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THE CENOZOIC

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Preface

The editors wish to thank the contributors for responding to the Call for Papers in such a timely manner. The papers represent a wide range of Cenozoic Era related topics contributed by our members and others. We would also like to thank Lance Grande for delivering the keynote address.

About the Cover

Artist reconstruction of the Boney Springs locality, Benton Co., MO. In the early 1970s Illinois State Museum scientists excavated the remains of 31 mastodons from this site, including the largest American mastodon on record. New radiocarbon dates suggest most of these animals died ~13,400 years ago. Image courtesy of the Illinois State Museum, artwork by Robert Larson.

Iowa City, Iowa
April 10, 11, & 12, 2015

John Catalani and Chris Cozart, Editors

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The Fossil Fish of Green River

Lance Grande

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The Green River Formation represents one of the largest documented accumulations of lacustrine sedimentary rock in the world. It extends over an area of more than 65,000 square kilometers (25,000 sq. miles) and averages about 600 meters (2,000 feet) in thickness. It covers portions of three states (Wyoming, Colorado and Utah), but most of the paleontological work in the Green River Formation has been done in Wyoming. Not only is the formation widespread, but at many localities there is an intricate record of both flora and fauna of the locality at the time of deposition. Several complex Eocene lake communities, containing organisms from the size of microscopic algae to 5-meter (16-foot) crocodiles, have been frozen in time for 40 to 50 million years to be reconstructed by paleoecologists today.

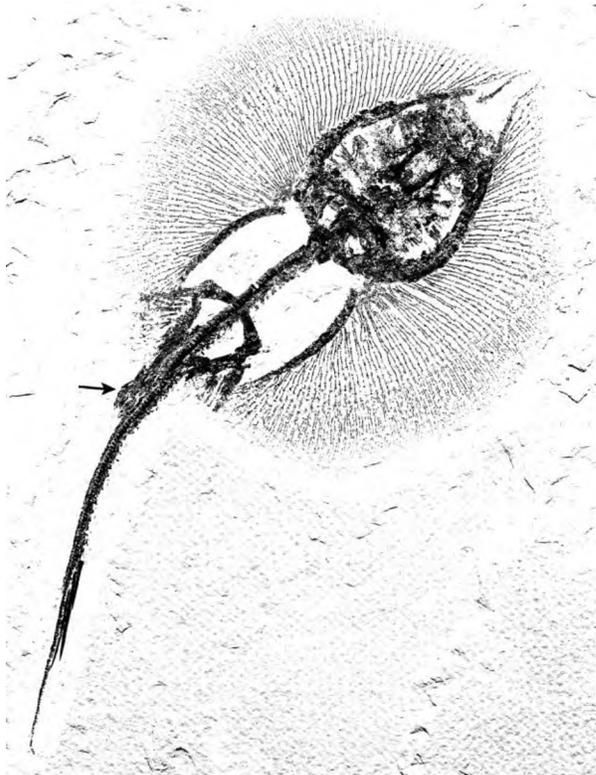
The Green River Lakes

The Green River system of Eocene lakes lay in a series of intermontane basins formed by geological events that uplifted the Rocky Mountains during early Tertiary time. These basins filled from the drainage of nearby tectonic highlands and eventually contained freshwater lakes supportive of a varied and abundant fauna. Large amounts of ash found in the lacustrine sediments indicate that volcanoes were particularly active periodically throughout the history of this lake system.



The lakes of the Green River Formation occupy parts of three U. S. States.

The Eocene climate of the Green River lake system was much different from the desert-like climate of that area today. Both the fauna (crocodiles, alligators, boa constrictors, and a few fish families whose extant members are subtropical) and the flora (such as large palm trees and balloon vines) indicate warm temperate to subtropical conditions. Roland Brown, E. W. Berry, and F. H. Knowlton, in various papers [and other authors] have concluded that the climate of most of the area was similar to the present climate of the Gulf Coast and southern Atlantic regions of the United States: subtropical with an annual rainfall of 75 to 100 cm (30 to 40 inches) and with essentially frostless winters. The average annual minimum temperature was over 2°C (36°F), and the overall average annual temperature was 15 to 21°C (60-70°F).

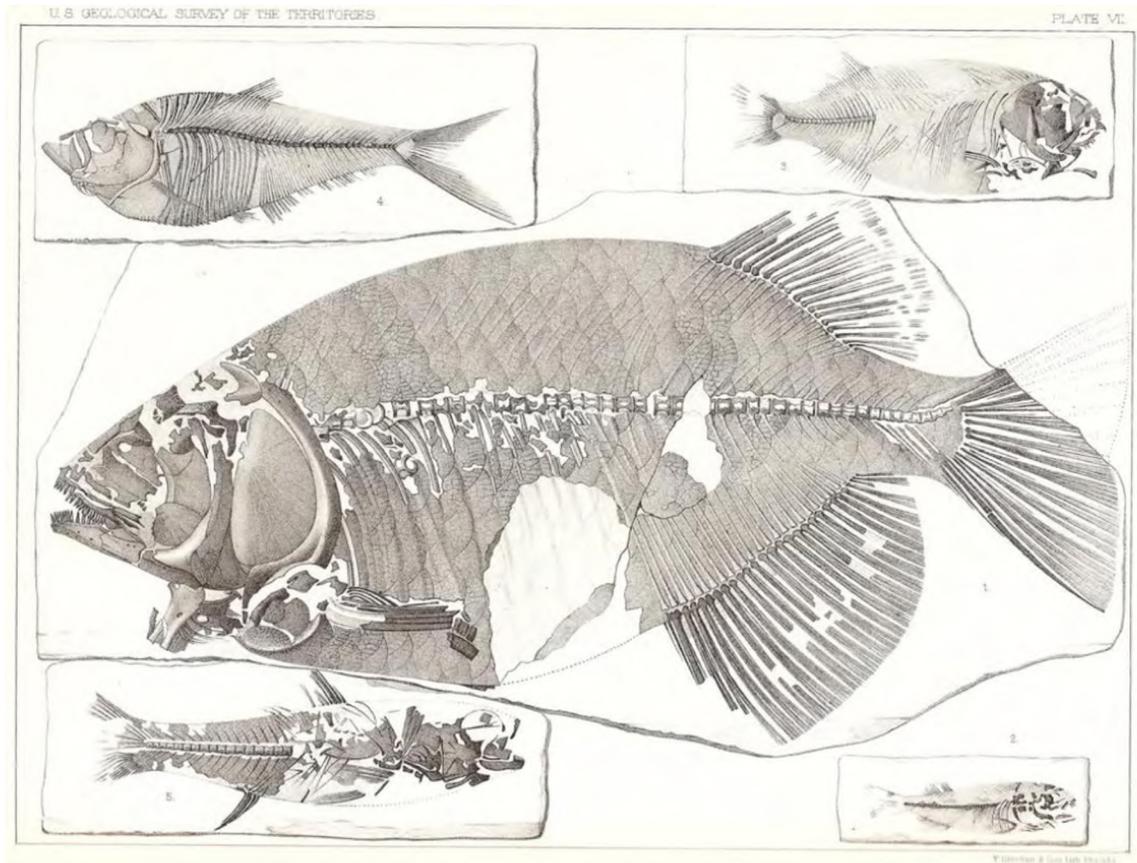


A male ray, *Heliobatis radians*, from Fossil Lake. The sex of the specimen is recognized by the presence of claspers (arrow). Claspers are modifications of the pelvic fins that are used to transfer sperm to the female during mating. This specimen is 38 cm (approx. 15 in) long (from Grande, 1984).

