

# FISH TAPHONOMY AND ENVIRONMENTAL INFERENCE IN PALEOLIMNOLOGY

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## Abstract

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The contribution of fish studies to paleoecology generally takes the form of (1) inference from analogies in modern fish faunas and (2) fish taphonomy — the pattern of death and dispersal of bones. (1) Modern fish faunas and associated organisms provide taxonomic, ecological, or functional analogues for interpretation of ancient limiting factors and behaviors. These inferences presume taxonomic conservatism. They also presume functional relationships between morphological form and feeding mode or habitat. They become weak with increased geologic age or phyletic distance between ancient subject and modern analogue. (2) Fish taphonomy may contribute information about limnology, community composition, life history, mortality, depositional environment, and preservation. Taphonomic reconstruction of ecology and preservation depends on the applicability of analogous processes in modern ecology and limnology.

In aquatic taphonomy, temperature is the most important factor in determining the fate of a carcass. Above about 16°C (depending on depth and pressure), most carcasses are made buoyant by bacterial decay gases and are transported to the surface where they may decay further and fall piecemeal into deepwater environments, or drift to beach environments where wave energy disarticulates, abrades, and scatters the bones. Below about 16°C, most carcasses remain on the bottom until buried; they may be disturbed by scavengers, depending on oxygen concentration in the hypolimnion.

## Introduction

Paleoecology attempts to reconstruct the relationships of ancient organisms to their biological and physical environments. It draws its information from many different fields of study in order to make inferences about the ancient geologic setting, climate, community structure, population dynamics, trophic relationships, and behaviors. Drawing reasonable inferences requires that we be able to (1) estimate the effects of physical and biological processes on the fossil assemblage and sediments, including evaluation of information

loss relative to the original, living community, and (2) discover critical similarities and differences between modern analogues and the ancient organisms and environments.

There are two ways in which paleoecological reconstruction can be approached: (1) by inference from taxonomically or structurally similar modern organisms used as analogues, which suggest limiting factors, behaviors, and trophic dynamics; and (2) by taphonomy (especially biostratigraphy — the events from death to burial): the limnological conditions, biological processes, and depositional systems affecting life, death, and preservation. Each of these

approaches has advantages and disadvantages, depending on the particular study. The inferences provided by one may sometimes test those of the other.

### The use of modern analogues

We first consider the use of analogy, its limitations, and its development in the fish paleoecological literature. Ecological characteristics of modern species (analogues) are attributed to fossil forms to provide explanations. The analogues may be phyletic relatives or functional counterparts. The most commonly applied attributes are environmental tolerances (salinity, temperature, substrate, current or wave energy, turbidity, depth), behaviors (feeding, spawning), and trophic relationships. The reasonableness of the inferred attribute depends on our confidence in either the phylogenetic or functional relatedness of the modern and fossil species. For example, to infer past climates from Recent distributions, we must assume that evolution of physiological tolerances in the past has been at least as conservative as appears in Recent representatives of the group in question.

Presently there are serious limitations in the use of morphology to infer ecological parameter states. Most environmental parameters do not affect the size and shape of fishes with sufficient regularity to allow confident inference of any conditions, for example, salinity or temperature, from body shape. The relationship between developmental temperature and number of serial parts is partly understood (e.g. Barlow, 1961; Johnson and Barnett, 1975; Lindsey and Arnason, 1981) but, because the means and the shapes of the curves vary between species, no inference about fossil species is possible with current knowledge. As a result of these limitations, inferences about environment have been based primarily on phyletic relatedness.

The relationships of morphology to feeding behaviors and other aspects of predator-prey relationships are somewhat better understood.

Inferences based on size and shape of jaws and pharyngeal arches, and size and shape of teeth (canine, crushing, grinding, etc.) are often accepted as reasonable (Grande, 1980).

Following the precedent successful in paleobotany (e.g. Dorf, 1930, 1970; Chaney et al., 1944; but see also Wolfe, 1971) it is assumed that if all living members of a genus or family are limited to a specific tolerance range that fossil members of those groups probably shared the same limitation. Confidence in the inference is a function of the number of living species in the group, the sharpness of the limitation, and the absence of exceptions. For example, the primary freshwater fish families (Myers, 1949) are thought to be indicators of a freshwater depositional environment. In a mixed fossil assemblage, reliability of the inference, however, depends on the proportion of primary freshwater representatives.

Similarly, northern hemisphere families whose species show rather sharp northern limits that are correlated with summer isotherms (Radforth, 1944) may be reliable indicators of length of growing season or of lower summer temperatures. Northern families whose southern limits are correlated with temperature may provide evidence bearing on maximum summer temperatures, provided that moisture and elevation are considered (Cross, 1970; Smith, 1978). Most such inferences have been based on fossil occurrences outside the species' modern range. Integration of diverse faunal evidence to reconstruct the seasonality of a paleoenvironment is possible for Pleistocene faunas containing both northern and southern Recent forms (Hibbard, 1955, 1960). Pliocene faunas (Smith, C. L., 1962) and Pleistocene faunas (Uyeno, 1963; Semken, 1966; Neff, 1975; Teller and Bardack, 1975; Teller-Marshall and Bardack, 1978) have also been studied in this way.

Cross (1970) discussed limitations to using fish alone to infer climate and showed that many papers (e.g. Smith, C. L., 1954; Smith, G. R., 1963) that inferred cooler climates could be interpreted otherwise to show wetter climates. He showed that fish fossils alone do not

allow us to distinguish between more water and cooler water. Climatic interpretation of cooler climates in the past is strengthened, however, when concordant with other elements in the flora and fauna. As usual, these methods depend on degree of relationship, number of recent species on which the generalization is based, and sample size in the fossil assemblage.

