantly different ($t=1.82$, d.f.=313; $p>0.05$).

Caudal peduncle depth to standard length ratio was found to be greater in specimens of *A. gosiutensis* than in *A. aggregatum* (Bruner 1991). Because I did not measure any body

dimensions other than standard length and body depth, I cannot directly compare Green River specimens with those from the H3 section. The reported difference between the species, however, was only significant at the p~0.01 level. If the sequential Bonferroni technique is used to correct for the number of statistical comparisons used by Grande *et al.* (1982), this value is no longer statistically significant.

The final character that Bruner (1991) found to distinguish *A. gosiutensis* from *A. aggregatum* is total number of vertebrae. Total number of vertebrae reported here for *A. aggregatum* of the H3 section is statistically different from the total number of vertebrae in the Green River Formation *Amyzon* (t-test, t=10.86, d.f.=187, p<0.0001). This study does, however, extend the range of total number of vertebrae for *A. aggregatum* to 30-37 (+ 4 Weberian). Therefore, the range of vertebral counts vertebrae of "*A. gosiutensis*" now falls completely within that of *A. aggregatum*. I agree with Bruner's explanation (1991) that the difference between the mean number of vertebrae can be explained by "Jordan's rule", the generalization that more northerly representatives of a species (at least in the northern hemisphere) tend to have higher vertebral counts than southerly members of the same species (Jordan 1892). This phenomenon is now better understood as being a function of temperature of development, and can be better stated as a trend for number of vertebrae to be negatively correlated with temperature at spawning time (Resh *et al.* 1976; Peden 1981; Lindsey 1988). The most common vertebral responses to increased temperature in many different species of fish are negative or V-shaped (references in Lindsey 1988). All else being equal, fishes of the same species that develop in colder water should therefore have higher vertebral counts. The climates during deposition of the Green River Formation and the Horsefly deposits were likely quite similar, although some fossil evidence suggests that the Green River Formation might have been warmer (*e.g.* the presence of palm fronds in the Green River Formation).

Given the variability that can exist in the number of vertebrae across the range of a species, it is not a good character on which to distinguish species, especially those that are separated by a large geographic difference. Because total number of vertebrae is the only character left to distinguish specimens of *Amyzon* of the Horsefly deposits from those of the Green River Formation, I strongly support Bruner's (1991) synonomyzation of the two

forms.

The H3 section is slightly younger than the H2 section, which are both dated as middle Eocene. Within the Green River Formation, specimens of *Amyzon* are found only at the base of the middle Eocene. In many meristic counts, however, specimens of the H3 section seem to be intermediate between those of the H2 section and those of the Green River Formation. This suggests an interesting geographic and temporal pattern of phenotypic variability in the species, but these questions cannot be addressed without better dating of the Horsefly sediments and a comparison to other localities of North America.

A. brevipinne.--*A. brevipinne* is the only other species in the genus conclusively known from the Eocene of British Columbia. The most significant difference between *A. brevipinne* and *A. aggregatum* is dorsal fin ray count, which can be used as a "sort of discriminant function with considerable confidence" to differentiate between the two species (Wilson 1974: p. 127). Dorsal fin ray counts for *A. brevipinne* range from 12-20 with a mean of 15.6 (note that the counts in the original description of the species [Cope 1894] are about 3 higher than would be counted by modern conventions [Wilson 1974] and are therefore not included in the ranges reported in Bruner [1991] or here). Dorsal fin ray counts of *A. aggregatum* from the H3 section range from 18-26 with a mean of 22.5. The mean dorsal fin ray count for specimens from the H3 interval is one ray lower than that reported for the species (Wilson 1977a). More importantly, the counts reported here include specimens with as few as 18 dorsal fin rays, overlapping significantly with the upper end of counts of *A. brevipinne*. In addition, I have counted some specimens attributed to *A. brevipinne* with up to 21 dorsal fin rays (unpublished data).

The other main character that distinguishes *A. aggregatum* from *A. brevipinne* is its "greater body depth to standard length ratio which is reflected in various other ratios [...]" (Wilson 1974: p. 261). The differences related to different body depth, however, might be a result of heterochronic development and taphonomic biases of the sites in which they are preserved. Specimens of *A. brevipinne* are much smaller than those of *A. aggregatum* (Wilson 1974, 1977a; Bruner 1991). In a preliminary study of 28 specimens of *A. brevipinne* from various sites around British Columbia, the standard length of specimens was 19.0 - 83.7 mm. with a mean of 38.1 mm (±2.8 standard error) (unpublished data).

Occasionally the deposits containing *A. brevipinne* (interpreted to be relatively shallow) also contain isolated bones of a large catostomid. Standard lengths of the specimens from the deep H3 deposits (this study) were 45-243 mm. with a mean of 151.0 mm. (±3.6 s.e.) (n=157) (with few small individuals preserved). Therefore, *A. brevipinne* is only known from small individuals, and *A. aggregatum* is known almost exclusively from large individuals. Future study should attempt to investigate whether *A. brevipinne* is a "dwarf species", or whether large individuals are simply not preserved. Future study should also compare small specimens of *A. aggregatum* with specimens of *A. brevipinne* to ensure that the differences in body proportions apply to young individuals of *A. aggregatum* as well.

Correlations

Of the 15 correlations between meristic counts that were statistically significant in this study, 14 can be explained by a lack of independence of characters. Eleven of the significant relationships involved two different vertebral counts, (which are all interdependent); two involved caudal fin ray subcounts that make up the total caudal fin ray count; and one involved the combined anal fin ray and pterygiophore series (which are closely associated during development). The only completely independent characters to be significantly correlated in this study are number of dorsal fin rays and number of anal fin rays.

Bell *et al.* (1985) found positive significant correlations among all four of the meristic characters that they measured on sticklebacks (dorsal fin spines, predorsal pterygiophores, dorsal fin rays and anal fin rays). The authors attempted to correct for temporal trends in these features by fitting time series to regression lines, but the correlations remained significant. However, complex time series cannot be fully expressed as regressions, and therefore all temporal data cannot be eliminated from the data. Even without correcting for temporal trends, most independent characters in this study were not correlated. Possible explanations for this are discussed below.

There was no evidence of pleomerism (positive correlation between vertebrae and standard length or negative correlation between body depth and vertebrae) through the H3

section. Lindsey (1975) found such correlations in different groups (populations, species, genera) within higher taxa. Reimchen and Nelson (1987) found some examples of pleomerism in populations within a species over several years, but these were largely due to microhabitat differences. This study, however, found no evidence of pleomerism within one population within a single habitat through a long period of time.

Temporal Trends

Temporal scale of variability.--Meristic series appear to vary over the 715-year interval, although there are few specimens in this sample. There is also temporal variation in meristic features over the 10 000 years represented by the H3 section. The considerable temporal variation in meristic counts (possibly on two different time scales) over this interval suggests that most other sediments (with lower temporal resolution) will be subject to temporal averaging of phenotypic variation.