The Green River system was composed of three lakes: Lake Uinta, Lake Gosiute and Fossil Lake. Lake Uinta was the first of the Green River lakes to form, and its Paleocene phase has been referred to as Lake Flagstaff. Lake Uinta gradually dried up in the south during the Late Paleocene time, but expanded eastward into what is now the Uinta Basin while two other lakes were forming in what is now Wyoming.

Lake Gosiute occupied the Green River and Washakie basins; shortly after, Fossil Lake formed in Fossil Basin, a long, narrow, north-south trending synclinal trough in southwestern Wyoming just west of Kemmerer. It is not known definitely that the lakes were connected, but published data suggest that Lake Gosiute could have been connected by a narrow channel to the southern end of Fossil Lake for a brief period, or periods.

Time ranges for these lakes differ. The short-lived Fossil Lake appears to have existed only in Early Eocene time [56-48 million years ago], whereas Lake Gosiute persisted from Early Eocene to Middle Eocene [56-40 mya], and Lake Uinta from Late Paleocene to late Middle Eocene [59-37 mya]. Besides occupying different time ranges, the three Green River lakes differ in geologic history and sedimentology.



A series of Green River freshwater fish as illustrated by the famous vertebrate paleontologist Edward Drinker Cope in 1884. Cope was a prolific writer, producing more than 1,200 scientific papers in his lifetime. He is perhaps best known for his competitive fossil collecting with Othniel Charles Marsh known as the “Bone Wars ”

Fossil Lake had the smallest surface area of the three lakes, and was relatively short lived. It was the deepest of the three lakes during much of its existence, in contrast to the extensive but shallow Lakes Uinta and Gosiute. Evidence from the edge of Fossil Basin indicates that Fossil Lake expanded and contracted several times. The majority of Green River fossil fish in both public and private collections are from the Fossil Lake area, where they have been commercially mined for more than a century. The two main fish-bearing units in Fossil Lake are the so-called “18-inch” and “split-fish” layers.

Lake Gosiute was a broad, shallow lake, currently thought of as a playa lake complex. There is strong evidence of large fluctuations in the position of the shoreline, and at times the lake became quite saline. It supported thick algal mats over much of its bottom during several stages of its history, and was probably more eutrophic than Fossil Lake. As with modern lakes, a eutrophic state made it productive of algae and plants, yet not supportive of the variety of fish species present in Fossil Lake. Suckers and catfish were plentiful in Gosiute, but the average size of the fish (such as herring) occupying the upper zones of the lake was smaller than in Fossil Lake. Gosiute suffered several periods of contraction due to deposition of alluvial sediments, and possibly to periods of decreased rainfall. In the Middle Eocene, Lake Gosiute disappeared.

Lake Uinta was the longest lived of all the Green River lakes, lasting for more than 17 million years, including its late Paleocene history as “Lake Flagstaff.” The sedimentary rock of Lake Uinta represents one of the thickest documented accumulations of lacustrine sediments in the world, with thicknesses greater than 2100 meters (7000 feet) in places. Throughout its history, Lake Uinta was very shallow, in spite of its huge geographic extent. Typically, Uinta was lagoonal to shallow lacustrine with many horizons of deltaic deposits, mudstones, shales, sandstone, and siltstones. The many zones exhibiting mud cracks interbedded with limestones indicate a fluctuating shoreline. Lake Uinta deposits include vast quantities of high-grade oil shale containing an estimated 290 billion barrels of oil. Although the economic potential for its oil has been well studied, far less is known of its paleontology than that of Fossil Lake and Lake Gosiute. The most frequently mined macrofossils from the Lake Uinta area are insects and plants. Unfortunately, due to the abundance of fish fossils in the Wyoming Green River Lake localities, the fish fauna of Lake Uinta has been essentially ignored. The main insect, plant, and vertebrate fossil localities of the Lake Uinta area are Middle Eocene (Bridgerian) in age.

Historical Background of Research

The first documented records of fossils from what is now called the Green River Formation were in various diaries, journals, and reports of early missionaries such as S. A. Parker (1840) and such explorers as J. C. Fremont (1845). They were reports of invertebrate fossils.

The first record of a fossil fish discovery in the Green River Formation was in 1856: Dr. John Evans, a geologist, collected a fossil fish from near what is now Green River, Wyoming, and sent it to Joseph Leidy, M.D., in Philadelphia. Leidy identified the fish as a herring, which he named *Clupea humilis* (1856), a name later changed to *Knightia eocaena*. Later, Ferdinand V. Hayden, director of the newly-established United States Geological Survey of the Territories, named this fossil locale the “Green River Shales” (1869).

During the late 1860s, the Union Pacific Railroad, while excavating about 2 miles west of Green River, Wyoming (in the area of Eocene Lake Gosiute), uncovered the first major fossil fish layer of the Green River Formation. A. W. Hilliard and L. E. Ricksecker, employees of the railroad, were first to discover the fish, and collected many specimens which they turned over to Hayden. Hayden referred to this site as the “Petrified Fish Cut” (1871). These specimens were later studied and described by the famous pioneer vertebrate paleontologist Edward Drinker Cope in Hayden’s 1871 report. The collection consisted of the genera *Phareodus*, *Knightia*, *Erismatopterus*, and *Asineops*.

Cope collected specimens from the Fossil Basin area in the later 1870's at "Twin Creek Site" (1884), and described them in several small papers and in his classic monograph (1884).

Meanwhile, geologists were reporting additional outcrops of the Green River Formation. In 1876, John W. Powell described sections of the Green River Formation in the foothills of the Uinta Mountains in northern Utah, and A. C. Peale discovered outcrops of the formation in northwestern Colorado. Both Powell and Peale turned their collected fish fossils over to Cope for study and description. Since publication of Cope's monumental works on the Green River fossil vertebrates, many authors have published papers on fossils of the Green River Formation.