The reliability of the analogy approach to paleoecology depends on the accuracy of the underlying systematics and functional morphology. Inferences become less certain when older periods of geologic time are involved and when large amounts of evolution have taken place. Because morphology is the result of long-term responses to physiological and ecological selection pressures, the method of using analogies is not easily amenable to direct experimentation or observation today; the inferences are not easily falsifiable, but are weakened by discovery of conflicting examples.

Although most papers on fossil fishes contain comments about habit or habitat, only a few authors have analyzed whole faunas or offered discussions of methods. Most applications of analogy have been restricted to Late Cenozoic (David, 1944; Smith, C. L., 1954, 1964; Smith, G. R., 1963, 1975; Gaudant, 1979a, b, 1981 and references therein), Early Cenozoic (Wilson, 1977, 1980; Grande, 1980; Buchheim and Surdam, 1981) and Mesozoic (Schaeffer, 1970; Waldman, 1971; Schäfer, 1972) faunas.

### *Salinity*

The most prolific use of the analogy approach to infer salinity in non-obvious circumstances has been by Gaudant (1979a, b, 1981). He analyzed paleosalinity in a number of Early Cenozoic European faunas and added inferences about temperature and depth. The various proportions of freshwater and marine taxa at different localities usually make it possible to determine the salinity of a depositional environment.

### *Temperature and climate*

Climate and water temperatures were studied by Smith, C. L., (1954, 1964) and Smith, G. R. (1963) in investigations of Great Plains fish faunas relative to Late Cenozoic climatic changes in North America. Interpretations of climates cooler than at present were based on fossil occurrence of genera and species that are now cool stenothermic, such as perch (*Perca*), muskellunge (*Esox*), and other northern groups. Similarly, the sequence of Pleistocene faunas from Hansen Bluff, near Alamosa, Colorado shows a local transition from coolwater fish (*Salmo*, presently northern) to warmwater fish (*Gila*, presently southern) that indicates a warming trend (Rogers et al., 1985). Pleistocene climate on the northern plains was inferred by Sherrod (1963) on the basis of an assemblage of fish bones in an ice-contact lake. Cooler Pleistocene climates were inferred by Swift (1968), Smith, M. L. (1981), and Smith, M. L. et al. (1975) for various localities farther south in North America. Earlier literature was reviewed by Miller (1965).

### *Stream gradient and habitat*

Smith, G. R. and Lundberg (1972) attempted to draw conclusions about stream gradient and related factors affecting the depositional environment of the Sand Draw local fauna in preglacial Nebraska. The data were drawn from both phyletic and structural analogies. The fish remains in the fauna belong to genera known from low-gradient, low-elevation habitats today. Furthermore, most of these genera, *Ictiobus* (buffalo fish), *Hiodon* (goldeye), *Chaenobryttus* (warmouth sunfish), *Lepomis* (sunfish), and *Morone* (white bass), are deep-bodied, laterally compressed fishes that grow to moderate or large size. These shape and size characteristics are found in fishes that inhabit slow-moving (low-gradient) waters usually at low elevations and usually large in volume. They are not common in high-gradient, small creeks (Smith, G. R. and Lundberg, 1972). Gradient, elevation, habitat volume, deposi-

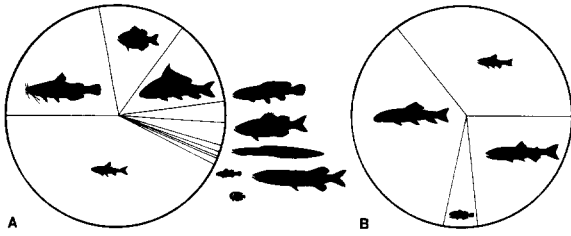


Fig.1. Classification, by shape, of fishes from five low-gradient stream habitats (A, in Michigan, Iowa, Kansas, Oklahoma, Alabama;  $N=4235$ ) and five high-gradient habitats (B, in British Columbia, Oregon, Idaho, Utah, New Mexico;  $N=2305$ ). Low-gradient streams have high diversity of taxa and body shapes, with an abundance of deep-bodied fishes. High-gradient streams have low diversity of taxa and shapes, and few if any deep-bodied inhabitants. Data from Division of Fishes, University of Michigan Museum of Zoology.

tional environment, and species richness are related in complex ways of major importance to interpretation of paleoenvironments (Fig.1). Elevation, high gradient, and suspended load (degradation), in concert, are generally negatively correlated with species richness, while low gradient, increased habitat volume, and stability are associated with high species richness (Smith, G. R., 1981). Other interpretations of habitat volume or gradient based on fishes include Smith, C. L. (1958), Uyeno and Miller (1962), Schultz (1965), Hibbard and Dalquest (1966), Lundberg (1967), Wilson (1968), Bell (1973), Ossian (1973), Eshelman (1975), and Bennett (1979).

Another example of the use of the analogy approach to infer habitat is Buchheim and Surdam's (1981) analysis of Lake Gosiute, in which they infer paleoenvironments, based in part on modern analogies of the fish fauna. This analysis is discussed in the taphonomy section below.