Variability of meristic series.--Although total number of vertebrae did not change dramatically over the section, there were some interesting trends in the subcounts. An increase in total number of vertebrae can be caused by an increase in number of precaudal vertebrae, an increase in number of caudal vertebrae or increases in both. Numbers of both caudal vertebrae and precaudal vertebrae are positively correlated with total number of vertebrae, but the correlation is much stronger with caudal vertebrae. A comparison of the meristic series through time also indicates that changes in total vertebrae are almost always associated with changes in number of caudal vertebrae (more so than number of precaudal vertebrae). This suggests that the caudal region is the more plastic part of the vertebral column.

A strong negative correlation between caudal vertebrae and precaudal vertebrae suggests that the relative position of the caudal region is somewhat variable. Such changes are not evident when examining temporal trends of each feature individually, but a principal component analysis of number of dorsal fin rays, number of anal fin rays, number of dorsal vertebrae, and number of caudal vertebrae (Fig. 3-6) reveals that the first principal

component is weighted heavily on caudal vertebrae and dorsal vertebrae but with little weight on total number of vertebrae. The first principal component, therefore indicates relative changes in the position of the caudal region. This principal component shows some temporal trends between the years 4000 and 7000 where the precaudal region appears to get longer at the expense of the caudal region.

Although the caudal region is more variable than the precaudal region, there are changes in the precaudal region of the vertebral column as well. Number of precaudal vertebrae is strongly correlated with number of dorsal vertebrae, and much less strongly correlated with number of predorsal vertebrae. Temporal trends in precaudal vertebrae are also accompanied by changes in number of dorsal vertebrae. This suggests that number of dorsal vertebrae is more plastic than the number of predorsal vertebrae. The relative position of the dorsal fin appears to also be somewhat plastic, as indicated by the first principal component of number of dorsal fin rays, number of dorsal vertebrae, number of predorsal vertebrae and total number of vertebrae (Fig. 3-7). The smoothing function of these elements indicates a posterior movement of the dorsal fin by about half a vertebrae (Fig. 3-5).

Within the entire vertebral column, the caudal elements are more plastic than the precaudal vertebrae. Within the precaudal vertebral region, any variation that occurs is due to changes in dorsal vertebrae (the more posterior elements). This study, therefore, indicates that any change in total number of vertebrae is more likely to occur at the posterior end of the fish. Ontogenetic studies have shown that the posterior end of the vertebral column of fishes is last to become ossified (with the exception of the last few vertebrae) (Itazawa 1963; Nagiec 1977; Lindsey 1988; Grande and Bemis 1998). Within the vertebral column, therefore, the last elements to ossify (the more posterior elements) are the more phenotypically plastic.

Variability of median fins, especially dorsal and anal fins, is much greater than that of number of vertebrae. Total number of caudal fin rays, which is the least variable of the median fin counts, appear to be most affected by changes in number of rays in the upper half of the fin. Lindsey's (1988) review of meristic experiments demonstrated that there is some ecophenotypic variability in caudal fin rays, but this was the least studied meristic

series. In sucker larvae (Catostomidae), which are free-swimming relatively early in development, the the ventral lobe of the caudal fin is the first to ossify (Lindsey 1988). Therefore, as with vertebrae, the last elements to develop in the caudal fin are also the most phenotypically plastic.

Finally, temporal variation was highest in the paired fin series. The repeatabilities of these counts were low, so any generalizations made from these data should be made with care.

Based on Lindsey's review of the embryogenesis of meristic traits (1988), I proposed in the introduction a gradient of meristic series from earliest to fix and most regimented to latest to fix and least regimented: paired fins, median fins, and then vertebrae. The meristic series that were used in this study certainly appear to follow this trend. The most variable series are the paired fins, with net changes of 10% and 17% through the interval. Median fins are less variable, with net changes of 4.5% to 6.2% through the interval. Finally, total number of vertebrae was relatively invariant through the H3 section, with a net change of 1.2% through the interval.

Comparison to environmental changes.--In chapter 2, I reconstructed paleoenvironmental changes in and around the lake represented by the H3 section based on changes in the preservation of the fishes (Fig. 3-9). Fishes from the H3 section are deposited at or near the bottom of a deep, usually stratified lake; therefore, reconstructions based on these fishes are most indicative of conditions on the bottom of this lake. The H3 deposit, however, contains few small individuals (almost no individuals less than a year old; see Wilson 1984), which suggests that the juveniles lived in a different part of the lake not represented in the currently exposed Horsefly deposits. Lakes, however, are relatively tightly linked ecosystems; therefore, changes in one part of a lake are more often than not associated with other changes in other parts of the lake. It is therefore worth comparing environmental and meristic trends through the H3 section for any consistent patterns.

The most obvious interval of change in meristic series occurs during the middle of the H3 interval, from the years 3000 to 6000, when most meristic series decline. This trend is illustrated most dramatically by pectoral fin ray count, but can also be seen in pelvic fin rays, dorsal fin rays, anal fin rays and anal pterygiophores. Number of vertebrae also

