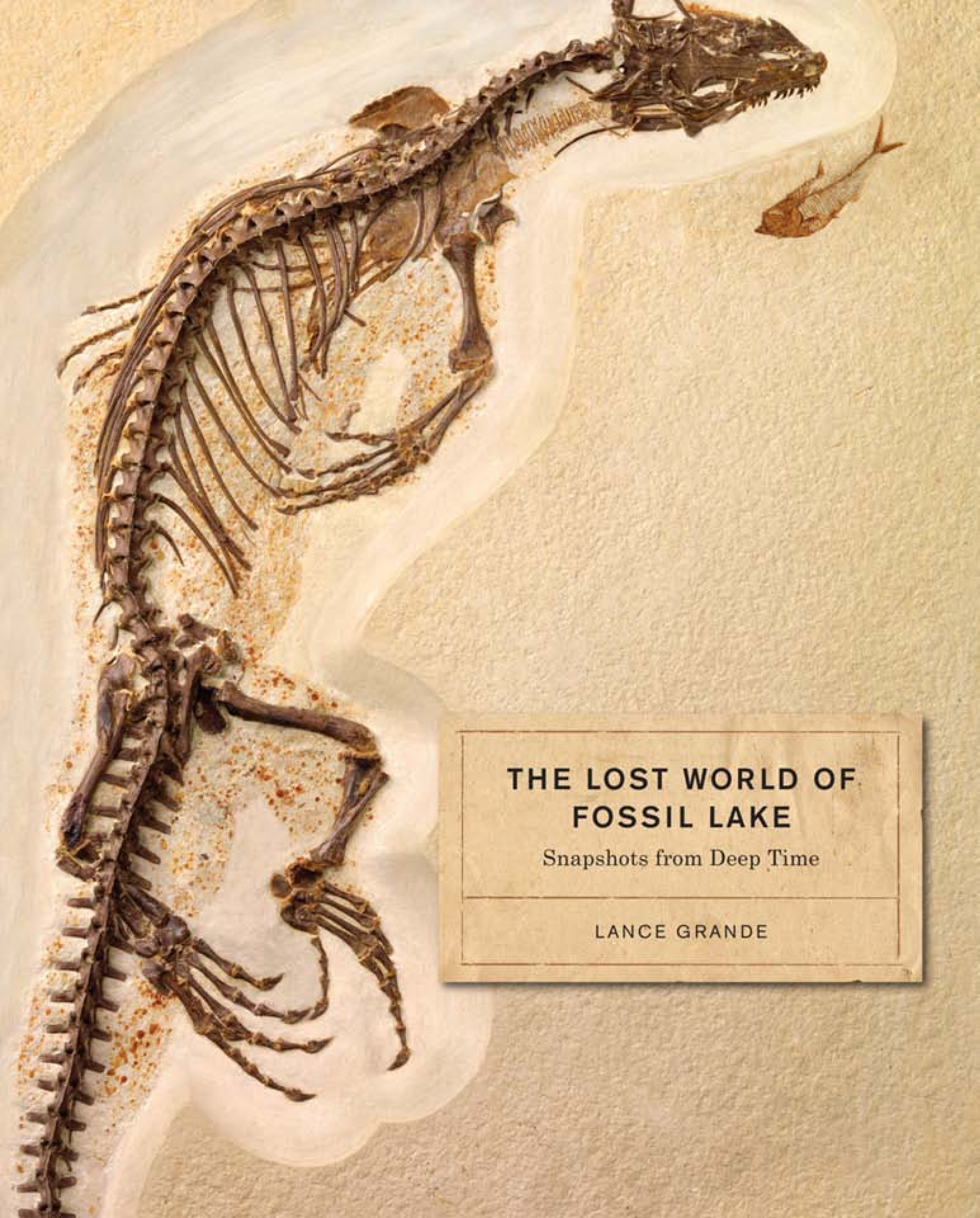
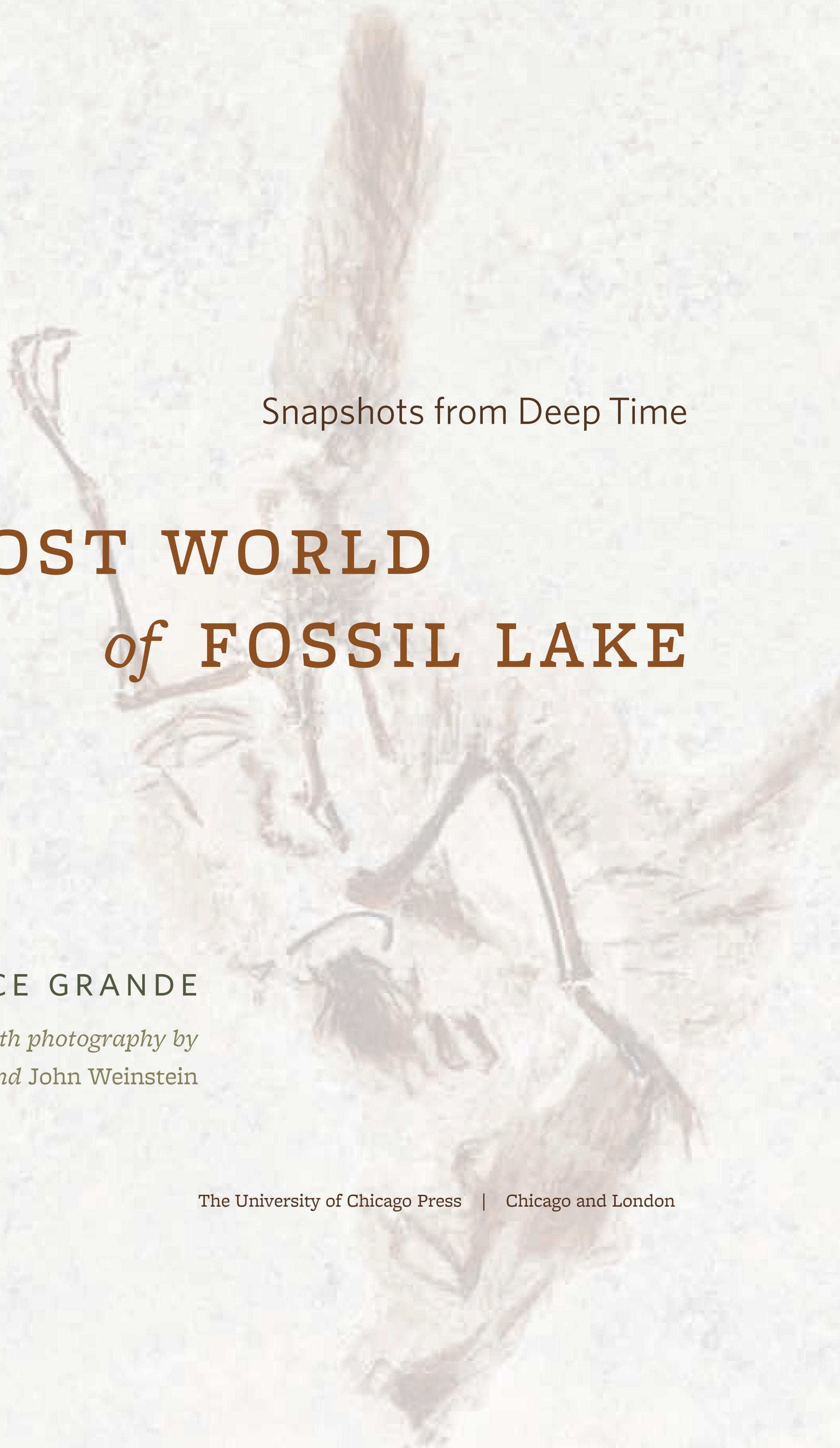


THE LOST WORLD OF FOSSIL LAKE

Snapshots from Deep Time

LANCE GRANDE



Snapshots from Deep Time

THE LOST WORLD *of* FOSSIL LAKE

LANCE GRANDE

With photography by
Lance Grande *and* John Weinstein

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Ray-Finned Fishes

(Superclass Actinopterygii)

The vast majority of fossils that have been mined from the FBM over the last century and a half have been fossil ray-finned fishes, or **ACTINOPTERYGIANS.** Literally millions of complete fossil ray-finned fish skeletons have been excavated from the FBM, the majority of which have been recovered in the last 30 years because of a post-1970s boom in the number of commercial fossil operations. Almost all vertebrate fossils in the FBM are actinopterygian fishes, with perhaps 1 out of 2,500 being a stingray and 1 out of every 5,000 to 10,000 being a **TETRAPOD.**

Some actinopterygian groups are still poorly understood because of their great diversity. One such group is the spiny-rayed suborder Percoidei with over 3,200 living species (including perch, bass, sunfishes, and thousands of other species with pointed spines in their fins). Until the living percoid species are better known, accurate classification of the FBM percoids (†*Mioplosus*, †*Priscacara*, †*Hypsiprisca*, and undescribed percoid genera) will be unsatisfactory.