### Trophic relationships

The morphology of jaws and teeth, and to a lesser extent, body size and shape, are often used with data from recent analogues to indicate predator-prey relationships and feeding behaviors. For example, fish in the Green River fauna have been ecologically classified

by Perkins (1970a) and especially by Grande (1980): flat, crushing teeth indicate mollusk and decapod feeding (*Heliobatis*); modern planktivory by paddlefish indicates the same in *Crossopholis*; predaceous teeth indicate predaceous habits in *Lepisosteus*, *Phareodus*, *Mioplosus*, and one species of *Amia*, while thick, short, styliform teeth indicate mollusk and crustacean feeding in another species of *Amia*; large pointed jaw teeth indicate predation on small fish and insects in *Eohiodon*; planktivory is inferred from clupeomorph mouth and body form (*Knightia* and young *Diplomystus*); ventral jaws and tooth loss indicate herbivory or scavenging (*Notogoneus*); slightly coniform pharyngeals in suckers indicate possible omnivory (*Amyzon*); similar teeth indicate similar diet in fossil and modern catfish, and in fossil and modern troutperch; small teeth indicate small prey (*Asineops*); obtuse, grinding pharyngeal teeth indicate feeding on mollusks and insects (*Priscacara*). Grande (1980) extended these inferences to trophic generalizations, and Perkins (1970a) used his classification to draw conclusions about community equitability.

Similarly, Smith, G. R. (1975) assigned trophic roles to Lake Idaho fishes based on feeding morphology and modern analogues: large, carnivorous teeth and large mouth and body size indicate a top carnivore (*Rhabdofario*); in suckers, a terminal mouth indicates a midwater planktivore (*Chasmistes*) and a ventral mouth indicates a benthic, small-particle omnivore (*Catostomus*); large size, large jaws, and long canine teeth indicate a top carnivore (*Ptychocheilus*); sharp, grinding pharyngeal teeth indicate herbivory (*Acrocheilus* and *Orthodon*); blunt, molariform teeth indicate molluskivores (*Mylocheilus*); small and medium-sized, midwater carnivory is inferred from analogy to similar Recent relatives (*Gila* and *Richardsonius*); molariform as well as grinding pharyngeal teeth indicate omnivory (*Idadon*); nocturnal scavenging and omnivory is inferred by analogy to similar modern relatives (*Ictalurus*); a medium-sized predator is inferred by analogy to a similar modern

relative (*Archoplites*); small benthic predators on crustaceans are inferred by analogy to similar modern relatives (Cottidae). Some trophic inferences are complex: in *Oncorhynchus*, numerous gill rakers indicate planktivory, but in the same form, piscivory is inferred from analogy with relatives; in *Prosopium*, relatively large jaws and large size indicate piscivorous habits, but also planktivory is inferred by analogy with relatives. Smith, G. R. and Todd (1984) extended these inferences to generalizations about broader aspects of the trophic interactions and the resulting selective pressures for defensive spines in Lake Idaho sculpins.

The use of analogy is more acceptable when similar congeners are being compared, such as within *Amia* and within *Lepisosteus* in the Eocene and Recent, and in most fish genera from the Pliocene, Pleistocene, and Recent. In most cases, however, the authors have been too willing to infer specialized feeding habits from specialized morphology. Ecological studies on modern specialists indicate extensive omnivory, especially in "herbivores" and molluskivores. Because digestion of plant material is not enzymatically efficient in fishes, and protein is too valuable to exclude from the diet, opportunistic feeding is probably selected for in fishes that can eat plants. Experimental studies (Liem, 1980) indicate that even morphological specialists may be behavioral opportunists.

### The use of taphonomy

Although taphonomy as a field of study has enjoyed increasing popularity in the past 10 years, recent summaries (Dodson, 1980; Olson, 1980) of the current state of the discipline do not discuss the taphonomy of the inhabitants of aquatic systems. Most workers have concentrated on fluvial transport and burial of animals from terrestrial ecosystems, or the transport and sorting of marine invertebrates. Unlike studies of transport, sorting, and abrasion based on hydrodynamic flow, studies of quiet water systems have had few guiding

principles except that transport may occur when carcasses float (Schäfer, 1972). Even this principle has been ignored or used inappropriately because of misconceptions regarding its physical basis and conditions of occurrence. Students of fish paleolimnology have relied upon traditional but questionable explanations for "good preservation": lack of scavengers, rapid sedimentation, anaerobic conditions, and, since Schäfer's work, occasional flotation. Nevertheless, aquatic taphonomy has been in the forefront of experimental discovery of processes of decay and burial, primarily through the work of Schäfer and other German workers on "Aktuopalaöntologie" (e.g. Richter, 1928; Schäfer, 1964, 1976).

Aquatic taphonomy had its beginnings in the work of Weigelt (1927) and Hecht (1933) who discussed processes contributing to decay and fossilization of many types of organisms, including fish. The classic work on mass mortality of fishes and the implications of this phenomenon for the fossil record is that of Brongersma-Sanders (1948, 1949, 1957). Gunter's observations (1941, 1942, 1947) of mass death on the Gulf Coast of North America also contribute to this area of study. Both Brongersma-Sanders and Gunter dealt almost exclusively with mass death in marine habitats. Gunter pointed out (1948) that many examples of mass death (inferred from multiple individuals on single bedding planes) are found in sediments with high organic content and in areas of probable former upwelling. This corresponds to Brongersma-Sanders' observations of recent mass death episodes caused by toxicity of dinoflagellate blooms in offshore areas of upwelling. Gunter's observations were of near-shore shallow habitats, in which fish and other marine organisms were killed by sudden temperature changes, for example, the swift passage of a cold front. He noted (1947) that these episodes of mass death may be recorded in the fossil record if nearby runoff is sufficiently strong to cause sedimentation or if low temperatures or strong salinities retard decay.