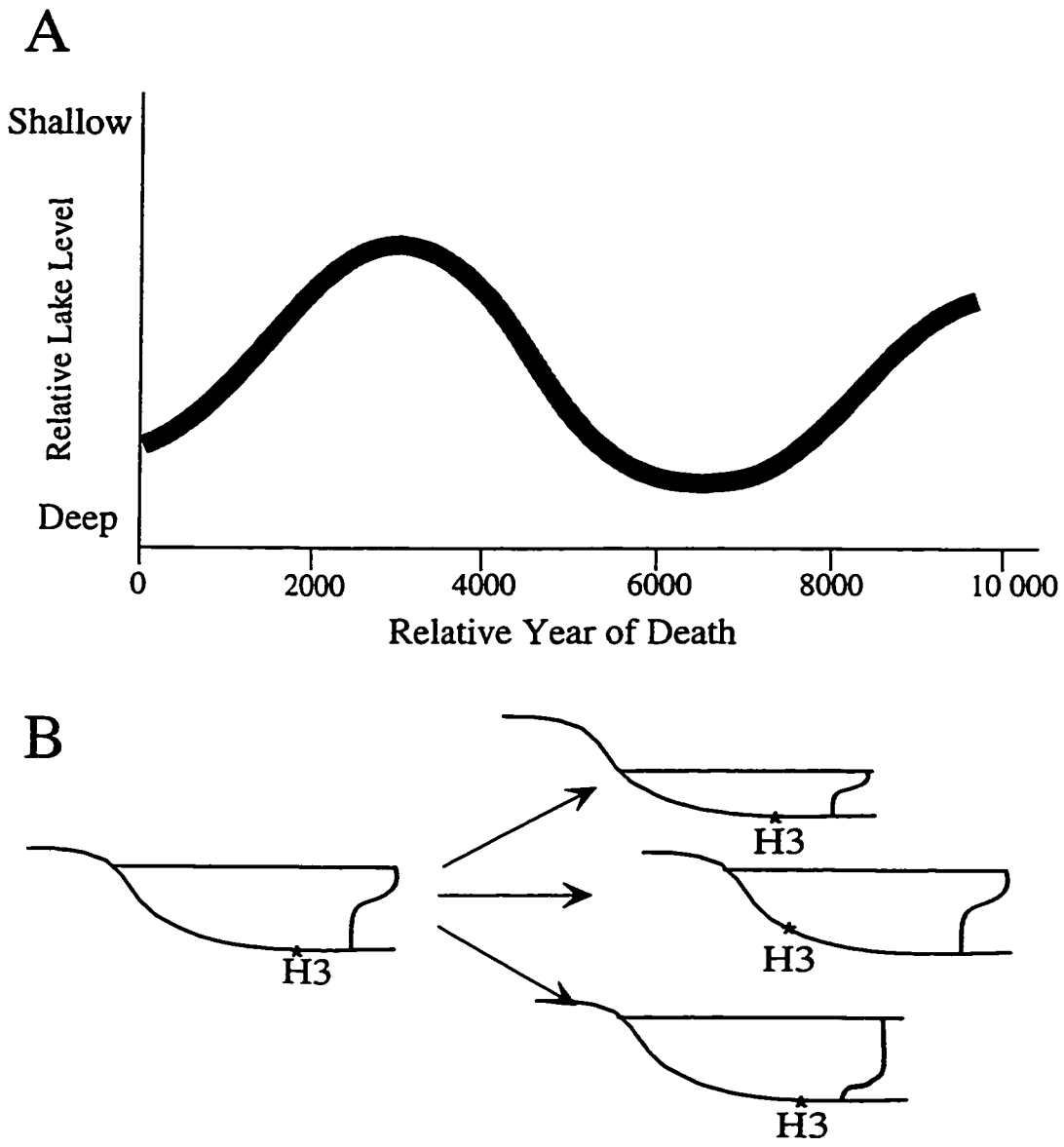


Figure 3-9: Relative changes in lake levels as reconstructed from changes in preservational patterns of fossil fish. A: Reconstructed relative lake level changes through the 10 000 year section represented by the H3 interval. B: Three different ways that the H3 section can become shallower. The position of the H3 deposit is indicated by the asterix, and the thermocline (and/or chemocline) by the gray line on the right. The entire lake can shallow (top), the lake can shift so that the position of the H3 section is more shallow (middle), or the thermocline can drop (bottom). All of these situations have the same results on preservation of fishes.

show a similar trend, with decreasing mean number of vertebrae per millennium through this interval (although the smoothing function shows an increase in total number of vertebrae at the start of this interval). Perhaps most interestingly, a strong component of the variation of number of dorsal fin rays, number of anal fin rays, number of dorsal vertebrae, and number of caudal vertebrae seems to support this trend, with a temporal change over this interval (Fig. 3-6). This analysis was repeated several times substituting other meristic counts, with the same general results produced (not shown).

This interval of meristic change coincides with one of the most dramatic intervals of change in the paleoenvironmental reconstruction of the lake (illustrated by changes in the taphonomy of fishes). I have postulated a relative deepening of the H3 section between the years 3000 and 6000 to account for a decrease in the amount of scavenging and a decrease in the amount of partial flotation of specimens due to the build-up of decay gases (partial flotation increases in warmer waters) (Fig. 3-9; see chapter 2). Such a trend, even if it is only the depth of the H3 deposit within the lake that was changing (as I suggested in chapter 2), is an indication of a broader environmental change in or around the lake. This broader environmental change is also likely to have an effect on the micro-environment in which fishes are developing.

The most common response of all meristic characters to increased temperature of development is negative (lower meristic counts at higher temperatures) (Lindsey 1988). Many of the other responses, however, are arched or V-shaped, which can represent a negative response across most of the temperature range of the species but which reverses at one or the other temperature extremes. Several species in Lindsey's review (1988) have negative responses to increased temperature in all (or nearly all) meristic series (*e.g.* *Brachydanio rario* and *Onchorhynchus mykiss*). All of the other species have negative responses to temperature for most meristic series. The coincident decrease in nearly all fin ray counts and total vertebrae counts in the interval from the years 3000 to 6000 therefore is most easily explained by increased temperature of development.

The combined trends during this interval, therefore, are increased relative depth of the H3 section, and increased temperature of development (in shallow waters). Based on the available information, it is impossible to determine an overall causal factor for these

coincident trends. We can, however, speculate on what kind of causal factors could have these results. One possible environmental change that could cause increased temperature at development and increased relative depth of the H3 section is decreased mixing of the lake by wind. Decreased mixing would result in the level of the thermocline rising in the lake, with several results. The surface waters could heat much more quickly (less water to heat), therefore increasing the temperature at which fishes are developing. It would also result in the position of the H3 deposit becoming relatively deeper (further from the thermocline or chemocline). A second possible cause of these changes is an increased absolute depth of the lake to include more shallow breeding habitat for the fishes (for example, a rise in lake levels to fill a floodplain). These shallow habitats would warm rapidly, increasing the temperature of development of the fishes. The increased depth in the lake would account for changes in preservation of fishes at the bottom. There is far too little information to support these speculations, but they do indicate that there are environmental changes that can easily account for these coincident changes in environment.

Causes of meristic variation.--One of the most encouraging aspects of this study is the principal component analysis of the four meristic counts with the highest sample sizes. The second principal component, which accounts for 31% of the variation of the factors, appears to be an indication of ecophenotypic variation in meristic series. It is possible that this component is indicative of selective responses in the fish to the changing environment, but it is unlikely that such selective responses would include nearly all meristic series at the same time. The possibility, however, cannot be eliminated. Environment can affect different meristic series in different ways, but timing of changes should be similar. Thus we might expect that such an ecophenotypic component of variation in all meristic series should be able to be isolated. Once this component is isolated, the remaining variation in meristic series should be a result of either evolutionary change or of differential survival (that could eventually lead to evolutionary change). Ideally, every meristic series could be included in a principal component analysis, but this would require many more specimens (at least more complete specimens) than I used in this study.

If we can use the second principal component of Figure 3-6 as an approximation of ecophenotypic change in the H3 section, there appears to be little environmental influence

on meristic series through the first 3000 years of the H3 section. Any meristic change in this interval, therefore, is likely caused by either selective pressures for certain meristic counts (differential fitness) or by true evolutionary trends. There are few meristic series that do change in this interval, which might be an indication of relative stasis in these features.

Future study.--Unfortunately, any further attempts to link meristic change to environment or evolutionary change would be reading too much into the results presented here. The Horsefly locality, however, has a great potential to further investigate these relationships. Several specific future studies could contribute essential information to studies of phenotypic change through the H3 interval.

Firstly, a better understanding of the environment of the H3 site would be very useful (see also Chapter 2). Ideally, an exposure of the site lateral to the current H3 deposit representing a shallow portion of the lake (above the thermocline) could provide direct information about the environment in which the fishes are developing (and therefore in which meristic counts are being determined). A detailed study of the changes in material being deposited in the lake represented by the H3 section could also generate information about paleoenvironmental changes in the lake. A study of changes in diatoms, which have proven to be powerful indicators of environmental change in modern lake systems (*e.g.* Smol *et al.* 1991; Dixit *et al.* 1992; Hui 1996; Pan *et al.* 1996; Vyverman *et al.* 1996) could certainly provide further indications of directions of environmental change in the H3 section.