Length measurements given here for actinopterygians were made from the tip of the snout to the very end of the tail fin (= total length). The FBM actinopterygian fishes presented below are as follows:

Superclass	Subclass, Super Division, or Series	Division or Subdivision	Order	Family	*(Common names of FBM taxa surveyed here)*
Actinopterygii	Chondrostei		Acipenseriformes	Polyodontidae	*(paddlefishes)*
	Holostei	Ginglymodi	Lepisosteiformes	Lepisosteidae	*(gars)*
		Halecomorphi	Amiiformes	Amiidae	*(bowfins)*
	Teleostei	Osteoglossomorpha	Hiodontiformes	Hiodontidae	*(mooneyes)*
			Osteoglossiformes	Osteoglossidae	*(bony tongues)*
		Ostarioclupeomopha	†Ellimichthyiformes	†Paraclupeidae	*(diplos)*
			Clupeiformes	Clupeidae	*(herrings)*
			Gonorynchiformes	Gonorynchidae	*(beaked sandfish)*
		Euteleostei	Esociformes	Esocidae	*(pikes and pickerels)*
			uncertain	†Asineopsidae	*(†asineops)*
			Percopsiformes	Percopsidae	*(trout-perches)*
			Perciformes	Latidae	*(perch-like)*
				Moronidae	*(temperate basses)*

Paddlefishes (Order Acipenseriformes, Family Polyodontidae)

Paddlefishes are relatively rare in the FBM, represented by the species †*Crossopholis magnicaudatus* (fig. 48). †*Crossopholis* has a very long snout region, or "paddle." Living paddlefishes are sometimes called "spoonbills," "spoonies," or even "spoonbill catfish." The last of those common names is misleading because paddlefishes are not closely related to catfishes and are instead close relatives of sturgeons. Living paddlefishes have tiny eyes, and the paddle is a sensory device lined with thousands of electroreceptor organs that allow paddlefishes to navigate and locate food, even in dark or cloudy waters. Grande and Bemis (1991, 73) found evidence that the FBM †*Crossopholis* also had such electro-sensory organs.

Paddlefishes, like their close relatives or SISTER GROUP the sturgeons, lack robust, solid vertebrae of the type found in other bony fishes of the FBM. The axial skeleton ("vertebral column") of paddlefishes is composed largely of soft tissues that do not preserve in the fossils. When first described from the FBM by Cope in 1883, †*Crossopholis magnicaudatus* was known only by a partial body and tail section lacking a head. In 1886 Cope described a second specimen consisting of a partial skull. It was not until almost a century later that the first nearly complete skeletons were reported (Grande 1980). One reason it took so

FIGURE 48

The Green River paddlefish †*Crossopholis magnicaudatus* Cope, 1883 (family Polyodontidae), from the FBM. This well-preserved specimen is 384 millimeters (1.3 feet) long and is from the sandwich beds of FBM Locality H (FMNH PF11897). *Top:* Entire fish. *Bottom:* Close-up of tiny scales in the abdominal region of the above fish. These tiny scales are each less than 0.5 millimeters (0.02 inch) in length. Scale bar equals 2 millimeters (0.08 inch).

long to discover a complete skeleton of †*Crossopholis* is that some of the commercial quarries did not recognize them, thinking them to be poorly preserved gars or some other badly preserved fish not worth collecting. The first complete paddlefish I reported in 1980 (Grande 1980, fig. II.8a) was assembled from discarded pieces I found in a scrap pile in a commercial quarry. Once *Bulletin* 63 (Grande 1980) was published and adopted as a field guide, many paddlefishes from the FBM began to show up, and today there are dozens of complete skeletons known (e.g., figs. 48, 49). Most of the paddlefishes come either from the Thompson Ranch sandwich bed quarries (e.g., FBM Locality H) or from the layers above the 18-inch layer near the K-spar tuff bed.

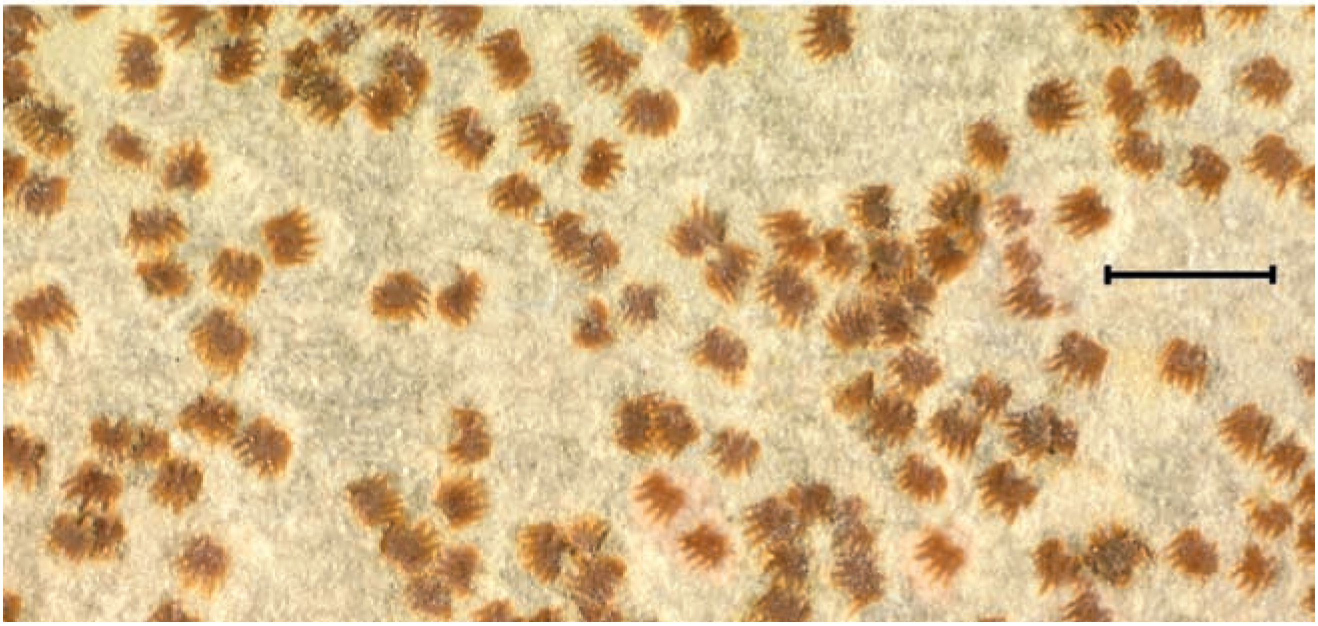


FIGURE 85
†*Mioplosus labracoides* Cope, 1877. This was a voracious species that fed largely on other fishes. Aspiration specimens (specimens preserved with fishes in their mouths or stomachs) are more common for this species than for any other fish species in the FBM. *Top:* †*Mioplosus labracoides* measuring 180 millimeters (7.1 inches) long, preserved with a †*Knightia eocaena* in its mouth; from the sandwich beds of FBM Locality H (FMNH PF10180). *Bottom:* Large †*Mioplosus labracoides* measuring 402 millimeters (1.3 feet) long, with a †*Diplomystus dentatus* preserved in its stomach region; from the 18-inch layer of FBM Locality G (FMNH PF15375).

FIGURE 89
†*Priscacara serrata* Cope, 1877. *Top:* A monstrously large individual of 414 millimeters (1.4 feet). *Bottom:* Close-up of gill arch region from above specimen showing the massive gill arch tooth plates covered with MOLARIFORM teeth; from the 18-inch layer of FBM Locality A (FMNH PF14929). These teeth were suited for crushing arthropods or mollusks.