The most important general work in aquatic taphonomy has been that of Schäfer (1972) who

stressed the importance of directly observing processes of death, decay, and burial. His monograph, *Ecology and Paleocology of Marine Environments*, serves as a seminal work in promoting experimental approaches to paleoecology. Investigating the preservation of North Sea fishes, he noted flotation in response to internal gas production and commented on the loss of body parts from floating carcasses.

Other works that describe the preservation of fish in ancient waters include Dence (1956), Breder (1957), Raynor (1963), Wilson (1968), Cavender (1969), Melton (1970), Perkins (1970b), Richardson and Johnson (1971), Zangerl (1971), Buchheim and Surdam (1977), Wilson (1978), Boyer (1981, 1982), and Franzen et al. (1982). David's (1957) annotated bibliography is a rich source of earlier works on fish preservation, paleoecology and mass mortality.

### *Environment of deposition*

#### *Pennsylvanian marine shales*

In the first comprehensive case history of fish preservation, Zangerl and Richardson (1963) studied the fish fauna of carbonaceous Pennsylvanian shales from the Illinois Basin of the United States. The authors were led by common assumptions about preservation to unusual conclusions about the environment. From restricted assumptions about causes of good preservation and disarticulated carcasses, they concluded that the shales were deposited in a lagoon covered by a floating mat of vegetation. To explain the disarticulated skeletons, they hypothesized feeding frenzies beneath this mat and common regurgitation of prey items. Under these circumstances, the excellent preservation required sedimentation rates to be several orders of magnitude greater than any known from similar depositional systems today (Sadler, 1981). But, to explain why carcasses were not totally disarticulated and why internal spaces of the bones were not filled with sediment during decay, the bottom was inferred to have been a combination of

soupy ooze over a hard surface presumably formed by synsedimentary compaction. In this model, the carcass would settle down in the soft ooze to the hard surface, where very quickly the sediments would compact around it before decay could occur. We would interpret the specimens to have dropped into deep water after floating and decaying at the surface. Partial articulation is attributable to undecayed connective tissue. The observed spaces were probably filled with tissue at the time of burial. The rationale for this alternate interpretation is developed in the sections to follow.

#### *Eocene lakes*

In a study of lacustrine sediments, Buchheim and Surdam (1981) drew on several lines of evidence including sedimentary structures, plant remains, insects, aquatic invertebrates, and paleoecology of the Green River Eocene fish fauna to infer two major paleoenvironments (nearshore and offshore) of Lake Gosiute. The lake was interpreted as shallow with oscillating water levels, both on geological grounds (alternating sedimentary packages) and on paleoecological grounds (alternating times of littoral and limnetic communities).

The nearshore littoral habitat is represented by shales displaying oolites, horsetail and cattail fragments, terrestrial insects, ostracods, juvenile fish, and fish fry. These shales are laminated, sometimes papery, and siliceous with aragonite or calcite. No bioturbation or root mottling was observed. The fry and juvenile fish are almost all *Knightia* and are very well preserved. The authors suggest that the finely preserved fish of this shallow-water area "...probably were seeking the protection of the shallows and aquatic vegetation..." (Buchheim and Surdam, 1981, p. 425) and that the cause of death was alkaline/saline shock. Figured examples (Buchheim and Surdam, 1981, fig.14-6E, F) show that the fish had jaw tetany, which is also known to occur from heat shock or anoxia.

There are several problems with the interpretation of this assemblage as indicative of a shallow water habitat. First, littoral areas

exhibit the greatest diversity within lakes, yet in this example, littoral diversity is low compared to the limnetic diversity. Second, the sediments are unbioturbated even though the waters were interpreted to be warm and shallow — and therefore hospitable to bottom-disturbing vegetation, benthic invertebrates, and fish. The excellent preservation of the fish is not consistent with warm shallow waters inhabited by scavengers. This point will be discussed in more detail in the next section.

The offshore limnetic (but not deepwater) habitat was characterized by the presence of well-laminated carbonate rocks containing a typical Green River fish fauna. Mass death layers of *Knightsia* are common, especially in the lower 10 m of the measured sections. These mass deaths are explained as the result of change in alkalinity/salinity conditions with zones barren of fish interpreted as indicating extreme conditions. The authors suggest that *Amyzon* was a bottom feeder along with the catfish *Astephus* and that both were scavengers on the mass death carcasses. However, this interpretation is not consistent with the functional morphology of *Amyzon*, which had a terminal, not ventral, mouth and was probably a midwater feeder on zooplankton. According to Buchheim and Surdam the numerous coprolites observed are attributable to the catfish *Astephus* and show that it was a bottom resident of this habitat when lake conditions were sufficiently fresh and oxygenated.

But the limited evidence for scavenging, of either the mass death layers of *Knightsia* or of *Astephus*, indicates limited oxygen conditions (see below) or bottom waters too saline or otherwise toxic to support scavenger populations. Coprolites, not necessarily of *Astephus*, need only be evidence of surface water populations.

This model of a differentiated water column is the same as Bradley's (1948) stratified lake with a saline and/or anaerobic hypolimnion, and is consistent with the ideas of Desborough (1978) and Boyer (1981, 1982). In this model, only rarely (such as during times of lake

turnover) could scavengers venture to the bottom. The alternation of occasionally scavenged mass-death layers and barren intervals supports this hypothesis.