Historical Background of Amateur Collecting

There is no way to list all of the thousands of amateur collectors of Green River Fossils, but there are records of a few major amateur collectors. Earliest major collecting by amateurs was confined mainly to 18-inch layer specimens in the Fossil Lake area.

Robert Lee Craig started digging in the 18-inch layer in about 1897 and continued through the late 1930's. David Haddenham joined Craig in about 1918, and the Haddenham family (son David F. and grandson Robert) continued working the area until about 1970. Carl Ulrich and his wife, Shirley, started digging in the area in 1947 and still work the area today with their son, Wallace.

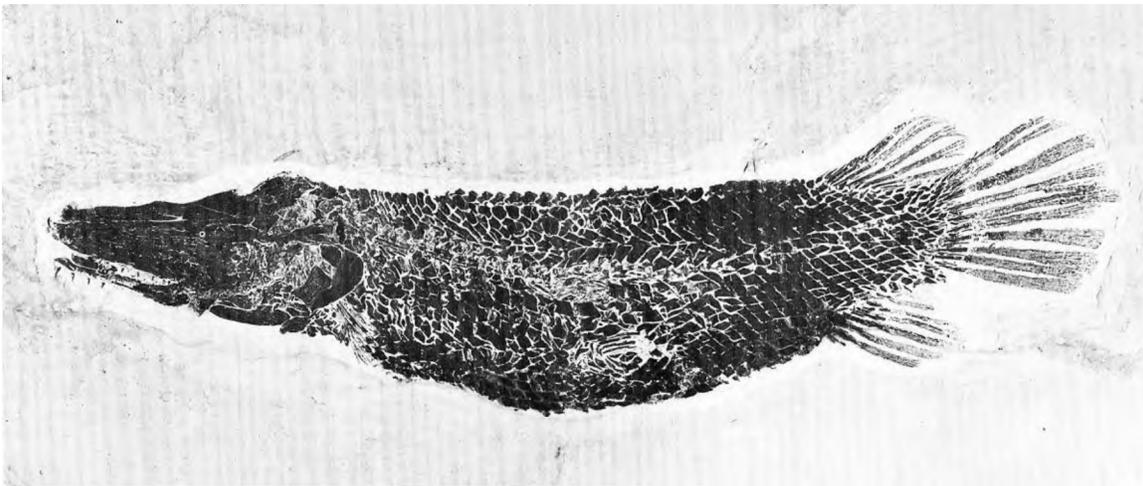
In 1970, Robert Tynsky and his family started digging in the split-fish layers of Fossil Basin. Today, the Tynsky family works on private land in the 18-inch layer and associated horizons. In the last twenty years, over a dozen new quarry operations have cropped up within the beds of the Fossil Basin, and the trade in Green River fossils has become extensive.



A typical quarry scene at Fossil Lake, where very large, thin sheets of rock can be lifted without breakage. The sheet being examined on its edge by the workers is only 2 cm (3/4 in) thick (from Grande, 1984).

The Taxa

The Green River Formation represents one of the earliest fresh water lake systems of North America which supported modern (teleost) fish fauna. Primary (strictly fresh water) fish families include the Polyodontidae [paddlefishes], Amiidae [bowfins], Ictaluridae [catfishes], Hiodontidae [mooneyes], and Catostomidae [suckers]. Marine derivatives include the Dasyatidae [rays], Clupeidae [herrings], Esocidae [pikes], Gonorynchidae [beaked salmon], and some percoids [perches]. Some of the marine derivatives such as *Heliobatis* may have entered the Eocene lake system in the early Flagstaff stages through connections with the sea. *Lepisosteus*, *Amia*, esocids, and a polyodontid are known in North American fresh water deposits as early as the Cretaceous, so their presence in the Green River Lake system is not surprising. The origin of most of the other members of the Green River fish fauna is poorly understood, primarily because of the extreme rarity of Paleocene fresh water fish deposits in North America.



A gar fish, *Lepisosteus simplex*, from Fossil Lake, with an obliquely compressed skull. The tough, diamond-shaped scales that protect the outer skin of the gar are clearly visible. Modern gars typically inhabit shallow weedy waters. This specimen is approximately 69 cm (27 in) long (from Grande, 1984).

The known specific richness of the Green River fish fauna, even at its highest (in the upper half of the Fossil Lake sediments with at least 28 species of fish), was considerably lower than that of modern lakes of similar longevity. African Lakes Malawi and Tanganyika (very large, deep lakes with durations of more than two million years) contain about 234 and 184 fish species, respectively. Not all Green River fossil species are described, and differences between the criteria used in specific separation of extant species and of fossil species probably also contribute to the relatively low number of fossil species. But the magnitude of the difference in specific richness between the Green River lakes and the African lakes is much too great to be attributed merely to yet undescribed fossil species or differences in specific criteria. The relatively low specific richness of the fish fauna inhabiting the Green River lake system could be the result of a highly fluctuating environment, where conditions were never stable long enough for teleost radiation to occur as explosively as it did in the

African lakes. It could also be at least partly an artifact of incomplete preservation (i.e., some species groups may be lumped together in a single Fossil Basin species because we are unable to distinguish the separate species based on the skeletons alone).

Arthropods (mostly insects and ostracodes, with a few branchiopods, malacostracans and arachnids) make up the largest part of the Green River invertebrate fauna. Nematode trails are also fairly common in some parts of the Green River Formation. The rest of the invertebrate fauna consists mainly of mollusks (gastropods and bivalves). [Single-celled protists, fungi, plants, frogs, turtles, lizards, snakes, crocodiles, (nonaquatic) birds, bats, opossums, tarsiers and other early primates, rodents, and early carnivorous and hoofed mammals are also identified from the Green River Formation.]

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Little Fossil Fish All Look the Same, or How to Successfully Identify Green River Herrings

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The Green River formation is one of the best-known fossil *Lagerstätten* sites in the world, preserving several Eocene lacustrine environments. The area was composed of three lakes in what is now northwestern Colorado, southwestern Wyoming, and northeastern Utah. Lake Uinta was the longest-lived of the three, lasting from late Paleocene to through mid Eocene. Fossil Lake is the smallest and shortest lived of the three. Despite this, most fossil fish are found there, particularly in the famed 18-inch and split-fish layers. This could be due to the fact that it was the deepest lake and provided the most stable environment (Grande, 1984). Lake Gosiute was a large, shallow, and probably eutrophic lake. The shoreline appears to have fluctuated many times during Gosiute's existence. Correspondingly, fish diversity was low, as were the relative sizes of the fish. Aside from fish, the area has yielded many other exceptionally well preserved fossils, including one of the earliest known fossil bats, crocodiles, alligators, massive palm fronds, and hosts of mollusks and arthropods (Grande, 1984), indicating that the area was once a warm, subtropical locality.