Birds

(Class Reptilia, Superorder Aves)

Birds are not the first thing one thinks of when the word "reptile" comes to mind. But as the kangaroo and the giraffe are part of the mammalian lineage, so the bird and the crocodile are part of the reptilian lineage. In fact, crocodiles are currently thought to be more closely related to birds than they are to lizards. Birds comprise a highly successful branch of dinosaurs that survived the Late Cretaceous mass extinction event, flourished, and diversified to more than 10,000 species living today. In the Mesozoic, there were still **PROTO-FEATHERED** tyrannosaurid dinosaurs and toothed birds. Today all surviving birds are toothless, and birds have become the most species-rich group of land vertebrates. Many are strong fliers, while others are primarily ground birds or even flightless. Some live in trees or shrubs, while others are aquatic. Birds play a critical role as pollinators, seed dispersers, prey, and predators.

Recently there have been significant efforts to incorporate more of the FBM birds into the evolutionary tree of modern birds, and it has been both enlightening and very challenging. Many of the identifications here are provisional until more in-depth studies can be undertaken. Much of the challenge is due to a lack of knowledge about the evolution of modern bird skeletons and also to the current lack of adequate descriptions for so many of the FBM bird species. Nevertheless, it appears that although the FBM is most famous for its fish fossils, the diversity of bird fossils there exceeds even that of the fishes by a considerable margin (see appendices B and C). There are 34 species (several yet undescribed) belonging to at least 27 different families reported and illustrated here. In addition, there are several other undescribed

species currently represented in private collections that I did not have access to for this book. The FBM contains some of the best fossil bird localities in the world, and we are only beginning to understand its scope. It clearly documents early diversification of the major lineages of living birds after the Late Cretaceous mass extinction. The presence of birds such as jacamars, mousebirds, and several species of parrot in the FBM are suggestive of a subtropical forested environment.

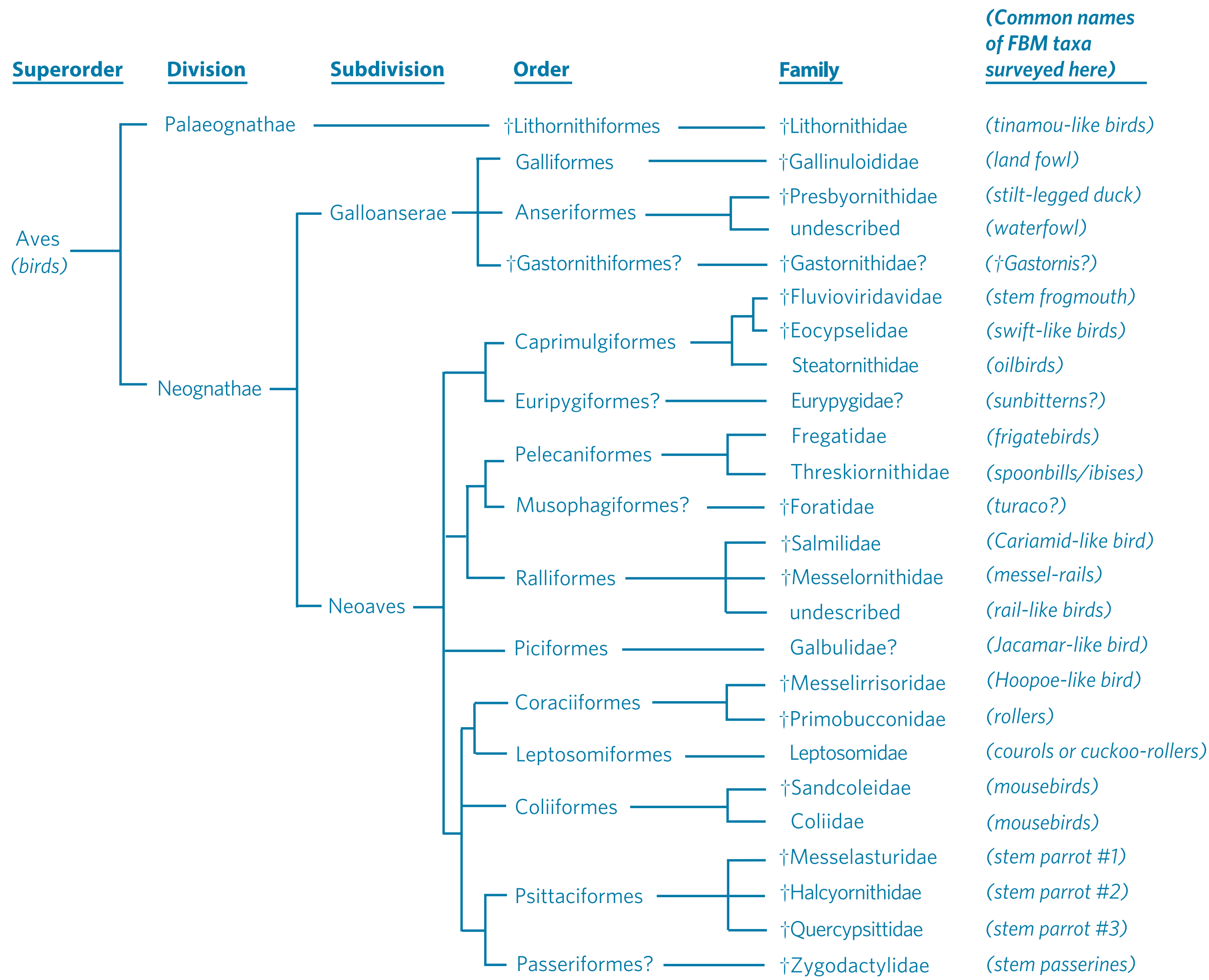
Isolated feathers are the most common of all bird fossils in the FBM. Some are intriguing because of their large size, indicating a giant bird lived near Fossil Lake that we have yet to find as a skeleton (fig. 114, *bottom*). This could possibly be a feather from the giant ground bird †*Gastornis* (also known as †*Diatryma*) found in other early and middle Eocene fossil localities in Wyoming. This giant bird stood over 1.8 meters (6 feet) in height and possessed powerful legs, large taloned feet, a massive head, and a fearsome beak several times larger than that of an ostrich. These huge birds are thought by some paleontologists to have been carnivores that fed on mammals and other vertebrates. Other paleontologists contend that they may have been herbivores that fed on large seeds, twigs, and other plant materials, although the large fearsome beak seems excessive for a strict herbivore. If †*Gastornis* was indeed a predator, it would have been at the top of the terrestrial food chain around Fossil Lake, because large predatory mammals had not yet evolved. These avian giants are currently thought to be closely related to Galloanserae (fowl) and evolved from birds that could fly. No bones of †*Gastornis* have yet been reported from the FBM.

FIGURE 114
Bird feathers from several FBM localities. *Top left:* Specimen measuring 52 millimeters (2 inches) in length, from the 18-inch layer of FBM Locality A (FMNH PA727). *Top middle:* Two feathers separated by a substantial period of time (11 laminar couplets probably representing several years) on the same small slab—a rare coincidence. Specimen is from the sandwich beds of FBM Locality L (FMNH PA785). Smaller feather is 40 millimeters (1.6 inches) long. *Top right:* Specimen from the 18-inch layer of FBM Locality G; feather is 70 millimeters (2.8 inches) long (FMNH PA784). *Bottom:* Large feather measuring 240 millimeters (9.4 inches) long from an unknown giant bird, possibly †*Gastornis* (Galloanserae). Specimen is from just below the K-spar tuff beds at FBM Locality A (FOBU 13445A).

The FBM bird skeletons are occasionally preserved with feathers, particularly in the mid-lake deposits (e.g., figs. 130, 143B, and frontispiece), but preparation of these feathers requires extreme meticulousness if they do not split out naturally when excavated. Occasionally, commercial preparators will enhance the damaged feathers with paint, which is easy to detect under magnification (e.g., fig. 131, *left*). The birds in figures 130 and 143B each took several months of full-time preparation under a microscope to properly reveal the feathers without requiring any restoration.