If the stratified lake model were to be rejected on other grounds, it would still be necessary to explain why the fish killed by saline shock in a shallow playa lake system did not float in the warm dense waters. This choice between lake models is discussed further in the sections on the Stratified Lake Model and Overturn and Fish Mortality.

#### *Temperature, bacterial decay, and flotation*

Experiments show (Smith and Elder, 1985), following Schäfer (1972), that the partial disarticulation of skeletons such as observed by Zangerl and Richardson (1963) is the result of bacterial decay and flotation in warm waters. Such carcasses lose elements and body regions piecemeal before sinking to the bottom as the gas escapes. The observed dispersion of elements for short distances in several directions from bottom carcasses (explained as predation injury) may indicate some scavenging activity (see below). Abnormal environmental conditions are not required to preserve these carcasses in the observed condition. Sufficient conditions are warm, relatively shallow water, occasional scavengers, and reasonable rates of sedimentation.

Smith, G. R. and Elder (1985) have shown that the undisturbed fossil fish of the Clarkia Basin in Idaho were not buried for at least several months after death. Other instances of this phenomenon can be observed in both the fossil record and recent lake bottoms. For example, skeletons resting uncovered at several meters depth and less than 15°C on the bottom of Lake Michigan have been observed to remain intact for several weeks though the flesh became partially decayed (J. A. Dorr, III, pers. comm., 1984). Carcasses may be moved by currents and scavenged by crayfish.

A pertinent contribution to this aspect of aquatic taphonomy is Waldman's (1971) study of the Koonwarra freshwater fauna from the

Lower Cretaceous of southeast Australia. Following the traditional assumptions about good preservation, he reached conclusions that bear reconsideration in light of experiments on temperature and flotation. Waldman envisioned a shallow arm of a lake that was cut off every winter by a sheet of cloudy ice, under which the waters became anoxic; the fish (including lungfish) died and their carcasses were covered by clay settling out during the winter months.

Because of the lack of scattering by scavengers, Waldman saw a need to postulate a mechanism for covering the carcasses and thus preventing disturbance by other organisms. Ice cover was the only hypothesis that seemed to explain the lack of disturbance. Other hypotheses — floating vegetation mat, salt crust, organic scum, or oil film — were considered and rejected because no evidence of their presence was found in the rock record. Waldman noted varved sediments that would normally indicate a seasonal cycle of stratification of the water body. But he rejected the possibility that an oxygen deficit at the bottom of a deep stratified lake protected the carcasses from scavengers (see below), because of a previous conclusion that the fish and associated insect fauna dwelt only in shallow waters. He assumed that they could not have inhabited (or withstood transport to) the center of a deep lake. Therefore, despite paleoclimatic evidence and the analogy of warm-water habitats of today's lungfish (Schaeffer, 1970), Waldman hypothesized cold waters and cold winters.

Reviewing the evidence, Wilson (1977) noted several inconsistencies in Waldman's hypotheses. Wilson suggested that in shallow waters, warmer temperatures of the following spring should have caused decay and flotation of the winter-killed fish. Furthermore, although flocculated, "glue-like", clay could have trapped fish, varves such as those seen in Waldman's section are only formed by unflocculated materials. These arguments suggest that the shallow ice cover model is untenable.

#### *The stratified lake model*

There is, however, much evidence at Koonwarra in favor of a stratified lake. In addition to the presence of undisturbed, varved sediments, Waldman also noted that there is little evidence for bacterial decay and gas rupture of the thoracic cavities. Experimental results of Smith, G. R. and Elder (1985; Elder, 1985) indicate that temperature and pressure control the buoyancy of decaying fish through regulation of bacterial gas production, and that suppression of gas bubbles is possible only in cold or deep waters, where bacterial metabolism is limited and bubbles are small. The observation of completely articulated fossil fish suggests cold or deep waters in which the fish were prevented from floating.

These results suggest that the Koonwarra fish carcasses, unlike the fishes in Zangerl and Richardson's Pennsylvanian shales, were not warm enough or shallow enough to float. Waldman noted that isolated elements and partial carcasses are rare. If cold or deep waters are accepted on the basis of similarity to experimental preservation in cold water, then the most plausible model for death and burial is that of a stratified lake in which fish settled into cold or deep waters, where they were rarely disturbed by scavengers because of oxygen depletion.

Wilson (1977, 1980) studied lacustrine sediments and fishes in Eocene deposits of British Columbia, Canada. Integrating climatic evidence with that from fishes, insects, varves, and flora he inferred death from circulation ("turnover") of a stratified, warm monomictic lake. Good preservation was attributed to exclusion of scavengers from an anoxic hypolimnion.

#### *Overturn and fish mortality*

McGrew's (1975) perceptive analysis of death and burial of fishes in the Eocene Green River Formation, citing Bradley's earlier work (1948), hypothesized that the fish died primarily from toxicity generated by summer algal blooms in a stratified lake. The stratified lake model has recently been challenged by Surdam



and various coworkers (Eugster and Surdam, 1973; Lundell and Surdam, 1975; Surdam and Wolfbauer, 1975; Buchheim and Surdam, 1977; Surdam and Stanley, 1979) but has received support from Desborough (1978) and Boyer (1981, 1982). The Green River lake system may have included both types of lakes; it comprised several separate basins of varying morphometry. Thus Lake Uinta and Lake Gosiute may have been playa lakes or lakes showing ectogenic meromixis (Boyer, 1981, 1982) or biogenic-chemical stratification (Desborough, 1978). The following discussion is based primarily on the preservational characteristics of fishes in Fossil Lake, which supported fish diversity that we do not believe to be possible in a playa lake.