The Green River Formation's clupeomorph fish, or herrings, are the most easily recognized fossils and perhaps the most plentiful vertebrate fossils on the planet (Grande, 1984). They are consequently common in museum and private collections worldwide. The most frequently encountered species, *Knightsia eocaena* Jordan, 1907, *K. alta* (Leidy, 1856), *Gosiutichthys parvus* Grande, 1982, and *Diplomystus dentatus* Cope, 1877, can be difficult to differentiate (Figs. 2-5). The characters defining each fish as a species are often subtle or difficult to see. Furthermore, some characters overlap between species due to natural variation within species (Grande, 1984), increasing the complexity and confusion.

To experts, a quick glance is all that is required to identify a fish. Unfortunately, as these people retire, new experts are rarely hired, even in large institutions such as the Smithsonian Institution. More jobs now open for those with backgrounds in molecular biology, whereas doors close for many taxonomists and morphologists (Bruce B. Collette, personal communication, 2006). This poses a potential problem for collections managers who are not experts in fish osteology. Identifying specimens to species level can be a time-consuming task. With some collections containing millions of specimens, making these painstaking identifications grows tiresome, and misidentifications could increase in frequency.

Certainly, there are some specimens that are quite easy to identify. *Diplomystus dentatus*, for example, grows substantially larger than the other mentioned species (Grande, 1982), so a Green River clupeomorph much more than 25 cm is undoubtedly *D. dentatus*. What about fossils of similar size? How can one quickly differentiate between two fish without meticulous inspection? This paper attempts to find a simple solution to this problem.

Materials and Methods

All fossils utilized are currently kept in the Paleontological Research Institution's (PRI) collection. Work was done entirely with a 10x hand lens, probe, and a ruler. While looking at these specimens, it was apparent that some were easy to tell apart in a qualitative sense, but many appeared so similar that a more quantitative method was necessary. Grande (1982a, b) had extensively revised these genera and provided detailed descriptions for each. Many distinctive characters, however, were difficult or impossible to see with the tools available. For example, a major feature distinguishing *Gosiutichthys* from *Knightsia* is the presence of two supramaxillary bones versus one, respectively (Grande, 1982b). Attempting to find two tiny bones on the anterior end of a three-centimeter fish proved frustrating and unrealistic with only a hand lens. A simpler, more efficient means was necessary.

Table 1. Grande's (1982, 1984) morphometric and meristic data.

Species	Body Depth Ratio Variation	Dorsal Fin Ray Count
<i>Knightsia eocaena</i>	0.20-0.29	11-12
<i>K. alta</i>	0.33-0.41	11
<i>Diplomystus dentatus</i>	0.33-0.42	11-12
<i>Gosiutichthys parvus</i>	0.28-0.37	9-10

An objective comparison of two measurements seemed a quick and reasonable way to identify a fish to species if the combination of measurements were unique to that species. Fortunately, Grande (1982b) reproduced some of his species variation data in convenient tables, allowing for a quick search of unique morphological features that were easy to measure. The most obvious character to use was the body depth to standard length ratio. Each species had a relatively distinct range of ratios (Table 1), although there was some overlap, indicating that at least one more trait was needed. Dorsal ray count seemed a logical choice, as there was little overlap between species (Table 1). This provided a combination of traits that should be unique to each species, assuming that Grande's range of variation was correct.

Fossils with a definite (no question mark following the name), up-to-date genus and species name in the PRI collection were considered correct, but were also tested. There were only two such fossils, and using the above method, they were found to be consistent.

Fin rays were counted first in an attempt to reduce bias. It was very easy to get a good impression of the species based on body depth ratio alone and counting fin rays became straining after an hour or so. This could lead one to make inaccurate ray counts in an attempt to achieve the desired result.

Table 2. Collected data.

Specimen	Standard Length (cm)	Body Depth (cm)	Ratio	Dorsal Fin Rays	Possible Identification	Label Identification
ACC 1251	3.4	1.1	0.32	9	<i>G. parvus</i>	<i>Knightsia</i> ?
"	2.9	1.0	0.34	9	"	"
"	3.3	1.1	0.33	9	"	"
ACC 1250	3.9	1.4	0.36	11	<i>K. alta</i>	<i>Knightsia</i> sp.
K13675	11.8	3.3	0.28	?*	<i>K. eocaena</i>	Clupeidae
ACC 2485	7.8	2.2	0.28	11	"	<i>D. humilis</i>
PRI50003	8.4	3.0	0.36	11	<i>K. alta</i>	<i>K. humilis</i>
ACC 1404	8.4	2.4	0.29	?	<i>K. eocaena</i>	none
ACC 1384	11.5	3.4	0.30	12	"	<i>K. eocaena</i>
PRI 45546	30.5	10.5	0.34	12	<i>D. dendatus</i>	<i>Copeichys dentatus</i>
ACC 2495	5.2	1.4	0.27	11	<i>K. eocaena</i>	<i>D. humilis</i>
ACC 1261	7.5	2.8	0.37	12	<i>D. dendatus</i>	<i>D. dendatus</i>
ACC 1334	10.2	2.2	0.22	11	<i>K. eocaena</i>	<i>K. eocaena</i>
K13673	6.0	2.3	0.40	11	<i>K. alta</i>	Clupeidae
K13674	4.8	1.7	0.35	11	"	Clupeidae
None	9.5	3.5	0.37	11	"	none
ACC 801	8.5	3.0	0.35	12	<i>D. dendatus</i>	<i>D. analis</i>
ACC 1261	13.0	4.5	0.35	12	"	<i>D. dentatus</i> (?)
"	7.8	2.2	0.28	?*	<i>K. eocaena</i>	<i>D. dentatus</i> (?)
ACC 1261	12.5	4.2	0.34	12	<i>D. dendatus</i>	<i>D. dentatus</i> (?)
ACC 1250	2.6	0.9	0.35	9	<i>G. parvus</i>	<i>K. diplomystus</i>
"	2.6	0.9	0.35	9	"	"
"	2.8	1.0	0.36	9	"	"
"	4.5	1.5	0.33	9	"	"
"	2.2	0.8	0.36	?*	"	"
K13677	4.0	1.4	0.35	9	"	<i>D. humilis</i>
"	3.5	1.1	0.31	9	"	"
K13678	3.7	1.2	0.32	9	"	"

*Fin ray count cannot be given. Species could be determined due to unique depth ratio and/or other fish found with it.