In the FBM, bird skulls and relatively complete articulated bird skeletons make up about .001 percent of the vertebrate fossils being excavated (about 1 in 10,000 vertebrates). Because there have been millions of vertebrate specimens mined from the FBM to date, there are well over 200 bird skulls and/or relatively complete articulated skeletons that have been discovered, some in museums and some in private collections. In addition, there are many smaller fragments of birds (e.g., isolated feet, wings, or other body parts) that are the result of postmortem disarticulation in water or possibly the remnants of a predator's meal.

The most common bird species in the FBM appear to be fish-eating, wading, and otherwise aquatic birds (e.g., frigatebirds and †presbyornithids), rail-like forms (e.g., †messelornithids), Palaeognathous birds (†lithornithids), and roller-like birds (†primobucconids); but the greatest amount of diversity appears to be among the small aerial species. However, because the sample size of birds studied from the FBM is still relatively small compared to that of the fishes, there is a great deal of diversity remaining to be discovered and described in the FBM bird fauna. The classification tree for living orders of birds that I follow here is after Hackett et al. (2008). The FBM birds presented below, in context with living relatives, are as follows:



Tinamou-like Birds (Order †Lithornithiformes, Family †Lithornithidae)

This extinct order and family of birds contains the only members of the Palaeognathae in the FBM. Today the Palaeognathae, named for their distinctive palate morphology, include ostrich, kiwis, rheas, cassowaries, emus, and tinamous. None of these groups occurs in North America today. The †lithorniforms superficially

FIGURE 115

†*Pseudocrypturus cercanaxius* Houde, 1988, from the extinct tinamou-like family †Lithornithidae; from the FBM sandwich beds. *Top:* Casts of the part and counterpart of "split-skull" from FBM Locality H before the two sides were glued together and prepared as a single piece (casts of original split slab are both numbered FOBU 11712). Head length is 97 millimeters (3.8 inches). These two splits were later glued together and prepared from both sides (see fig. 116). *Bottom:* A complete skeleton from FBM Locality M. Original specimen WDC CGR-108 with a head length of 99 millimeters (3.9 inches). A cast of this specimen is FMNH PA732.

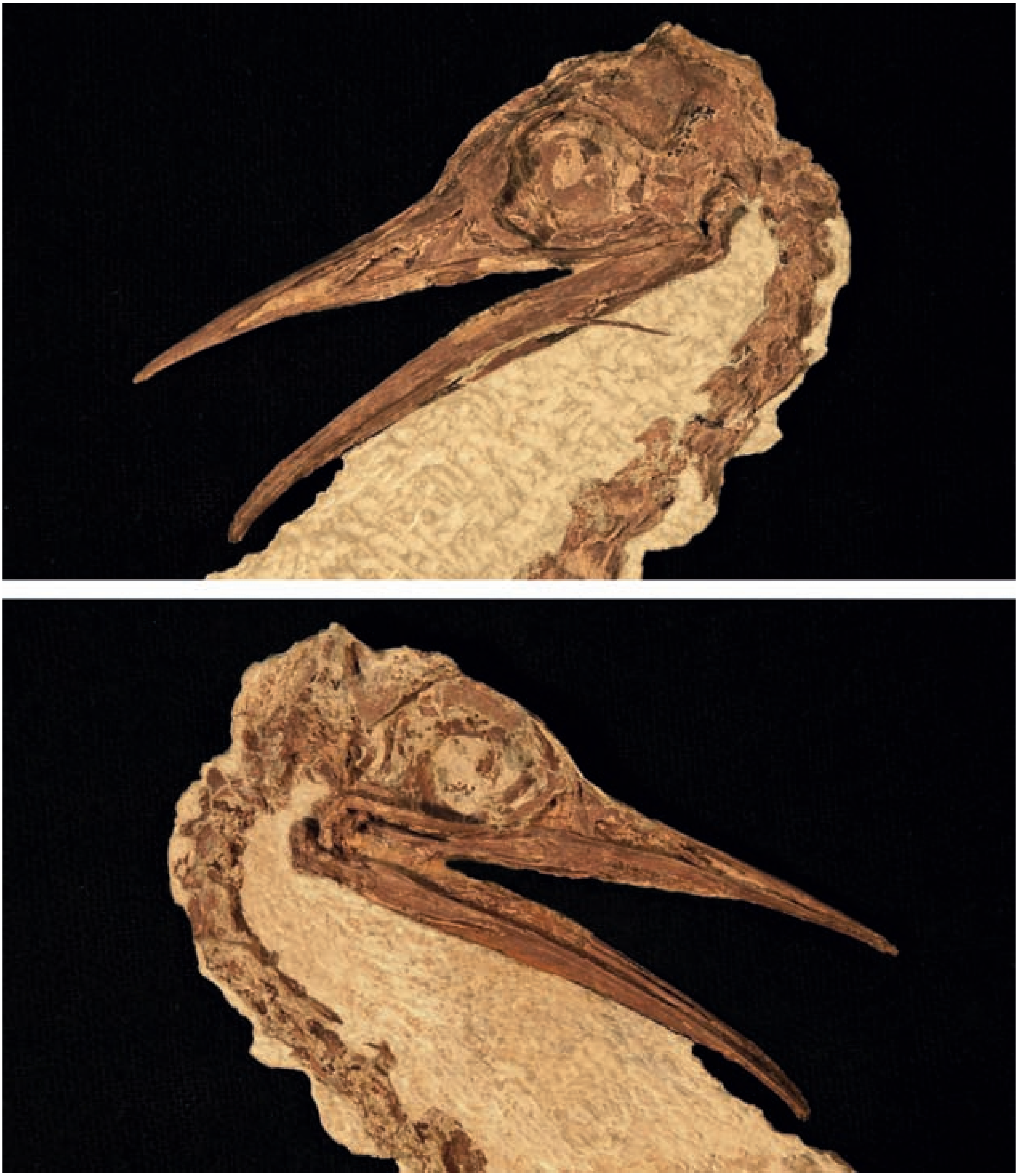


FIGURE 116
†*Pseudocrypturus cercanaxius* Houde, 1988, HOLOTYPE, prepared by gluing the two split skull pieces together (see fig. 115, *top*). Once the two sides were reconnected to each other, the skull was acid-prepared from both sides (UNSM 336103). Skull length is 98 millimeters (3.9 inches). *Top:* Left side. *Bottom:* Right side.

FIGURE 117
†*Pseudocrypturus* sp., an undescribed tinamou-like species of †Lithornithidae. Beautifully preserved complete skeleton, from the sandwich beds of FBM Locality H, with a skull length of 98 millimeters (3.9 inches) (SMA 0186).

resemble tinamou, a neotropical group of the Americas. They are so far known by seven species from the late Paleocene to mid-Eocene of North America, and one species from the early Eocene of Europe. †Lithornithid species are known as early as late Paleocene, but appear to have become extinct by the late middle Eocene. In the FBM, there is one described species of †lithornithid, †*Pseudocrypturus cercanaxius* (figs. 115, 116). The holotype for this species is a skull and neck prepared from both sides (fig. 116), which was made after gluing two sides of a Thompson Ranch "split-skull" together (fig. 115, *top*). Later a complete skeleton of this species was discovered (e.g., fig. 115, *bottom*). †*Pseudocrypturus cercanaxius* had long legs and a relatively long, narrow beak. It may have used this beak for probing along shorelines and shallow waters for insects and other invertebrates. Its wing