McGrew was the first to attempt to determine season of death based on preservation pattern. [In Waldman's (1971) hypothesis, season of death was a corollary of his hypothetical cause of death.] McGrew noted that it is common to find the greatest disarticulation in the head and anterior half of the body in Fossil Lake fishes. The sequence of disarticulation was estimated to proceed from the antermost vertebrae forward to the head and backward to the tail at different rates. The most posterior part of the body is commonly undisturbed. This was explained as the result of easy access for bacteria in the gill region and orifices of the head.

Noting that the fishes in the mass mortality layers are not disarticulated, McGrew proposed that mortality and preservation were caused by one event and suggested that rapid burial following an algal bloom would be one way to accomplish this. [In lakes, circulation of water and nutrients may be followed by an algal bloom that depletes the water of carbon dioxide, causing precipitation of carbonates. The algae may also release metabolites that may become toxic to fishes (Prescott, 1948).] Postulating a summer algal bloom, fish mortality, and a sequence of decay and disarticulation of carcasses, he suggested that the amount of disarticulation is directly proportional to the amount of time the fish lay on the bottom before the next carbonate precipitation event.

But unburied fish will not remain on the bottom unless cold or under pressure, and the amount of disarticulation depends primarily on other factors. In the Fossil Lake fishes, the disarticulation patterns are mostly consistent with the scavenging preferences of the larger necrophages such as snails and crayfish that prefer the head and gut cavities to the muscular areas of the body (see below).

Perkins (1970b) favored a model in which unseasonably low temperatures in summer cause circulation of toxic  $H_2S$  from the hypolimnion of a normally dimictic lake. An alternate interpretation may apply to Fossil Lake — a warm monomictic lake with winter circulation in a warm-temperate to subtropical climate. The warm monomictic model assumes moderate eutrophication. The fish would be killed whenever circulation brought hydrogen sulphide into the epilimnion from the hypolimnion as the lake cooled in winter. The fish would settle to the bottom in cold water and be disturbed by scavengers when sufficient oxygen was present. In spring the surface waters would warm up and stratify once more. The hypolimnion would remain cold and spring algal growth would cause carbonate precipitation accompanied by oxygen depletion. In deep waters, carcasses could be covered completely to lie without further disturbance; in shallower areas, they would be exposed to further scavenging or flotation. The biased nature of the Fossil Lake collections, towards the occasional deep-lake strata with well-articulated individuals, should be recognized. Flotation and scattering of isolated elements may have been more frequent than represented in museums.

#### *Seasonality*

Three tests of season of death may be done, disarticulation sequence, seasonal bone growth (Wilson, 1977; Smith, 1985; Elder, 1985), and population structure (Wilson, 1977). One can extend McGrew's principles, sequencing the disarticulation and then calibrating the rate of disarticulation using experimental results, obtained under different conditions of temperature, current energy, and scavengers.

Experiments show that at low temperatures (4–6°C) with no current energy or scavengers, lepidotrichia (fin ray bones) require at least four weeks to disarticulate (Smith, G. R. and Elder, 1985). One may estimate a minimum time from death to burial and check this against the hypothetical sequences of lacustrine events.

Alternatively, one can examine individual bones and scales for growth annuli (McGrew, 1975; Wilson, 1977; Smith, G. R., 1985). Season of death will be recorded by the place in the cycle where growth stopped. Thus, a fish bone whose edge displays a dense band with no rapid growth beyond it indicates an individual that overwintered (at least partially) but which did not survive through the following spring. An incomplete light band of rapid summer growth indicates summer mortality.

Wilson (1977) used standard length as a proxy for body size and noted that a histogram of the most numerous taxon, the sucker *Amyzon*, showed distinct polymodality in an Eocene lake in British Columbia. This suggested that death was catastrophic and occurred at a single time each year, thus sampling distinct year-classes. This yearly event fits his model postulating a warm monomictic lake with winter circulation. Analysis of Wilson's preservational patterns (Elder, 1985) in light of the experimental demonstration of fish flotation only at higher temperature and low pressure (Smith, G. R. and Elder, 1985) and patterns caused by scavenging and currents (Elder and Smith, G. R., 1984) confirm Wilson's conclusions.

*Disarticulation by scavengers and transport by currents.*

The importance of evidence of disturbance has been emphasized in the previous discussion of paleoenvironmental studies. Because presence or absence of scavengers may provide information about oxygen and other important aspects of lakes, it is necessary to distinguish among possible causes of skeletal disturbance and rearrangement. Experimental evidence,

interpreted with the help of some principles from information theory, aids in the discrimination. Viewed in the framework of information theory, taphonomy attempts to retrieve environmental information from the pattern of loss of organic organization after death and the new information added to the system by the taphonomic processes themselves (Tasch, 1965). As the processes of death, decay, and burial destroy information about the organism, they add information about its organic and physical environment and its history in that environment.

A first step towards quantifying the information in a dispersed skeleton is the measurement of distance between bones with known initial relationship, e.g. paired bones. The correlation between positions of members of pairs and the frequency distribution of the distances and directionality of transport of series of pairs allow us to use information theory to measure attributes of transport and burial processes, such as direction and heterogeneity of the energy responsible for transport and the rate of burial.