Even if every aspect of the environment were known throughout the entire history of the lake, there would still be gaps in our understanding of the effects of these environmental changes on meristic series. Lindsey and Arnason's (1981) atroposic model is a good first step in attempting to understand the relationship between meristic and environmental variables, but this model needs to be tested and validated before it can be of any use in studies such as these. It would also be interesting to know whether there were any phylogenetic patterns to meristic responses to changing environment. If there are, studies on extant catostomid species contribute a lot to our understanding of meristic changes in *Amyzon*. If more individuals of other species from the H3 locality could be

collected and analyzed for temporal trends in meristic counts, these patterns could then be compared to those of *Amyzon*. Even if specific meristic responses to changing environment of the two species differ, they should still show coincident meristic changes (possibly in different directions) during environmental change.

Finally, a large sample of complete individuals from the H3 interval would allow a complete principal component analysis on all the meristic series. Such an analysis could isolate ecophenotypic changes without any assumptions of directionality of meristic variation in response to environmental effects. Preliminary results of such a PCA reported here for a few meristic counts are encouraging, and suggests that there are intervals in which ecophenotypic changes is higher than in other intervals. A principal component analysis will also allow this ecophenotypic variation to be isolated (and removed), leaving only variation caused by other factors.

Conclusions

Varved lacustrine sediments from the Horsefly locality, British Columbia, are among the most promising localities for microstratigraphic studies of phenotypic change through time. A detailed microstratigraphic analysis of changes in meristic counts has generated several specific conclusions:

1. This study addresses some of the problems caused by low repeatabilities of meristic counts. Some characters are much easier to count (and have greater repeatability) than others, and care should be taken when using meristic counts in any study.
2. This study includes some extensions to published ranges of meristic counts in *Amyzon aggregatum*. These results strongly support Bruner's (1991) synonomyzation of "*A. gosiutensis*" with *A. aggregatum*, and also suggest that further work be done to distinguish *A. brevipinne* from *A. aggregatum*.
3. Few (independent) meristic counts were correlated (either positively or negatively) with each other in specimens of *Amyzon aggregatum* from the H3 interval of the Horsefly locality. There is no evidence of pleomerism through the H3 interval.

4. Meristic series that are the first to develop ontogenetically also tend to be the most phenotypically plastic in specimens of *Amyzon* from the H3 interval.

5. Within the H3 interval, there are clear temporal trends over two different time scales (centuries and millennia) in some meristic series. Many of these trends were likely caused by ecophenotypic responses of meristic series to environmental changes. The most obvious interval of meristic change in the middle of the H3 interval, which is likely mostly caused by ecophenotypic changes, corresponds to the interval of greatest environmental change in the lake. There are intervals, however, in which ecophenotypic variation is low, and meristic variation is likely due to either evolutionary changes in the fishes, or a differential fitness associated with certain meristic counts that might eventually lead to evolution. Before more precise patterns and rates of evolution can be determined, however, more has to be learned about the relationships between environment, genetics and determination of meristic counts.

Literature Cited

Algeo, T. J. 1993. Quantifying stratigraphic completeness: a probabilistic approach using paleomagnetic data. Journal of Geology 101:421-433.

Anders, M. H., S. W. Krueger, and P. M. Sadler. 1987. A new look at sedimentation rates and the completeness of the stratigraphic record. Journal of Geology 95:1-14.

Anderson, R. Y., and W. E. Dean. 1988. Lacustrine varve formation through time. Palaeogeography, Palaeoclimatology, Palaeoecology 62:215-235.

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes. Systematic Zoology 10:105-117.

Beacham, T. D. 1991. Developmental stability, heterozygosity, and genetic analysis of morphological variation in pink salmon (*Onchorhynchus gorbuscha*). Canadian Journal of Zoology 69:274-278.

Beacham, T. D., and C. B. Murray. 1986. The effect of spawning time and incubation temperature on meristic variation in chum salmon (*Onchorhynchus keta*). Canadian Journal of Zoology 64:45-48.

Beardmore, J. A., and S. A. Shami. 1976. Parental age, genetic variation and selection. Pp. 3-22 *in* S. Karlin and E. Nevo, eds. Population genetics and ecology: proceedings of the conference held in Israel, March, 1975. Academic Press, New York.

Behrensmeyer, A. K. 1982. Time resolution in fluvial vertebrate assemblages. Paleobiology 8:211-227.

Bell, M. A. 1973. Pleistocene threespine sticklebacks, *Gasterosteus aculeatus* (Pisces) from southern California. Journal of Paleontology 47:479-483.

——— 1988. Stickleback fishes: Bridging the gap between population biology and paleobiology. Trends in Ecology and Evolution 3:320-325.

Bell, M. A., and T. R. Haglund. 1982. Fine-scale temporal variation of the Miocene stickleback *Gasterosteus doryssus*. Paleobiology 8:282-292.

Bell, M. A., and P. Legendre. 1987. Multicharacter chronological clustering in a sequence of fossil sticklebacks. Systematic Zoology 36:52-61.

Bell, M. A., J. V. Baumgartner, and E. C. Olson. 1985. Patterns of temporal change in single morphological characters of a Miocene stickleback fish. Paleobiology 11:258-271.

Bell, M. A., M. S. Sadagursky, and J. V. Baumgartner. 1987. Utility of lacustrine deposits for the study of variation within fossil samples. Palaios 2:455-466.

Bruner, J. C. 1991. Comments on the genus *Amyzon* (Family Catostomidae). Journal of Paleontology 65:678-686.

Campbell, W. B., J. M. Emlen, and W. K. Hershberger. 1998. Thermally induced chronic developmental stress in coho salmon: integrating measures of mortality, early growth, and developmental instability. Oikos 81:398-410.

Carroll, R. L. 1997. Patterns and processes of vertebrate evolution. Cambridge University Press, Cambridge.

Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. Journal of the American Statistical Association 74:829-836.

Cope, E. D. 1894. Fossil fishes from British Columbia. Proceedings, Academy of Natural Sciences of Philadelphia 1893 45:401-402.

Dingus, L., and P. M. Sadler. 1982. The effects of stratigraphic completeness on estimates of evolutionary rates. Systematic Zoology 31:400-412.

Dixit, S. S., J. P. Smol, J. C. Kingston, and D. F. Charles. 1992. Diatoms: powerful indicators of environmental change. Environmental Science and Technology 26:23-33.

Dunn, J. R. 1983. Developmental osteology. Pp. 48-50 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson, eds. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication Number 1. Allen Press, Lawrence, Kansas.

Durham, J. W. 1967. The incompleteness of our knowledge of the fossil record. Journal of Paleontology 41:559-565.

Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82-115 *in* T.J.M. Schopf, ed. Models in paleobiology. Freeman, San Fransisco.

Ferguson, M. M., and A. P. Liskauskas. 1995. Heritability and evolution of meristic variation in a naturalized population of brook charr (*Salvelinus fontinalis*). Nordic Journal of Freshwater Research 71:217-228.

Flessa, K. W., A. H. Cutler, and K. H. Meldahl. 1993. Time and taphonomy: Quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. Paleobiology 19:266-286.

Gingerich, P. D. 1976. Paleontology and phylogeny: patterns of evolution at the species level in early Tertiary mammals. American Journal of Science 276:1-28.