FIGURE 119

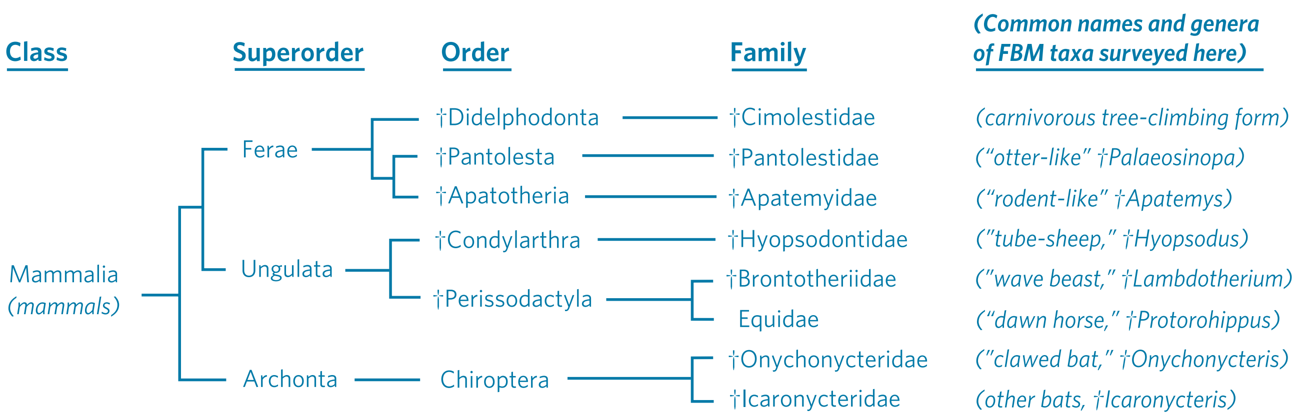
†*Presbyornus* sp., an as yet-undescribed long-legged waterfowl species of the extinct family †Presbyornithidae, from shoreline deposits of FBM Locality N. This species is so far known only on the basis of bone beds from Eocene nesting sites. Although no articulated skeletons have yet been found in the FBM, a composite skeleton has been made based on hundreds of isolated bones prepared out of the bone beds. *Left:* A composite skeleton mount made from the bone bed material (UMNH uncataloged). Skull length is 90 millimeters (3.5 inches). *Right top:* A skull 89 millimeters (3.5 inches) long still in matrix from the bone bed (UMNH uncataloged). *Right bottom:* A slab from the bone bed (bones were later prepared out and are in the collection of UMNH). Photos courtesy of Mark Loewen.

Mammals

(Class Mammalia)

There are literally hundreds of Eocene mammal localities in North America, but the FBM localities have one very significant advantage over most of the others: the FBM fossils are almost always complete, articulated skeletons. Even pieces that are now incomplete appear to be that way because the quarrier did not collect the rest of the specimen in the field (e.g., fig. 151). Most other Eocene mammal localities were formed in high-energy environments such as rivers and streams, and produce mainly isolated teeth, jawbones, and other fragments. In fact, many Eocene mammal species have been described and named based solely on teeth, and the form of the skeleton remains completely unknown. And many isolated bones have been found that cannot be assigned to a tooth-based species because no complete skeletons exist to show which body and limb bones go with which teeth. Thus there is much to be learned about extinct mammalian groups from the beautifully preserved complete skeletons from the FBM. Some of the FBM skeletons provide a Rosetta-stone-like key to correlating teeth and isolated body bones for certain extinct families of mammals. That said, mammal fossils are extremely rare from the FBM, except for one of the bat species †*Icaronycteris index*, now known by about 50 skeletons. Most other mammal species from the FBM are known by only one or two specimens each (most illustrated in this book), and mammal skeletons other than bats from the FBM have come to light only within the last several decades (e.g., after publication of Grande 1984). However, with the intense level of quarrying activity currently under way, I am sure that the FBM will yield many more mammal species in the years to come.

The most common mammals in the FBM by far are bats (many of these in private collections). The second most common form is the otter-like †*Paleosinopa*, currently known by three skeletons. †Brontotheres are also known from the FBM by two partial skeletons and one articulated foot. Other mammal taxa known from the FBM are each represented by a single specimen as far as I was aware of at the time of writing this. The broader mammal classification used here roughly follows that of Rose (2006). The FBM mammals presented below are as follows:



Carnivorous Tree-Climbing Form (Order †Didelphodonta, Family †Cimolestidae)

In the 1980s there was a very peculiar but beautifully preserved complete mammal skeleton discovered in the nearshore Thompson Ranch FBM Locality H (figs. 144, 145). It is evidently a tree-climbing carnivorous form not seen before. It has an extremely long and PREHENSILE tail that adapted it to be able to grasp tree branches. It is the earliest prehensile tail known for any placental mammal, and the tail has more vertebrae than in any other known mammal (Michelle Spaulding, pers. comm., 2011). Together with its long fingers and toes, the tail would

FIGURE 144
An undescribed species of tree-climbing carnivore in the extinct family †Cimolestidae. Beautifully preserved complete skeleton (partly enlarged in the next figure). Note the extremely long tail, which has the largest number of vertebrae of any known mammal (Michelle Spaulding, pers. comm., 2011) and is the earliest known example of a prehensile tail in mammals. Specimen is from the sandwich beds of FBM Locality H and has a head length of 56 millimeters (2.2 inches) (FMNH PM1095).

The many species of †*Hyopsodus* were small rat-size to raccoon-size species of mammals ranging from early through late Eocene time in North America, Asia, and Europe. The very few known specimens with postcranial skeletons preserved indicate that †*Hyopsodus* had a strange, weasel-like body shape. This profile has led to the common name of "tube-sheep" occasionally used for these animals, although they were clearly smaller than sheep in size. In addition to its narrow body shape, †*Hyopsodus* had a muscular chest, claws, and short limbs, suggesting a propensity for digging or rooting. It is also thought to have lived part of its life in trees. It may also have been a swimmer because it is commonly found in near-shore deposits of the Bridger Formation. The teeth of †*Hyopsodus* suggest that its diet was that of a generalist. It could have fed on plants and small animals, and because it inhabited lakeshore regions, it may have been another of the many animals that relied on aquatic animals for food. The disappearance of the great Eocene Lake systems may have been part of what led to the decline of the family in the late Eocene. †*Hyopsodus* evidently favored a subtropical climate, and as the climate began to cool in the late Eocene, its numbers declined until the end of the Eocene, when it appears to have became extinct.

Currently the FBM specimen of †*Hyopsodus wortmani* is being studied by Dunn and Rose (Ken Rose, pers. comm., 2010), and a detailed description of it is forthcoming.

Brontotheres and Horses (Order †Perissodactyla, Families †Brontotheriidae and Equidae)

There are two known species and families of perissodactyl that have been found in the FBM: the "wave beast" †*Lambdotherium popoagicum* (family †Brontotheriidae) and the "dawn horse" †*Protorohippus venticolus* (family Equidae). The order Perissodactyla today contains horses, tapirs, and rhinoceroses, but also includes over a dozen extinct families. The order is otherwise known as the "odd-toed ungulates," and ungulates are the "hooved mammals." "Odd-toed" refers to the character of having a single toe or a middle toe that is larger than the toes on either side, rather than having an even number of toes. Perissodactyls are thought to have evolved in Asia, and the earliest known fossils of the order are thought to be early Eocene in age.

There are two partial skeletons of †*Lambdotherium popoagicum* known from the FBM; an 18-inch layer specimen from FBM Locality B (fig. 151, *left*) and another specimen from the sandwich beds of FBM Locality I (fig. 151, *right*). Unfortunately, the skeletons were each only partly collected by the commercial quarrier who found them, because their importance or value was not initially recognized. (Under the covering layer of rock, only a few bumps could be seen, and they were originally thought to be disarticulated fishes, which the commercial quarriers rarely bother to collect). In addition to the two partial skeletons illustrated