Experiments with scavengers (e.g. gastropods; Elder, 1985) indicate that fish bones are normally moved in all directions and are without preferred orientation (Fig.2). The distance of displacement is not correlated between paired bones nor does it seem correlated with the hydrodynamic character of the bone. Observation of this pattern in the fossil record indicates scavenger effects (Fig.3). Its absence may indicate conditions unsuitable for scavengers, such as anoxic bottom waters. Experiments show that anoxic waters do not prevent decay or flotation, contrary to Schäfer (1972), but can preclude scavenging.

Experiments with currents (Elder, 1985) show a more unimodal distribution of dispersal directions. Often the elements exhibit a preferred orientation. There is a correlation between distances moved by members of pairs and between elements having similar shapes. A set of bones used in current experiments is diagrammed in Fig.4 with histograms of log difference in distance moved. The distribution shows, for example, that in 22 out of 30

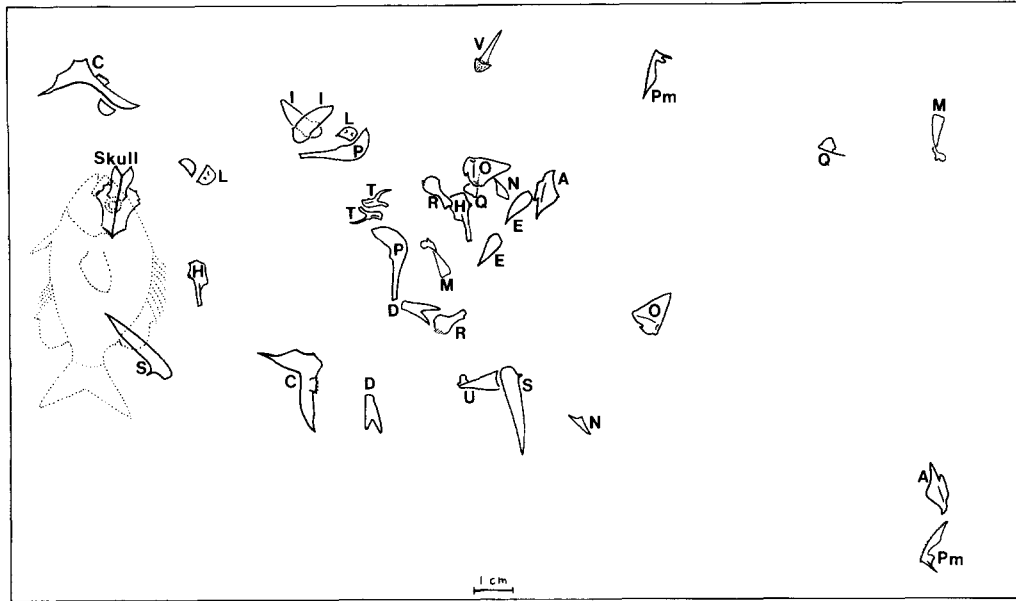


Fig.2. Distribution of major bones of a sunfish, ca. 5 cm long, after 14 days of scavenging by eight 5–12 mm gastropods. The fish's starting position is outlined on the left. Identification of bones drawn: *A* = angular; *C* = cleithrum; *D* = dentary; *E* = ectopterygoid; *H* = hyomandibula; *I* = interopercle; *L* = lacrima; *M* = maxilla; *N* = pharyngeal; *O* = opercle; *P* = preopercle; *Pm* = premaxilla; *Q* = quadrate; *R* = ceratohyal; *S* = subopercle; *Skull* = frontals and parietals; *T* = supratemporal; *U* = urohyal; *V* = vomer.

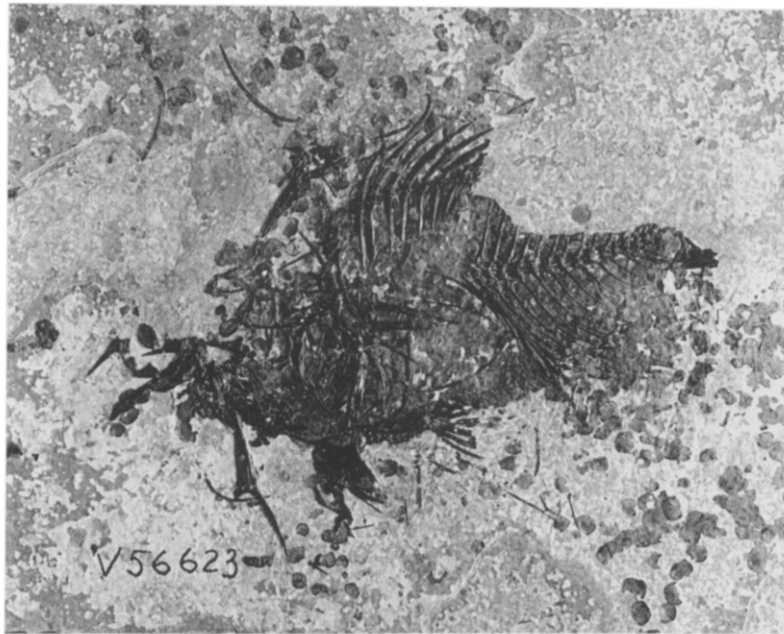


Fig.3. *Priscacara* sp., Green River Formation, Fossil, Wyoming, University of Michigan Museum of Paleontology V56623, ca. 14 cm. Note multidirectional scatter of bones and scales, especially from the head and abdomen, indicating scavenger transport.