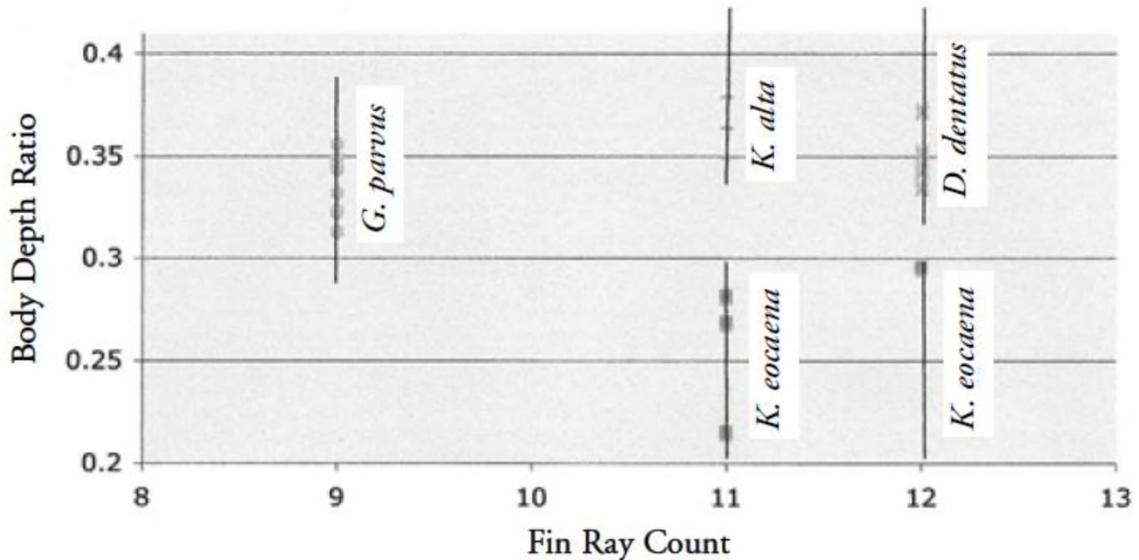


Fig. 1. Tables 1 and 2 graphed.

After a count was complete, the maximum depth of the fish was measured, to the nearest tenth of a centimeter, as was the standard length of the fish. The standard length is a measure from the anterior-most end of the fish to the end of its caudal peduncle (essentially where the tail ends and the caudal fin rays begin; Fig. 2). Dividing the maximum body depth by the standard length obtained the desired ratio. These data are compiled in Table 2.

Analysis and Discussion

The results in Table 2 were graphed with ray count on the x-axis and depth ratio on the y-axis (Fig. 1). Vertical lines representing the variation ranges as outlined by Grande are also plotted on the graph. All of the points grouped by their probable species fall on their respective lines. A second line for *Knightsia eocaena* was added because one specimen had 12 dorsal rays (normal for the species; Grande, 1982b).

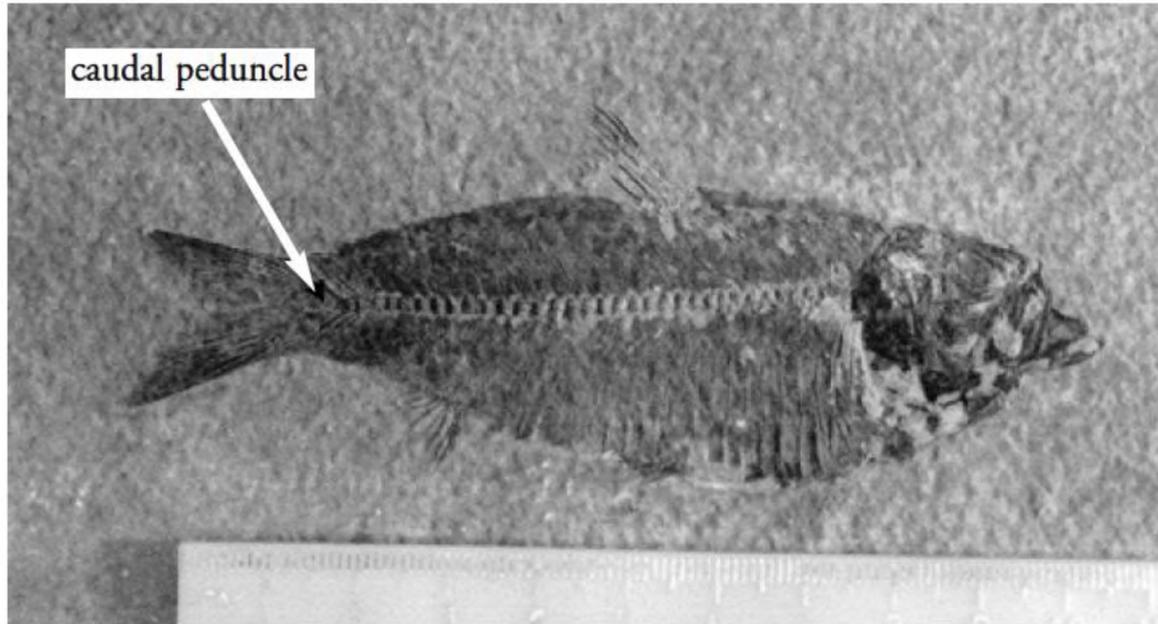


Fig. 2. *Knightsia alta*, showing the caudal peduncle.



Fig. 3. *Gosiutichthys parvus*. Note that the pencil used for scale is about 10 cm long.

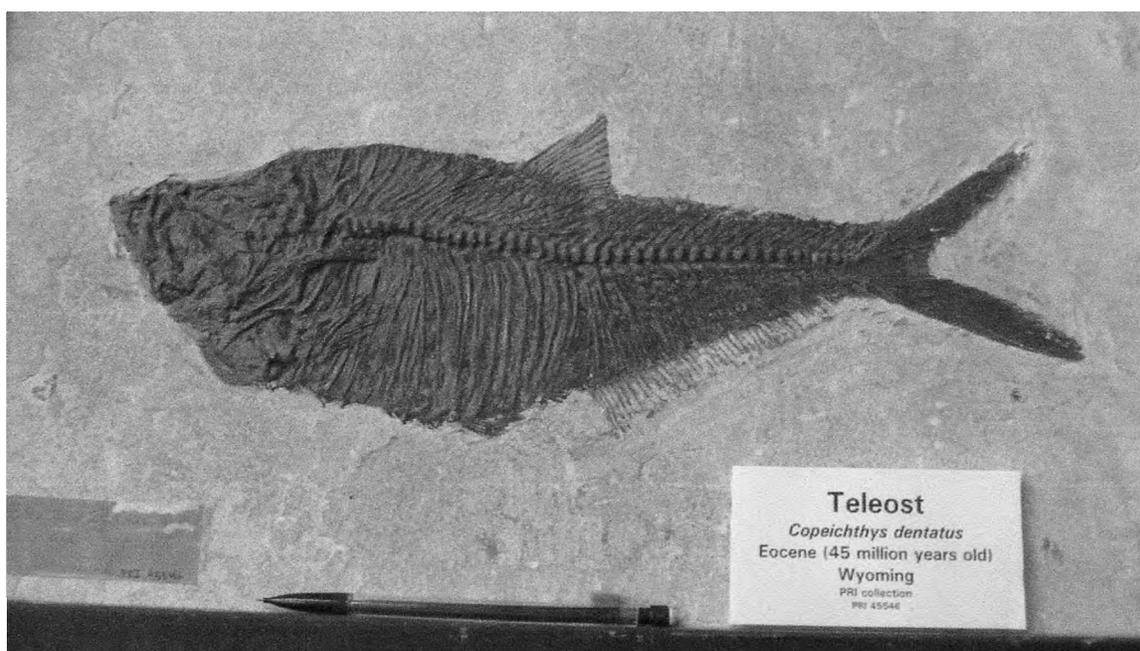


Fig. 4. *Diplomystus dentatus*. Note that the pencil used for scale is about 10 cm long.