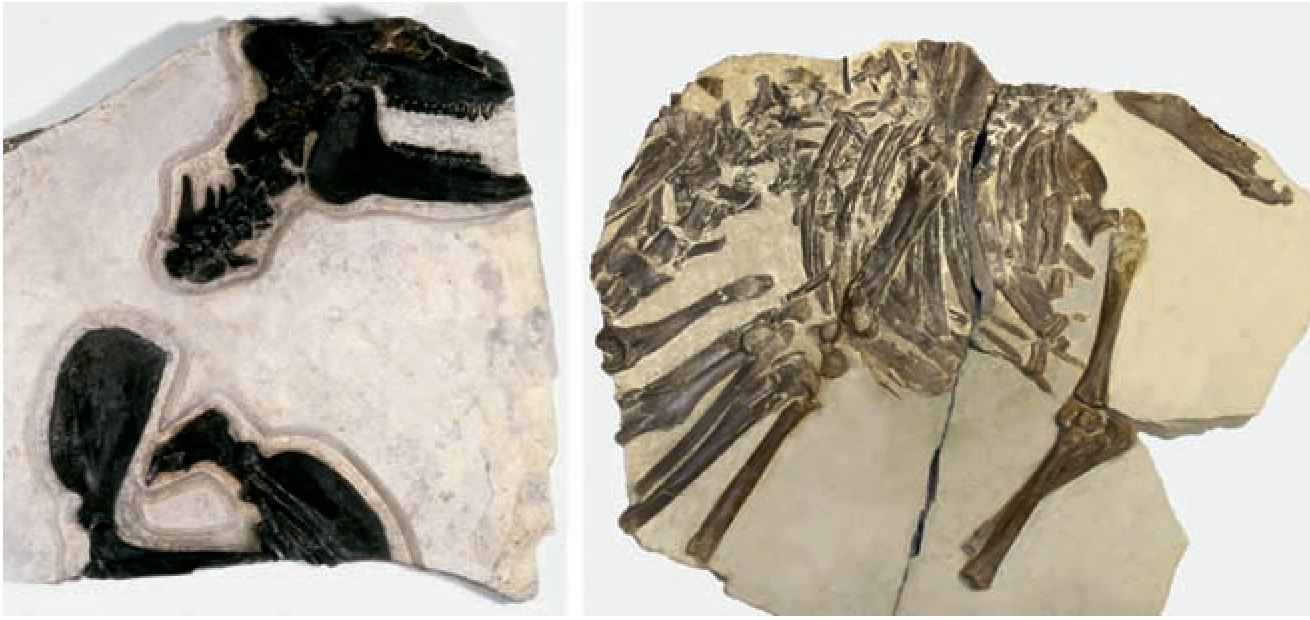


FIGURE 151
†*Lambdotherium popoagicum* Cope, 1880, a mammal species in the extinct family †Brontotheriidae. Two skeletons that were probably both originally complete skeletons. They were, unfortunately, incompletely collected in the commercial quarries where they were found. *Left:* Head, neck, and shoulder girdle of an incompletely collected specimen. Currently in a private collection, but a detailed cast of this specimen is FMNH PM61126. Original is from the 18-inch layer of FBM Locality B, and the length of the lower jaw is 134 millimeters (5.3 inches). *Right:* Lower jaw and partial postcranial skeleton of another incompletely collected specimen from the sandwich beds of FBM Locality I (UW 21883); lower jaw is 112 millimeters (4.4 inches) long. Image courtesy of Michael Cassiliano.

here, there is also an articulated foot from the 18-inch layer in the collection of the Department of Geology at the University of Wyoming (UW 40362).

†*Lambdotherium* is sometimes considered to be in a separate family, †Lambdotheriidae, but Rose (2006) considers it to belong with the †brontotheres in the †Brontotheriidae. The closest living relatives to the †Brontotheriidae are horses, which together with †Brontotheriidae make up the suborder Hippomorpha. The name "wave beast" comes from some of the larger species of the family, the †brontotheres (or †titanotheres), which were immense creatures and some of the largest land animals of Cenozoic time. The family †Brontotheriidae are thought to have become extinct in North America at the end of the Eocene and slightly later in Eurasia. There was a trend for increasing size in the family, with the smaller forms such as †*Lambdotherium* known in the early Eocene and the largest forms in the late Eocene.

†*Lambdotherium* was the earliest genus of the family †Brontotheriidae. The teeth suggest it fed on coarse vegetation such as leaves and twigs. The appearance of the †*Lambdotherium* in a mid-lake deposit is surprising because there is no evidence that †*Lambdotherium* was a swimmer, but the partial disarticulation of the skeleton suggests that the animal's carcass may have been transported some distance to the mid-lake region by currents.

One of the most remarkable finds of recent years in the FBM was the discovery of a complete skeleton of a "dawn horse" (figs. 152, 153). The nomenclature (i.e., taxonomic names) of fossil horses is in flux right now. Previous names that

FIGURE 152
†*Protorohippus venticolus* (Cope, 1881), the "dawn horse" in the extant family Equidae. Beautifully preserved specimen on a slab with †*Knightia eocaena* and †*Diplomystus dentatus* is currently in a private collection, but a detailed cast of it is FMNH PM61117. Original specimen is from FBM Locality D; the horse has a head length of 150 millimeters (5.9 inches).

have been used for the dawn horse are †*Eohippus* and †*Hyracotherium*, but both of these names have been found to belong more correctly to other animals, so the most recent name applied to the FBM species is †*Protorohippus* (also occasionally referred to as the "mountain horse") and the species appears to be †*Protorohippus venticolus* (Aaron Wood, pers. comm., 2010). †*Protorohippus* belongs to the horse family, Equidae, which today contains seven living species, including horses, donkeys, and zebras.

The FBM specimen is the most complete articulated skeleton of a dawn horse ever discovered. How it got to the middle region of the Eocene lake (FBM Locality D) is a tantalizing question, particularly given the perfect articulation of all the bones. Horses have the ability to swim, although they are not aquatic

Non-Eudicot Flowering Plants

(Phylum Angiospermophyta; Subclasses Magnoliids, Monocotyledons, and Ceratophyliids)

The flowering plants (angiosperms, phylum Angiospermatophyta) are the most diverse group of land plants living today. They are characterized by a number of uniquely derived features, including the ability to produce flowers, fruit surrounding the seeds, and an ENDOSPERM within the seed. By the Late Cretaceous, angiosperms had replaced ferns and cycads as the dominant land plants, and from the Late Cretaceous through early Eocene, large canopy-forming angiosperm trees became more and more dominant in forest environments formerly dominated by conifers. There is such a wide variety of flowering plants represented in the FBM that I divide them into two organizational sections here: non-eudicot flowering plants in this section (subclasses Magnoliids, Monocotyledons, and Ceratophyliids) and eudicot flowering plants in the next section (subclass Tricolpates). The major groups of angiosperms known from the FBM are as follows:

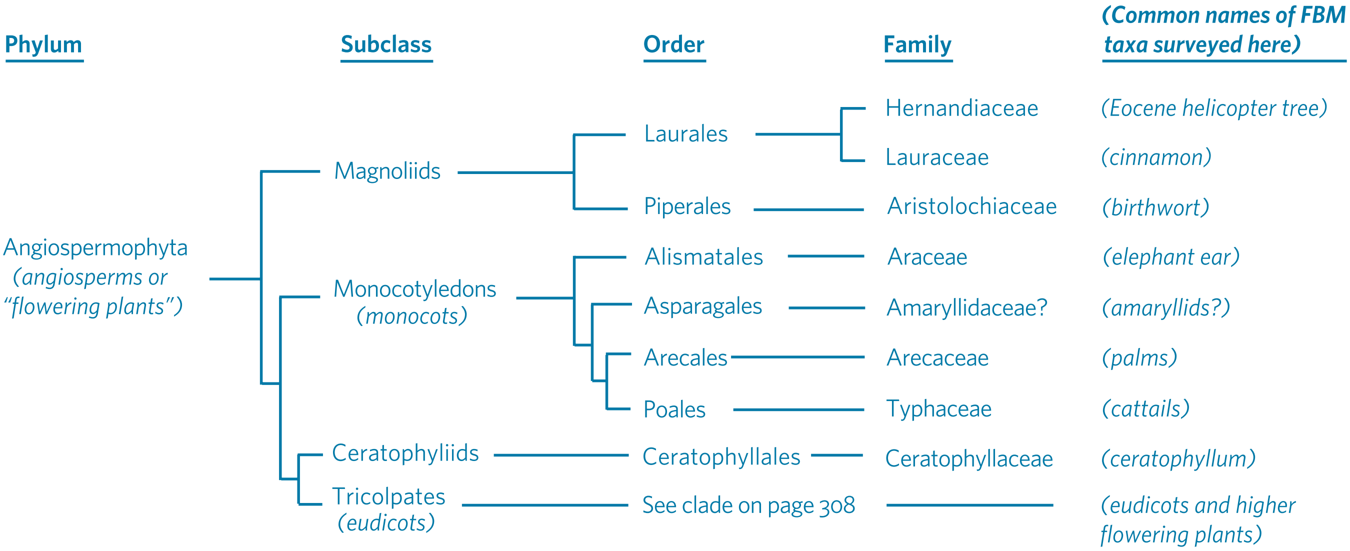


FIGURE 165

Gyrocarpus sp., from the 18-inch layer of FBM Locality A. *Left:* Trilobed variant of a very large leaf (family Hernandiaceae). Total length is 300 millimeters (11.8 inches) (FMNH PP53567). There is much variation in shape for this species (see fig. 157), but note the very long PETIOLE, smooth leaf margins, and PALMATE VENATION. *Right:* Winged seed measuring 60 millimeters (2.4 inches) in length that possibly belongs to this species (FMNH PP 54857).