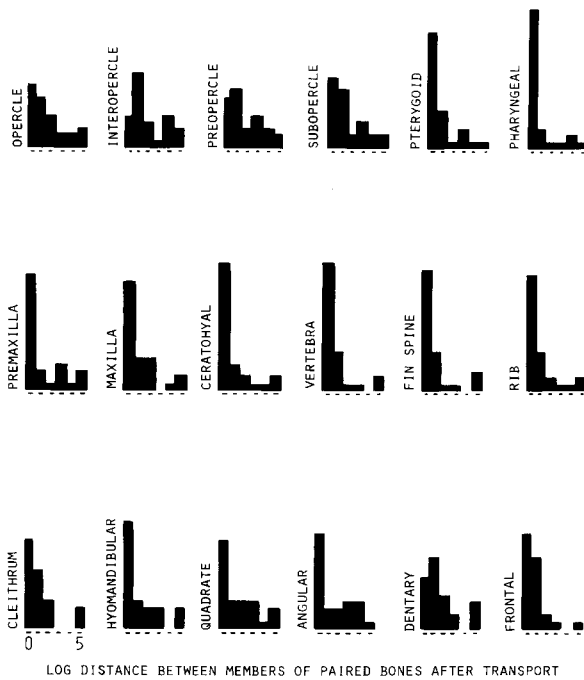


Fig.4. Frequency distributions of distances (log cm) between paired bones after transport by currents in an experimental tank. Certain shapes, especially elongate bones, show correlated responses to current, providing taphonomic information. Thirty trials represented.

experimental trials the pharyngeal bones travelled together. This distribution is generally the same for most of the elongate elements and those of more 3-dimensional shape, such as the frontals. Some of the highly 3-dimensional bones do not show this distribution so clearly because they are hydrodynamically more stable only in certain positions. Members of the pair become set in the stable position at different times and thus become more separated than simpler bones. The flat bones of the opercular series show a random pattern.

Fossil fish may be interpreted as having been under a flowing current when we observe, for example, directional scatter of scales or lepidotrichia (Fig.5), or when we observe clear indication of correlation of distances moved by disarticulated, paired elongate elements. Evidence for gentle, directional, and relatively homogeneous disturbance (in unburrowed sediments) also implies that the fish was not buried during the time of decay (Smith, G. R. and Elder, 1985). From measurements of decay of fish under different conditions, we may infer how long a fossil fish remained uncovered, an aspect of sedimentation rate.

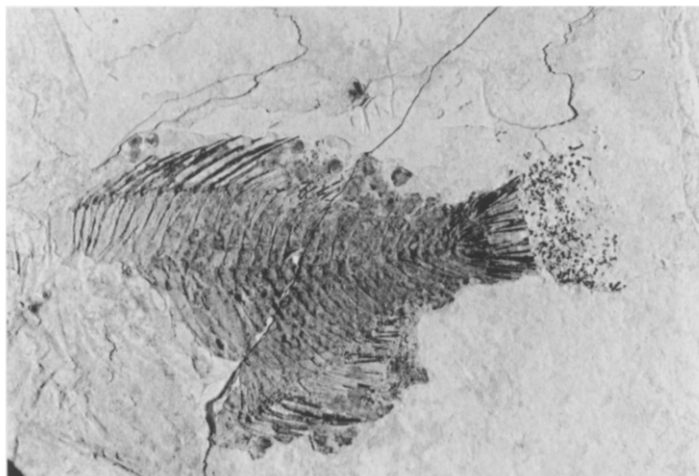


Fig.5. *Plioplarchus* sp., Sentinel Butte, North Dakota, University of Michigan Museum of Paleontology V83213, ca. 10 cm. Scales and lepidotrichia show nearly unimodal dispersal and correlated positions of similar elements, indicating current transport.

Evidence for the action of both processes is found in those specimens exhibiting multidirectional scatter and loss of many hydrodynamically light elements, such as lepidotrichia and scales, from the area. A scavenger that disturbs a skeleton after current activity may destroy the characteristic pattern of correlation and cause an overprint of the multidirectional scatter pattern. In contrast, a current acting after scavenging would not be likely to create a pattern of distance correlation among already scattered bones. This may allow distinction of the sequence of disturbance.

## Discussion

Interpretation of fossil skeletal patterns of disarticulation, disorientation, and displacement (according to the results of observable aquatic processes) allows the possibility of determining temperature and depth of lakes, inferring types of lake stratification (if any) and seasons and causes of death, and of estimating oxygen conditions and something of the chemistry and rate of sedimentation. A major advantage of using a taphonomic approach to paleoecology is its testability. There are two approaches. The traditional one has been the comparative approach to preservation systems, regarding them as natural experiments in which some factors were kept constant and others varied. This approach may be misleading when examples are chosen to illustrate conclusions drawn previously.

On the other hand, the experimental approach attempts to test taphonomic hypotheses using Recent analogies in controlled systems (Schäfer, 1972). Ancient systems may then be interpreted by the similarities of their preservation to results obtained by known processes, involving factors such as time, energy, and water.

Experimental studies offer the surest way to discover reliable generalizations about preservation of aquatic as well as terrestrial organisms in lakes and rivers. Decay, transport, and burial can be experimentally studied as pro-

cesses in which information is lost, reorganized, or stored under the control of biological activity or hydrodynamic energy. Because potential taphonomic information is correlated with the structural complexity of the organisms, fish skeletons are rich sources of data. Information loss is proportional to the number of ways in which parts of the system (various bones) can be taphonomically arranged, and increases as physical factors such as time, energy, chemical reactions, and scavengers increase the system's entropy. The several distinctive ways in which parts of the fish skeleton may be rearranged (e.g. by bacteria, currents, or scavengers) provide new information.

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