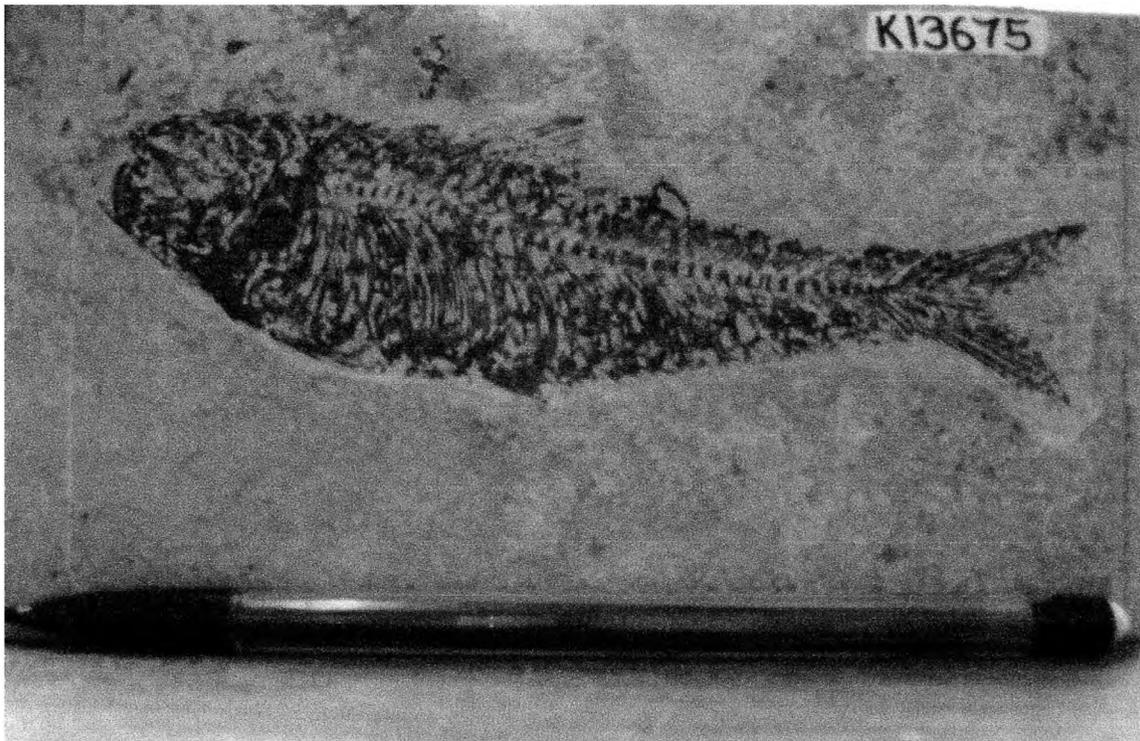


Fig. 5. *Knightia eocaena*. Note that the pencil used for scale is about 10 cm long.

Conclusions

This method for identification was relatively successful. It was simple to perform and required very few tools, which were inexpensive and easy to obtain. There were, however, several limitations.

First, it assumes that one has a general concept of what a clupeomorph fish is. Without this knowledge, identification would be quite difficult because there are no doubt many fish with these same morphological characters. Additionally, this only works on relatively well preserved, whole specimens. The dorsal fin is a relatively delicate feature and might no longer be present on the fossil, or it might not be extended enough to accurately observe the number of rays. This happened a number of times as shown by Table 2. Counting rays was also difficult on mass deathbeds because the fish were often layered on top of each other, covering up the essential character.

Several assumptions were also made. Grande's published variation data was taken as fact. If there is greater variation within these species that causes overlap between them, then this method would no longer work. One must also assume that the fish are not distorted. That is, they are neither depressed/expanded dorsoventrally nor shortened/elongated anteroposteriorly. This would lead to incorrect representations of life body depth ratios. There was also fin ray overlap between *Knightia alta* and *Diplomystus dentatus*, as well as depth ratio overlap. The basis for differentiation lies in the assumption that Grande's (Table 1) variation data were correct in that *K. alta* only has 11 fin rays and *D. dentatus* usually has 12.

Although equipment was very cheap and low tech, some slight improvements would have been useful. It would have been very helpful to have a more powerful hand lens, because staring at fin rays for long periods of time can be very straining. A sensitive probe would have been beneficial as well, because it is sometimes easiest to count fin rays by touch rather than sight. Lastly, digital calipers would have been useful in yielding more accurate measurements. A tenth of a centimeter miss-measurement can dramatically change the depth to body ratio, giving inaccurate results.

Overall, the technique is an over-simplification of anatomy, but one that has proven to be quite useful despite its mentioned shortcomings. Further study would no doubt allow for changes and improvements.

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Ted Hermann was a sophomore at Cornell University in Fall 2006 when he completed this project for Warren Allmon's "Paleobiology" course. He is a member of the class of 2009. Originally printed in *American Paleontologist*, Spring 2008, 16(1):21-23 – reprinted here with permission.

Articulate Crinoids of the Cenozoic

Thomas Williams

Subclass Articulata was first proposed by Miller in 1821 and is one of six subclasses of crinoids proposed by Moore and Teichert in 1978 in the current classification system. Articulate crinoids believed to have arisen in the Triassic from an Inadunate Cladid ancestor with members of the subclass still present today (Sims 1993). This makes articulate crinoids the survivors of 500 million years of evolution in the oceans and survivors of multiple major extinctions including severe changes in sea levels. Over 6000 individual species involving 800 genera are present in geologic history, hitting their peak in numbers and types during the Carboniferous period. Crinoids nearly went extinct at the end of the Permian with only a few survivors which opened the door for the rise of articulate crinoids to evolve. Today there are over 600 species most of which are, “free living feather stars or comatulids.” Eighty species exist with a calyx on a stem attached to the sea floor looking exactly like the crinoids we see in fossilized specimens (Hess 1999).