Reading the Pages of Deep History

So how do we interpret this extinct community, so beautifully preserved within the FBM? The diverse assemblage of fossils presents us with **EMPIRICAL** data with which to reconstruct deep history. It raises a number of questions as well.

The Paleoecology of Fossil Lake: What Was Life Like 52 Million Years Ago in Southwestern Wyoming?

The fossils in the FBM make up a collage of 52-million-year-old "snapshots" documenting a biologically diverse freshwater lake surrounded by subtropical lowlands and more distant temperate upland regions. The plants and animals were transitional species between the age of the dinosaurs and modern day. The early Eocene included the warmest global temperatures of the Cenozoic era (Wilf 2000); and the warm, humid climate of Fossil Lake was similar to the present climate of the Gulf coast and southern Atlantic regions of the United States, with an annual rainfall of 30 to 40 inches and nearly frostless winters (Bradley 1929, 1948; MacGinitie 1969). That ecosystem and ecology contrast sharply with the cool mountain-desert climate that exists in the region today (fig. 213). There were active volcanoes about 120 miles north of the lake that had several major eruptions during the lake's existence and left thin ash layers within the FBM. Occasionally these eruptions caused massive forest fires and catastrophic mass kills in the lake, as evidenced by occasional beds that are heavily blackened with carbon and charcoal occurring just above or below fish mass-mortality layers.

A natural balance of prey and predator existed in the lake for millennia as part of a complex food chain. Algae such as *Pediastrum* sp. were the PRIMARY PRODUCERS that converted sunlight and carbon dioxide into sugar and served as the primary food source of the lake. PRIMARY CONSUMERS included vast schools of the filter-feeding fish †*Knightia eocaena*. This species existed in the lake by the billions and fed on primary producers such as algae and other microorganisms. It was the most common of all the fish species in the lake, and it reproduced in great numbers, providing one of the most abundant food sources for higher links in the food chain. SECONDARY CONSUMERS included predaceous fishes (†*Crossopholis*, *Lepisosteus*, *Amia*, *Atractosteus*, †*Phareodus*, †*Diplomystus*, †*Priscacara*, and †*Mioplosus*), as well as frigatebirds, bats, trionychid turtles, aquatic lizards, small crocodilians, the otter-like †pantolestid, and many other animals. †*Knightia* was the primary link in the food chain that fueled this level of the ecosystem. And at the top there were TERTIARY CONSUMERS such as the large crocodiles, alligators, monitor lizards, and giant trionychid turtles that preyed on the secondary consumers. On shore the primary producers were land plants and shallow-water plants that were fed upon by herbivores ranging from insects to the small horse †*Protorohippus venticolus*. Insects were, in turn, fed upon by secondary consumers like birds, bats, fishes, and insectivorous mammals; and perhaps †*Protorohippus* occasionally fell prey to the large crocodiles in the lake.

Near the shore there were aquatic organisms such as water lilies, floating ferns, ceratophyllum, and many kinds of swimming insect larvae and nymphs. Along the shoreline were cattails, horsetail, elephant ear plants, ferns, sumac, balloon vines, and palms. An abundance of very large well-preserved palm fronds in the FBM indicate that large groves of palm trees must have grown close to the water's edge. Dragonflies and damselflies filled the air along the shoreline while clouds of march flies and small biting gnats swarmed over the water. The nearshore aquatic plants helped provide nursery grounds for the many schools of baby fishes that dwelt there. The lake was filled by water flowing down from the uplands, including a major river to the northeast. This resulted in some river inhabitants showing up in the northern nearshore FBM quarries from time to time, like the pickerel †*Esox kronneri*, the Eocene mooneye †*Hiodon falcatus*, the trout-perch †*Amphiplaga brachyptera*, clams, the otter-like †*Palaeosinopa*, as well as freshwater shrimp and crayfish.

FIGURE 213

Fossil Lake, then and now. *Top:* Reconstruction of near-eastern shore as it may have looked 52 million years ago. The two dawn horses (†*Protorohippus*) drink at the water's edge while being viewed by a crocodile (†*Borealosuchus*), and out in the lake frigatebirds (†*Limnofregata*) dive to the surface to snatch small herring (†*Knightia*) for dinner. Palms (†*Sabalites*) and elephant ear plants (*Colocasia*) line the shore near the lake's edge, with climbing ferns (*Lygodium*) on some of the palm trunks. Cattail (*Typha*) and water lotus (*Nelumbo*) grow in the water near shore. In the far distance, part of the surrounding highlands is visible. *Bottom:* What remains of Fossil Lake today: the limestone of the FBM at the tops of isolated buttes with eroded valleys in between. The remaining record of Fossil Lake is encapsulated in the sedimentary rock layers being mined there.

The river also carried cooler-climate vegetation into the lake. The more temperate, cooler-climate plants in the distant highlands—including conifer, plane trees, and sweetgum—shed their leaves and fruits into streams and rivers flowing down the mountains.

Around the lake were small groups of the three-toed "dawn horse," †*Protorohippus venticolus*, which grazed on vegetation. The palms and other trees were filled with a diverse array of birds, insects, and small carnivorous mammals. The large true carnivores of today of the mammalian order Carnivora had not yet evolved, and those mammalian forms occupying that niche were very different than those of today. One such form was a small carnivorous tree-climbing mammal, the first to have developed a prehensile tail allowing it an agile life in the trees (fig. 144). It swung freely through the tree canopy with its long tail and graceful arms and legs, feeding on small animals along the way. The top predators of the time continued to be reptilian, such as the large crocodiles and monitor lizards, as well as the giant 2-meter-tall flightless bird †*Gastornis*. The daytime skies contained frigatebirds that swooped down from the sky to feed on fishes and other small vertebrates in the lake. Rails, rollers, and birds that resembled a cross between ducks and flamingos were common shorebirds, and many species of parrots inhabited the trees surrounding the lake. It is hard today to think of Wyoming as a hotspot for parrot diversity! There were colonies of bats near the north end of the lake, where most of the 35 or so fossil bat specimens have been discovered. Today, bats use echolocation as a way to navigate and find food in the dark. One of the bat species that lived near Fossil Lake, †*Onychonycteris finneyi*, appears to have lacked the ability to echolocate and may have been a day flier also inhabiting nearshore trees.

From palm trees to crocodiles, the FBM fossils provide a quasi-photographic record of a lost world. There are more than just a few isolated plant and animal species preserved here; there is a complex and vibrant ecosystem locked in stone.