——— 1983. Rates of evolution: effects of time and temporal scaling. Science 222: 159-161.

Gingerich, P. D., and G. F. Gunnell. 1995. Rates of evolution in Paleocene-Eocene mammals of the Clarks Fork Basin, Wyoming, and a comparison with Neogene Siwalik lineages of Pakistan. Palaeogeography, Palaeoclimatology, Palaeoecology 115:227-247.

Gould, S.J. 1982. The meaning of punctuated equilibrium and its role in validating a hierarchical approach to macroevolution. Pp. 83-104 *in* R. Milkman, ed. Perspectives in evolution. Sinauer Associates, Sunderland, Mass.

——— 1995. Tempo and mode in the macroevolutionary reconstruction of Darwinism. Pp. 125-144 *in* W.M. Finch and F.J. Ayala, eds. Tempo and mode in evolution. National Academy of Sciences, Washington, D.C.

Gould, S. J., and N. Eldredge. 1977. Punctuated equilibria: The tempo and mode of evolution reconsidered. Paleobiology 3:115-151.

——— 1993. Punctuated equilibrium comes of age. Nature 366:223-227.

Graham, R. W. 1993. Processes of time-averaging in the terrestrial vertebrate record. Pp. 102-124 *in* S. M. Kidwell and A. K. Behrensmeyer, eds.

Grande, L., and W. E. Bemis. 1998. A comparative phylogenetic study of Amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Journal of Vertebrate Paleontology 18 (supplement to number 1):1-690.

Grande, L., J. T. Eastman, and T. M. Cavender. 1982. *Amyzon gosiutensis*, a new catostomid fish from the Green River Formation. Copeia 1982:523-532.

Hills, L. V., and H. Baadsgaard. 1967. Potassium-Argon dating of some Lower Tertiary strata in British Columbia. Bulletin of Canadian Petroleum Geology 15:138-149.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandanavian Journal of Statistics 6:65-70.

Hubbs, C. L. 1922. Variations in the number of vertebræ and other meristic characters of fishes correlated with the temperature of water during development. American Naturalist 56:360-372.

Hubbs, C. L., and K. F. Lagler. 1964. Fishes of the Great Lakes region (second edition). University of Michigan Press, Ann Arbor, Michigan.

Hubert, W. A., and C. B. Alexander. 1995. Observer variation in counts of meristic traits affects fluctuating asymmetry. North American Journal of Fisheries Management 15:156-158.

Hui, J. 1996. Diatoms from the surface sediments of the Skagerrak and the Kattegat and their relationship to the spatial changes of environmental variables. Journal of Biogeography 23:129-137.

Itazawa, Y. 1963. The ossification sequences of the vertebral column in the carp and the snake-head fish. Bulletin of the Japanese Society of Scientific Fisheries 29:667-674.

Jordan, D. S. 1892. Relations of temperature to vertebrae among fishes. Proceedings of the U.S. National Museum for 1891 14:107-120.

Kidwell, S. M., and A. K. Behrensmeyer. 1993a. Taphonomic approaches to time resolution in fossil assemblages: introduction. Pp. 1-8 *in* S.M. Kidwell and A.K. Behrensmeyer, eds.

——— (eds.) 1993b. Taphonomic approaches to time resolution in fossil assemblages. Short Courses in Paleontology Series, Number 6. S. J. Culver, series ed.

Kirpichnikov, V. S. 1979. Genetic bases of fish selection. translated by G.G. Gause (1981). Springer-Verlag, Berlin.

Koch, C. F. 1991. Sampling from the fossil record. Pp. 4-18 *in* N. L. Gilinsky, and P.W. Signor, eds. Analytical paleobiology. Short Courses in Paleontology Series, Number 4. S. J. Culver, series ed.

Lee, J. C. 1982. Accuracy and precision in anuran morphometrics: artifacts of preservation. Systematic Zoology 31:266-281.

——— 1990. Sources of extraneous variation in the study of meristic characters: The effect and size of inter-observer variability. Systematic Zoology 39:31-39.

Lindsey, C. C. 1975. Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body length. Journal of the Fisheries Resource Board of Canada 32:2453-2469.

——— 1988. Factors controlling meristic variation. Pp. 197-274 *in* W. S. Hoar, and D. J. Randall, eds. Fish physiology Volume XI-B. Academic Press, New York.

Lindsey, C. C., and A. N. Arnason. 1981. A model for responses of vertebral numbers in fish to environmental influences during development. Canadian Journal of Fisheries and Aquatic Sciences 38:334-347.

Lindsey, C. C., A. M. Brett, D. P. Swain, and A. N. Arnason. 1984. Responses of vertebral numbers in rainbow trout to temperature changes during development. Canadian Journal of Zoology 62:391-396.

MacGregor, R. B., and H. R. MacCrimmon. 1977. Evidence of genetic and environmental influences on meristic variation in the rainbow trout, *Salmo gairdneri* (Richardson). Environmental Biology of Fishes 2:25-33.

MacLeod, N. 1991. Punctuated anagenesis and the importance of stratigraphy to paleobiology. Paleobiology 17:167-188.

Malmgren, B. A., W. A. Berggren, and G. P. Lohmann. 1983. Evidence for punctuated gradualism in the Late Neogene *Globorotalia tumida* lineage of planktonic foraminifera. Paleobiology 9:377-389.

——— 1984. Species formation through punctuated gradualism in planktonic foraminifera. Science 225:317-319.

Martin, R. E., and R. C. Wright. 1988. Information loss in the transition from life to death assemblages of foraminifera in back reef environments, Key Largo, Florida. Journal of Paleontology 62:399-410.

Mathews, W. H. 1964. Potassium-argon age determination of Cenozoic volcanic rocks from British Columbia. University of British Columbia Department of Geology Report 2.

Maxwell, W. D., and M. J. Benton. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. Paleobiology 16:322-335.

McCune, A. R. 1987a. Towards the phylogeny of a fossil species flock: semionotid fishes from a lake deposit in the Early Jurassic Towaco Formation, Newark Basin. Peabody Museum of Natural History (Yale University) Bulletin 43:1-108.

——— 1987b. Lakes as laboratories of evolution: endemic fishes and environmental cyclicity. Palaios 2: 446-454.

——— 1990. Evolutionary novelty and atavism in the *Semionotus* complex: relaxed selection during colonization of an expanding lake. Evolution 44:71-85.

——— 1996. Biogeographic and stratigraphic evidence for rapid speciation in semionotid fishes. Paleobiology 22:34-48.

McCune, A. R., K. S. Thomson, and P. E. Olsen. 1984. Semionotid fishes from the Mesozoic Great Lakes of North America. Pp. 27-44 *in* A. A. Echelle, and I. Kornfield, eds. Evolution of fish species flocks. University of Maine at Orono Press.

Nagiec, C. 1977. Ossification of the axial skeleton and fins in the whitefish, *Coregonus lavaretus* L. Acta Biologica Cracoviensia. Series Zoologia 20:155-179.

Nenashev, G. A. 1966. Heritability of several morphological (diagnostic) traits in the Ropsha common carp. Izvestiya Gosudarstvennogo Nauchno-issledovatel 'skogo

Instituta Ozernogo i Rechnogo Rybnogo Khozyaistva 61:125-135.