Articulates which were first described by Miller as, “The joints resting on the first superior columnar joint and forming the cup containing the viscera, articulate by liplike and transverse process having a minute perforation” (Moore and Teichert 1978, Sims and Sevastopulo 1993). Articulates became the first group of crinoids to be established, however, has had the least amount of revisions. Miller in his initial studies observed clearly and used the existence of “well developed muscular and ligament fossae on the radial–brachial articular rather than the presence of an axial canal in the radials...” to distinguish Articulata from the other crinoids (Sims and Sevastopulo 1993). Muller in his 1843 study of *Pentacrinus* and other forms characterized articulates by the, “moveable articulation between the radials and the primibrachs.” Another key characteristic is the lack of an anal plate in the cup of adults which is now considered a primary classification key in Articulata from Paleozoic crinoids (Sims and Sevastopulo 1993). Miller proposed the name Articulata to what he alluded to as a joint that he thought existed between the viscera and the cup. However, lots of problems exist with the group Articulata classification problems include classification based on post Paleozoic crinoids and leaving out observations made by Miller in 1821. Classification of Articulata has revealed reoccurring descriptions of characteristics found in Paleozoic crinoids, thus indicating a shared ancestry (Sims and Sevastopulo 1993).

These crinoids in terms of forms still living can be divided into three basic categories those that live on stalks throughout their life which are Isocrinida, Bourgueticrinida and Millericrinida. Next is a group that lives on a stalk as juveniles and then loose there stalk as adults the Cyrtocrinida, and finally those which cement a cup directly to the substrate which includes Cyrtocrinida (Moore and Teichert 1978, Baumiller 1996). The Uintacrinida were stemless crinoids, an Order once believed to have been pelagic but more recent research has shown this group may have settled into the substrate for sessile existence. There are no living members of this group to study the lifestyle as they became extinct at the end of the Cretaceous (Ausich, and Webster 2008). Order Roveacrinida, described as small pelagic crinoids went extinct as well at the end of the Cretaceous (Moore and Teichert 1978). Moore and Teichert 1978 currently have seven orders of Articulata which include:

Class:	Crinodea	Cambrian-Recent
Subclass:	Articulata Zittle 1879	Lower Triassic- Holocene
Order:	Millericrinida Sieverts-Doreck 1952	Middle Triassic-Holocene
Order:	Cyrtocrinida Sieverts-Doreck 1952	Lower Jurassic-Holocene
Order:	Bourgueticrinida Sieverts-Doreck 1953	Upper Cretaceous-Holocene
Order:	Isocrinida Sieverts-Doreck 1952	Lower Triassic-Holocene
Order:	Comatulida Clark 1908	Lower Jurassic-Holocene
Order:	Uintacrinida	Upper Cretaceous
Order:	Roveacrinida	Middle Triassic-Upper Cretaceous

General Description

Articulates based upon have a wide variety with seven orders of diversity and habitat where they are encountered. Generally cups of articulates (Figure 1) are dicyclic, monocyclic, or cryptocyclic with five infrabasals, five basals and five radials with variations of this design rare but possible. The number of plates and the design of plates and the arrangements of the plates is monocyclic or dicyclic which has a third set of plates. Cryptocyclic describes a condition in which a dicyclic cup lost part of the innermost, lowest most cirlet of infrabasals. Cryptocyclic cups show a definite similarity to Cladids, Flexibles, and Diplobathrid crinoids (Sims and Sevastopulo 1993, Moore and Teichert 1978).

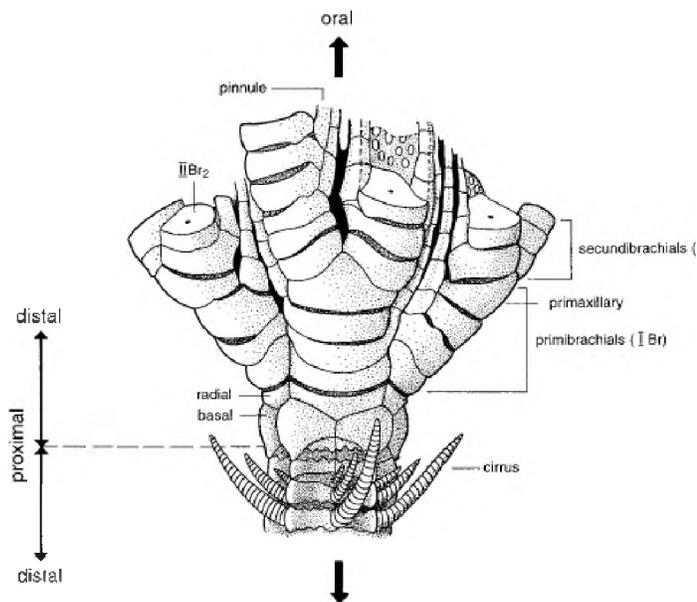


Figure 1. Order Isocrinida *Metacrinus* showing low and wide cup configuration with generally large basal plates up to the beginning of the arms (Hess 1999).

Cup design does show some variance such as in Uintacrinida, with some types showing fusion or reduction in the basal plates. Comatulida basal plates may be strongly reduced and transformed (See Figure 2). Basal plates are missing in Cyrtocrinida (Figure 3) and these crinoids when might first look at them ne may be inclined to look at them as being something other than crinoids. Anal plates and compound radials appear to be completely missing as well as a lack of plates separating or basals. Generally the arms of articulates are uniserial but distal brachials can be wedged shaped. Arms most of the time divide at the primibrachs and commonly further divide and are usually free however, they connect to the inter-brachial plates. Length of the arms is variable from very short to extremely long in length as compared to the cup size. The tegmen is always flexible and large oral

plate may be present and be made up of many small polygonal plates. Columnals to the crinoid can be circular five sided or elliptical without cirri on the nodals. Many articulates appear to attach themselves to the substrate distal or radix ciria or terminal disc (Moore and Teichert 1978).

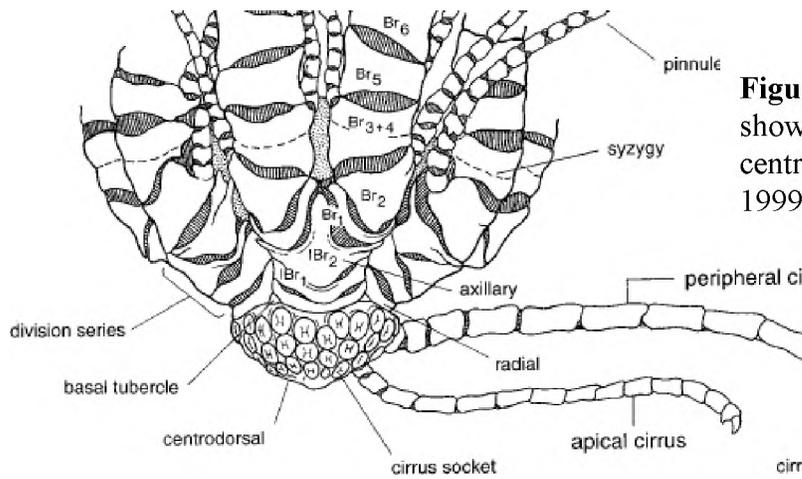


Figure 2. Order Comatulida showing the structure of centrodorsal and cirri (Hess 1999).