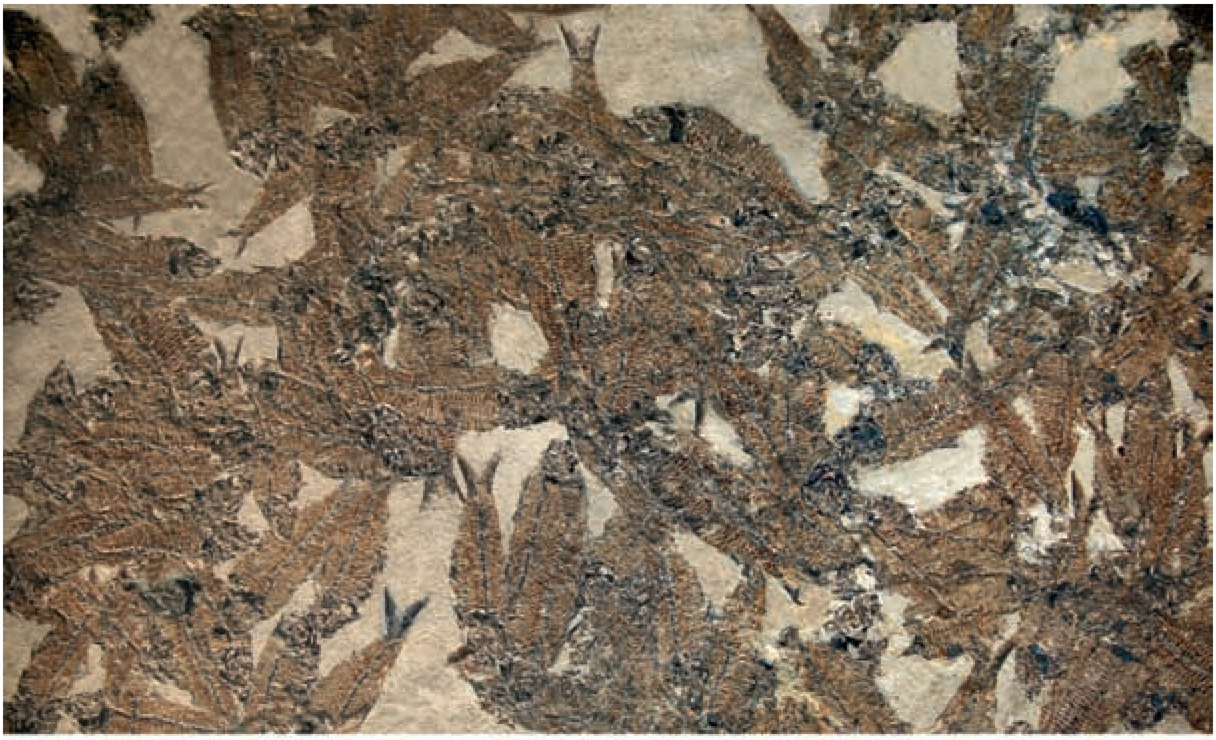
Death and Mass Mortality in Eocene Fossil Lake: What Killed Everything?

The spectacular abundance of fossils in the FBM and their often life-like preservation raises the question: What killed these organisms? There are many possible explanations. Many catastrophic deaths were due to mass-mortality events that killed thousands or even hundreds of thousands of individuals at a time. Other deaths were clearly due to individual causes such as predation. Then there are specimens in which the cause of death is still a mystery.

Ecological catastrophes are not rare in nature. In fact, throughout Earth's history, and even today, catastrophic events involving mass mortalities in aquatic environments are common. But it is rare that documentations of geologically ancient catastrophes are as well preserved as they are in the FBM. Ecological catastrophes occur at many different scales, and they could be classified as one of two basic types: *global mass extinction* or *regional mass mortality*. Global mass-extinction events are rare phenomena that involve the extinction of 50 percent or more of all species on the planet and can take hundreds or even thousands of years from start to finish. There have been at least five of these in the last 540 million years, and a good example is the one at the end of the Cretaceous, discussed on page 2. The FBM captures a picture of the early recovery of the North American BIOTA, roughly midway between the post-Cretaceous global mass-extinction event and today.

The FBM mortalities were not global in nature. Instead, the many mortality layers of the FBM represent regional mass mortalities. Regional mass mortalities are relatively common ecological events. These events are localized rather than global in scale and take place quickly, usually in a matter of hours, days, or weeks. Today, these type of mortality events commonly occur in aquatic environments and result from factors ranging from an overly warm summer day in a shallow bay to an oil spill in the ocean. There are several places where the regional rapid die-off of millions of fishes and aquatic organisms occurs repeatedly, even annually (e.g., Scott and Crossman 1973, 126). Smith (1949) described modern examples of bays where the bottom was covered with a solid mass of fish carcasses. Although localized die-offs in nature are not uncommon, conditions that allow fossilized preservation of these mass mortalities are very rare.

Several scientific explanations have been offered for the localized mass mortalities that occurred within the FBM. It is important to remember that the FBM is not a single mass mortality. The FBM spanned at least many thousands of years, and within it there are some layers with millions or billions of fossils, and others with very few fossils. Many different regional mass mortalities occurred throughout the duration of Eocene Fossil Lake. Within the mid-lake quarries, these are represented by several different zones, including many consisting almost exclusively of †*Knightia eocaena*. The †*Knightia* "death layers" represent enormous schools that were quickly killed, and some layers contain up to hundreds of bodies per square meter. There is one †*Knightia eocaena* mass-mortality zone that occurs on parts of Fossil Ridge at the base of the 18-inch layer (e.g., fig. 214, *top*), one that occurs near the K-spar tuff layer (fig. 74), and several others in between. Within the 18-inch layer, there are also several mass mortalities of the percoid fish †*Cockerellites liops*, the most prominent of which is a layer just above a volcanic ash (bentonitic) layer about one-third of the way down in the 18-inch layer of the mid-lake deposits (e.g., fig. 93). There is also a mass-mortality layer of small specimens of the percoid †*Mioplosus* near the K-spar tuff zone in FBM Locality A (fig. 83, *bottom*). All of these species-specific mass mortalities represent mass kills of enormous schools of fishes over a short period of time, sometimes covering areas of thousands of square meters or more. This brings us back to the question: What caused the mass mortalities in the FBM?



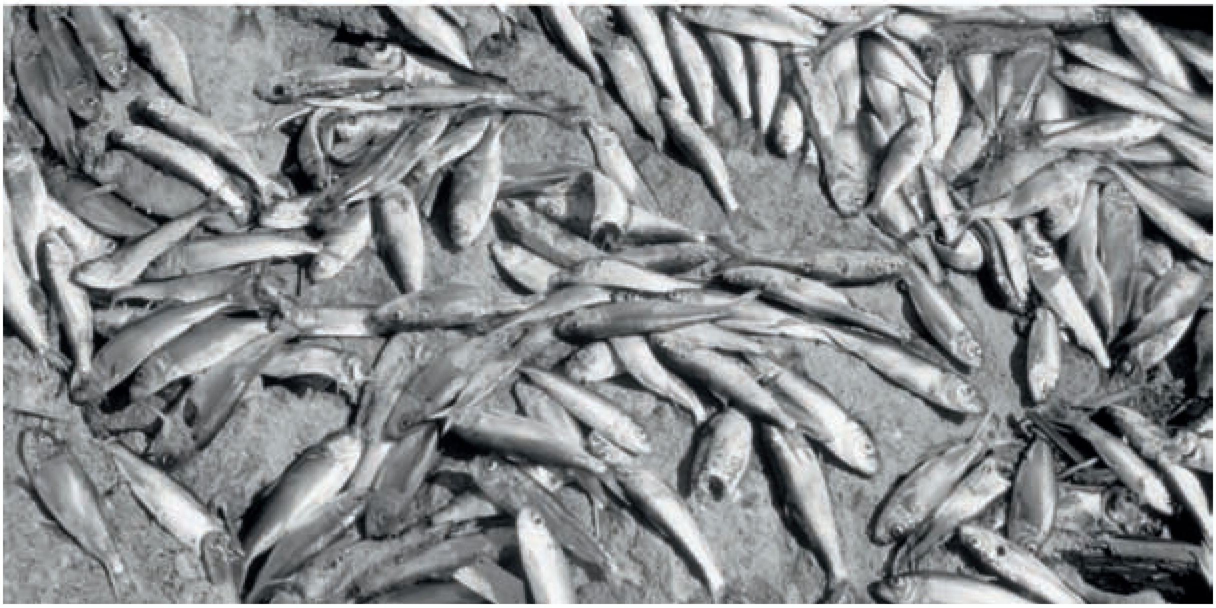


FIGURE 214

Mass mortality of the herring family, Clupeidae, past and present. *Top:* Mass mortality of †*Knightia eocaena* from the base of the 18-inch layer on Fossil Butte. At this particular site, this layer has a density of several hundred fishes per square meter, with each fish averaging about 100 millimeters (3.9 inches) in length. Slab is AMNH 13101. *Bottom:* A mass mortality of the cludeid *Alosa pseudoharangus* (also called the alewife) that was typical during the summer in Lake Michigan during the 1960s. This kill, like the fossil illustrated above, has a density of several hundred fishes per square meter with each fish also averaging about 100 millimeters (3.9 inches). Photo taken on a Chicago beach, but mass kill also covered part of the lake bottom. Clupeids have had a long history of sensitivity to abrupt fluctuations in environmental conditions.