Nisbet, I. C., T. J. Baird, D. V. Howard, and K. S. Anderson. 1970. Statistical comparison of wing length measured by four observers. Bird-banding 41:307-308.

Orska, I. 1963. The influence of temperature on the development of meristic characters of the skeleton in Salmonidae. I. Temperature-controlled variations of the number of vertebrae in *Salmo irideus* Gibb. Zoologica Poloniae 12:309-339.

Pan, Y., R. J. Stevenson, B. H. Hill, A. T. Herlihy, and G. B. Collins. 1996. Using diatoms as indicators of ecological conditions in lotic systems: A regional assessment. Journal of the North American Benthological Society 15:481-495.

Peden, A. E. 1981. Meristic variation of four fish species exhibiting lowest median counts in Georgia Strait, British Columbia. Canadian Journal of Zoology 59:679-683.

Raup, D. M. 1987. Major features of the fossil record and their implications for evolutionary rate studies. Pp. 1-14 *in* K.S.W. Campbell, and M.F. Day, eds. Rates of evolution. Allen & Unwin, London.

Raup, D. M., and R. E. Crick. 1981. Evolution of single characters in the Jurassic ammonite *Kosmoceras*. Paleobiology 7:200-215.

Reimchen, T. E., and J. S. Nelson. 1987. Habitat and morphological correlates to vertebral number as shown in a teleost, *Gasterosteus aculeatus*. Copeia 1987:868-874.

Resh, V. H., D. S. White, S. A. Elbert, D. E. Jennings, and L. A. Krumholz. 1976. Vertebral variation in the emerald shiner *Notropis atherinoides* from the Ohio River: An apparent contradiction to "Jordan's Rule". Bulletin. Southern California Academy of Sciences.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Rouse, G. E., and W. H. Mathews. 1961. Radioactive dating of Tertiary plant-bearing deposits. Science 133:1079-1080.

Rouse, G. E., W. S. Hopkins, and K. M. Piel. 1971. Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. Geological Society of America Special Paper 127:213-246.

Schindel, D. E. 1980. Microstratigraphic sampling and the limits of paleontological resolution. Paleobiology 6:408-426.

——— 1982. Resolution analysis: a new approach to the gaps in the fossil record. Paleobiology 8:340-353.

Schmidt, J. 1917. Racial investigations. I. *Zoarces viviparus* L. and local races of the same. Comptes Rendus des Travaux. Laboratoire Carlsberg 13:279-396.

Schmidt, J. 1919a. La valeur de l'individu a titre de générateur apprecies suivant la méthode du croisement diallele. Comptes Rendus des Travaux. Laboratoire Carlsberg 18:1-71.

Schmidt, J. 1919b. Racial investigations. III. Experiments with *Lebistes reticulatus* (Peters). Comptes Rendus des Travaux. Laboratoire Carlsberg 14:1-8.

Sheldon, P. R. 1990. Rates of evolution - living fossils. Pp. 106-110 *in* D. E. G. Briggs, and P. R. Crowther, eds. Palaeobiology: A synthesis. Blackwell Scientific Publications: London.

Smith, A. B., and C. Patterson. 1989. The influence of taxonomic method on the perception of patterns of evolution. Evolutionary Biology 23:127-216.

Smith, K. 1921. Racial investigations. VI. Statistical investigations on inheritance in *Zoarces viviparus* L. Comptes Rendus des Travaux. Laboratoire Carlsberg 14:1-60.

Smol, J. P., I. R. Walker, and P. R. Leavitt. 1991. Paleolimnology and hindcasting climatic trends. Verhandlugen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 24:1242-1246.

Svärdson, G. 1945. Polygenic inheritance in *Lebistes*. Arkiv foer Zoologia 36A:1-9.

Swain, D. P., and C. C. Lindsey. 1986. Meristic variation in a clone of the cyprinodont fish *Rivulus marmoratus* related to temperature history of the parents and of the embryos. Canadian Journal of Zoology 64:1444-1455.

Symons, D. T. A., and M. R. Wellings. 1989. Paleomagnetism of the Eocene Kamloops Group and the cratonization of Terraine I of the Canadian Cordillera. Canadian Journal of Earth Sciences 26:821-828.

Tartarko, K. I. 1968. Effect of temperature on the meristic characters of fish. Problems of Ichthyology 8:339-350.

Tave, D. 1984. Quantitative genetics of vertebrae number and position of dorsal fin spines in the velvet belly shark, *Etmopterus spinax*. Copeia 1984:794-797.

Valentine, D. W., M. E. Soulé and P. Smallow. 1973. Asymmetry analysis in fishes: A possible statistical indicator of environmental stress. Fisheries Bulletin U.S. 71:357-370.

Velleman, P. F. 1992. Data Desk Statistics Guide. Data Description, Inc., Ithica, N.Y.

Vrba, E. S. 1980. Evolution, species and fossils: how does life evolve? South African Journal of Science 76:61-84.

Vyverman, W., R. Vyverman, V. S. Rajendran, and P. Tyler. 1996. Distribution of benthic diatom assemblages in Tasmanian highland lakes and their possible use as indicators of environmental changes. Canadian Journal of Fisheries and Aquatic Sciences 53:493-508.

Wilson, M. V. H. 1974. Fossil fishes of the Tertiary of British Columbia. PhD Thesis. Geology Department, University of Toronto.

——— 1977a. Middle Eocene freshwater fishes from British Columbia. Life Sciences

Contributions, Royal Ontario Museum 113:1-61.

——— 1977b. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. Canadian Journal of Earth Sciences 14:953-962.

——— 1980. Eocene lake environments: depth and distance-from-shore variation in fish, insect, and plant assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology 32:21-44.

——— 1984. Year classes and sexual dimorphism in the Eocene catostomid fish *Amyzon aggregatum*. Journal of Vertebrate Paleontology 3:137-142.

——— 1988a. Taphonomic processes: information loss and information gain. Paleoscene #9. Geoscience Canada 15:131-148.

——— 1988b. Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 62: 609-623.

——— 1993. Calibration of Eocene varves at Horsefly, British Columbia, Canada, and temporal distribution of specimens of the Eocene fish *Amyzon aggregatum* Wilson. Kaupia - Darmstädter Beiträge zur Naturgeschichte 2:27-38.

Wilson, M. V. H., and D. G. Barton. 1996. Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. Paleobiology 22:535-542.

Wilson, M. V. H., and A. Bogen. 1994. Tests of the annual hypothesis and temporal calibration of a 6375-varve fish-bearing interval, Eocene Horsefly Beds, British Columbia, Canada. Historical Biology 7:325-339.

CHAPTER 4:

CONCLUSIONS

Over the past few decades, paleontologists have become increasingly interested in the study of patterns of change over short time intervals in the fossil record. These microstratigraphic studies can help to determine the amount of variability within individual samples in most other paleontological studies (preserved without such excellent temporal resolution). Microstratigraphic studies have several important applications: to understand the amount of temporal averaging occurring within other stratigraphic intervals, to better understand environmental changes and the different scales and degrees of change that occurred in the past, and to better understand patterns and rates of phenotypic change within and across lineages in the hopes of better understanding patterns and processes of evolution.

Fossil sites, however, need to have some very specific attributes in order to be able to study such microstratigraphic patterns. Most importantly, a site has to have excellent temporal resolution: a high sedimentation rate with no gaps or variations in rate of deposition, and no temporal averaging. Several other features are important, depending on the specific questions that are being addressed: a method of determining absolute time spanned by the deposit, and abundant and morphologically complex fossils. Unfortunately, few stratigraphic intervals meet all the conditions required for microstratigraphic studies.

The varved lacustrine sediments of the Eocene Horsefly Mine locality in central British Columbia, do meet all these criteria, and are therefore ideal for microstratigraphic study. Lacustrine deposits have among the highest continuity of deposition of any depositional environment (Schindel 1980). This is especially true of varved lakes, whose sediments are preserved in yearly laminations (Bell *et al.* 1987; Anderson and Dean 1988). The presence (and preservation) of varves is a clear indication that there is no temporal averaging of the

sediment. The total absolute time represented by varved intervals (and between specimens in varved intervals) can be easily determined by simply counting years from the sediment. The H3 section, a 10 000-year varved interval in the Horsefly deposits, contains abundant fossils of numerous taxa (including plants, diatoms, insects, and fish). In a total of about four weeks of collecting from the H3 interval, some 698 specimens of fossil fish have been collected. Many of these specimens are preserved well enough to allow microstratigraphic study of phenotypic change. There is some variation in preservation, which can be used to reconstruct environmental change in or around the lake represented by the H3 interval.

Paleoenvironmental Reconstructions

Variation in preservation of the most common species of fish, *Amyzon aggregatum*, are indicative of several changes in and around the lake represented by the H3 section.

The vast majority of varved sediments are deposited in meromictic lakes (Anderson *et al.* 1985) because the conditions provided by the perennially isolated anoxic waters at the bottom exclude all bioturbation, and prevent resuspension of sediments during overturn events. The polymodality of specimens of *Amyzon* and the preservation of nearly every specimen in the dark portion of the varves suggests that the vast majority of specimens die in the winter. As Wilson (1977) has suggested for the H2 section, this could be caused by starvation during winter months, or could be the result of anoxia as the lake overturns in the fall or winter. The high amount of tetany displayed by specimens seems to indicate the latter. Stratification and yearly cycles in the lake represented by the H3 section can be reconstructed using these features. The bottom was perennially anoxic, probably isolated by a chemical gradient (chemocline). The water above the chemocline was likely monomictic as Wilson (1993) and Wilson and Barton (1996) have proposed for the H2 section, and therefore overturned in the fall or winter, accounting for a seasonal kill of fishes.

Variations in preservational patterns (disarticulation of skull, abdomen and fins) and tetany of specimens allow a reconstruction of (relative) lake level changes through time. Intervals in which skull disarticulation (which was used as an indication of scavenging) is

high, abdominal disarticulation (which was used as an indication of partial floatation) is high, and tetany is low indicate a relatively shallow interval in the lake history. Other features of the site, such as the distribution of fishes and other fossils and the relative size of *Amyzon* support these reconstructions, and in some cases, suggest the way in which the deposit was becoming more shallow (*e.g.* a relative movement of the H3 section closer to shore was suggested by a smaller size of *Amyzon*). There appears to by a cyclicity of lake level changes in the H3 section, with a deepening trend until about the year 3000, followed by a shallowing trend to the year 6000, followed by a deepening trend to the end of the section (year 10 000).

Phenotypic Change

I also took advantage of the excellent temporal resolution provided by varves for a microstratigraphic study of phenotypic change through the H3 section. There is no obvious variation in osteological characters through the section, therefore I focused on meristic series, which can change over a much shorter time intervals (Svärdson 1945; Kirpichnikov 1979).

Bell and his colleagues identified changes in meristics and osteological characters through tens of thousands of years in sticklebacks (Bell 1973, 1988; Bell and Haglund 1982; Bell *et al.* 1985, 1987; Bell and Legendre 1987). Environment cannot directly affect the development of some of the osteological characters (e.g. pelvic structure), therefore much of the change that Bell reports can be attributed to evolution (or at least selective pressures that might lead to evolution). Most of the phenotypic change in the characters that Bell and his colleagues examined had a "stepped pattern" with phenotypic change occurring in fairly short intervals (Bell *et al.* 1985), separated by periods of relative stasis. Near the end of the section, all characters change rather dramatically. The authors attribute this sudden change (estimated to be over about 30 years) to migration of new populations into the basin (Bell and Legendre 1987).

In this study, I found very little change in meristic elements that could not be attributed to ecophenotypic change. The interval of greatest environmental change (a deepening trend

between the years 3000 and 6000) was also associated with the period of greatest meristic change. A principal components analysis suggests that much of this change is associated with ecophenotypic responses to environmental change. The interval at the start of the H3 section (years 0 to 3000), however, has very little change that can be attributed to ecophenotypic change, and therefore all changes in this interval should be a result of selective pressures or evolution. There is very little change in any meristic series in this interval, however, which might be an indication of a period of relative stasis.

Concluding Remarks

The microstratigraphic studies presented here demonstrate variation in taphonomy and phenotypic change in fishes on a combination of scales that has never before been observed: both hundreds and thousands of years. Wilson and Barton (1996) demonstrated taphonomic changes over hundreds of years in another interval in the Horsefly deposits. Other studies have shown variation in meristics on scales of thousands and tens of thousands of years (Bell and Haglund 1982; Bell *et al.* 1985, 1987; Bell and Legendre 1987). All of these studies suggest that much of the variation within other sites (not preserved with such excellent temporal resolution) is a result of temporal averaging.

There are several gaps in our knowledge of the paleoenvironment of the H3 section that, if filled, could increase our understanding of causes and implications of changes of both taphonomy and phenotype of fishes. A detailed study of the sedimentology of the site can provide direct information about changes in material being deposited into the lake through time. Changes in diatoms that make up most of the varved sediment can provide at least an indication of timing of environmental change in the lake. Increased lateral and vertical exposure of the site can allow testing of some of the hypotheses generated here. Such a holistic approach to the study of the varved lacustrine deposits at Horsefly, British Columbia could vastly improve our knowledge of causes and implications of microstratigraphic changes in the lake.

Literature Cited

Anderson, R. Y., and W. E. Dean. 1988. Lacustrine varve formation through time. Palaeogeography, Palaeoclimatology, Palaeoecology 62:215-235.

Anderson, R. Y., W. E. Dean, J. P. Bradbury, and D. Love. 1985. Meromictic lakes and varved lake sediments in North America. U.S. Geological Survey Bulletin 1607:1-19.

Bell, M. A. 1973. Pleistocene threespine sticklebacks, *Gasterosteus aculeatus* (Pisces) from southern California. Journal of Paleontology 47:479-483.

——— 1988. Stickleback fishes: Bridging the gap between population biology and paleobiology. Trends in Ecology and Evolution 3:320-325.

Bell, M. A., and T. R. Haglund. 1982. Fine-scale temporal variation of the Miocene stickleback *Gasterosteus doryssus*. Paleobiology 8:282-292.

Bell, M. A., and P. Legendre. 1987. Multicharacter chronological clustering in a sequence of fossil sticklebacks. Systematic Zoology 36:52-61.

Bell, M. A., J. V. Baumgartner, and E. C. Olson. 1985. Patterns of temporal change in single morphological characters of a Miocene stickleback fish. Paleobiology 11:258-271.

Bell, M. A., M. S. Sadagursky, and J. V. Baumgartner. 1987. Utility of lacustrine deposits for the study of variation within fossil samples. Palaios 2:455-466.

Kirpichnikov, V. S. 1979. Genetic bases of fish selection. translated by G.G. Gause (1981). Springer-Verlag, Berlin.

Schindel, D. E. 1980. Microstratigraphic sampling and the limits of paleontological resolution. Paleobiology 6:408-426.

Svärdson, G. 1945. Polygenic inheritance in *Lebistes*. Arkiv foer Zoologia 36A:1-9.

Wilson, M. V. H. 1977. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. Canadian Journal of Earth Sciences 14:953-962.

——— 1993. Calibration of Eocene varves at Horsefly, British Columbia, Canada, and temporal distribution of specimens of the Eocene fish *Amyzon aggregatum* Wilson. Kaupia - Darmstädter Beiträge zur Naturgeschichte 2:27-38.

Wilson, M. V. H., and D. G. Barton. 1996. Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. Paleobiology 22:535-542.

APPENDIX

Specimens of *Amyzon aggregatum* examined in this study:

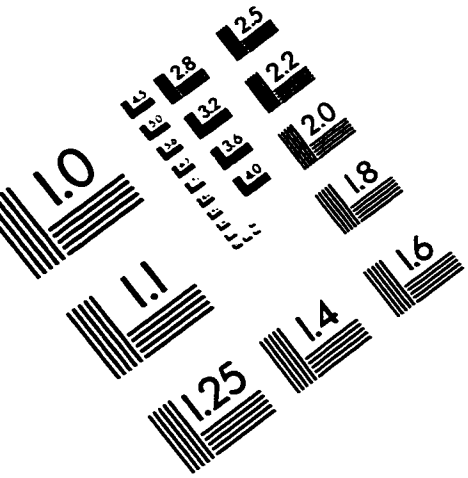
UALVP (University of Alberta, Laboratory for Vertebrate Paleontology):
23444-23451,
23453-23454,
23456-23468,
23470-23478,
31113-31116,
31118-31120,
31122-31123,
31125-31138,
31140-31143,
31145-31158,
31160-31161,
31164-31165,
31169-31174,
32032,
32035-32039,
32041-32049,
32051-32056,
32058-32069,
32265-32268,
32270-32274,
32295-32386,
33050-33103,
33105-33119,
33120-33131,
33133-33144,
33160,
33198-33210,
40761-40763,
40765-40780,
40782-40826,
40828-40831,
40833-40847,
40851-40917,
40919-40936,
40938-40950,
40957-40967,
40969-40979,
40981-41009,
41013,
41015-41053,
41055-41064,
41066-41074,
41076-41150,

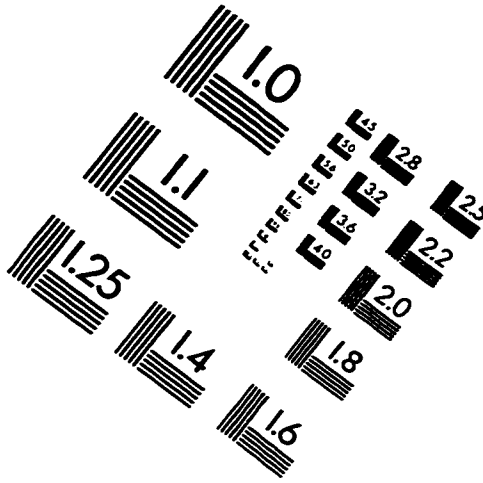
UALVP (cont.)

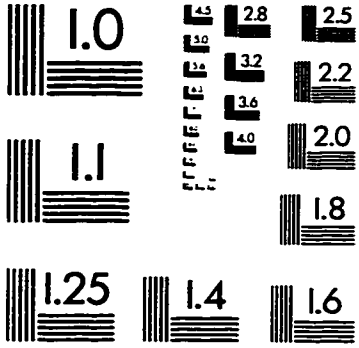
41166-41169,
41171-41176,
41178-41191,
41193-41211,
41218-41220,
41229-41230

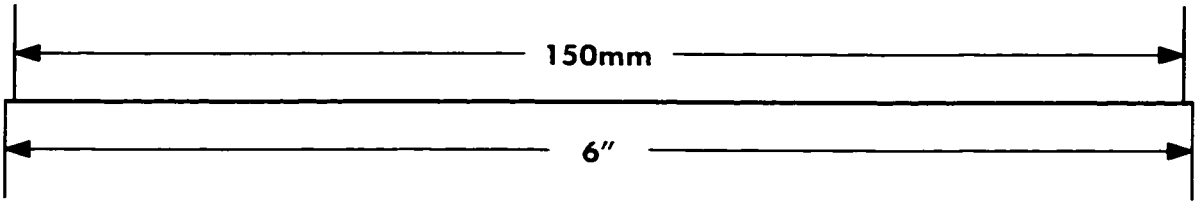
Royal British Columbia Museum
rbcm.eh.997.003.01-rbcm.eh.997.003.62

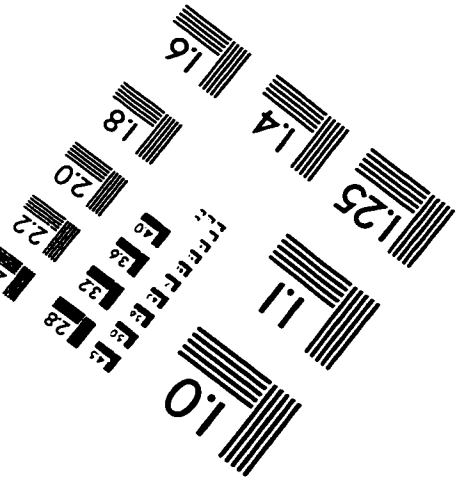
IMAGE EVALUATION TEST TARGET (QA-3)

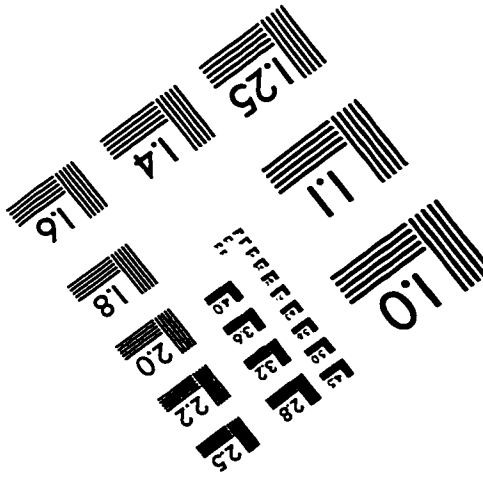












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