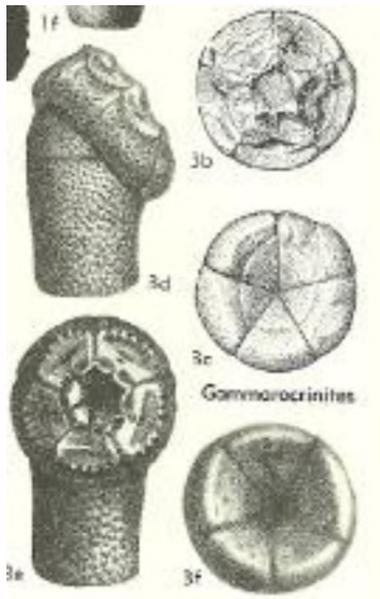


Figure 3. Order Cyrtocrinida *Gammarocrinites* showing side and top view (Moore and Teichert 1978).

Cenozoic Articulata Orders

Order Bourgueticrinida is a stalked crinoid with a small compact slender cup which is commonly fusiform conical, pyriform and has been described as funneled in shape (See Figures 4-6, 17 and 18). The cup has five basals and five radials surrounding a central canal, however, some specimens however, some specimens can have four or six radials or arms. The basal and radial plates close up on the sutures and can fuse as a ring or cup. Arms are undivided or branched on the primibrachs but some variations is possible. The columnals are circular or elliptical and appear to have attached to the substrate with a holdfast structure as opposed to cirri on a stem (See figure 4). This order has

strong representation in the Mesozoic Era but there are few individuals represented in the fossil record (Moore and Teichert 1978).

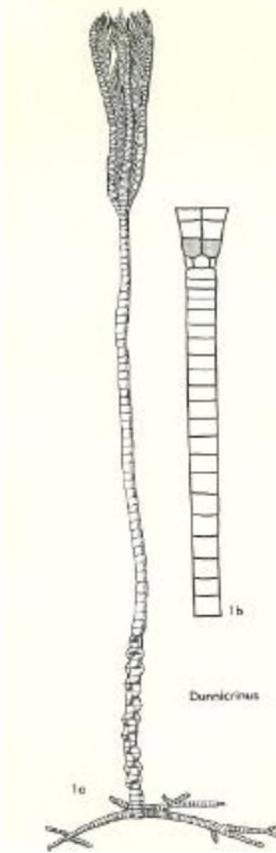


Figure 4. Order Bourgueticrinida *Dunnicrinus mississippiensis* stalked Articulate crinoid with small low cylindrical cup.

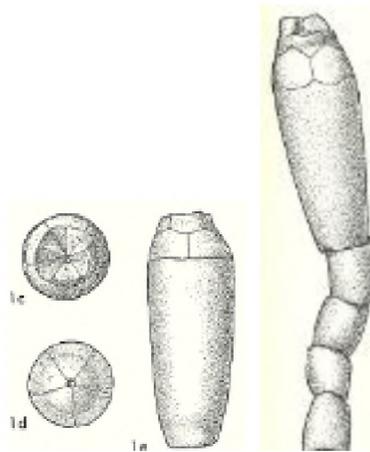


Figure 5. Order Bourgueticrinida *Bourgueticrinus*.

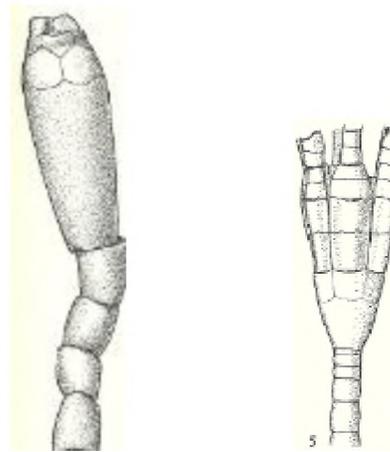


Figure 6. Order Bourgueticrinida *Rhizocrinus* showing conical funnel shaped cup (Moore and Teichert 1978).

Family Bourgueticrinidae has been reported from the upper Cretaceous through the Eocene in both Europe and the United States. Family Bathycrinidae is composed of six genus and represented from the Upper Cretaceous through Holocene is a well represented family. *Dunnicrinus mississippiensis* described by Moore 1967 has well documented specimens from the Upper Cretaceous of Mississippi in the Prairie Bluff Chalk (See Figure 4). This crinoid shows what could be described as a return to simplicity in form with some resemblance to early Inadunate forms in the lower Paleozoic. *Dunnicrinus* has a small cylindrical shaped cup with five uniserial pinnulate arms forming a slender elongate crown. It is this long slender crown to its overall proportionality to its height with its unbranched arms which a very simple but successful design and appears to be a return to a more simplistic design (Moore 1967). Overall Family Phynocrinidae occurs in modern specimens in the North Atlantic and Japan at depths of 600 – 2,400 meters and Porphyrocrinidae appears in recent specimens in the in the Pacific Ocean both have similar cup design as to other members of this order (Moore and Teichert 1978).

Order Isocrinida, a very successful order of crinoids that first appeared in the Lower Triassic, is still present today (See Figures 1, 7-10). This order appears to be the first order of articulates reported and potentially the most successful with many representatives from the Jurassic to recent. *Endoxocrinus parrae* (Figure 7) and *Cenocrinus asterius* (Figure 9) are well represented in today's oceans and bear the basic fundamental Isocrinida features which date back to at least the Jurassic. *Endoxocrinus* and *Cenocrinus* display their arms in a large parabolic fan structure and also spread their cirri out along the stem which extends from the substrate. Some of the complete specimens in the fossil record have long arms extending from the cup as well as long stems with preserved cirri (Hess 1999).



Figure 7. Living Isocrinida *Endoxocrinus parrae* in life position (Hess 1999).



Figure 8. Isocrinida *Raymondicrinus oregonensis*.



Figure 9. Living Isocrinida *Cenocrinus asterius* with arms forming parabolic fan oral side up with stem attached to hard ground (Hess 1999).



Figure 10. Isocrinida *Pentacrinites fossilis* Jurassic of southern England (Hess 1999).

Family Isocrinidae generally has a small dicyclic cup described as cryptocyclic with some variety among the infra-basal with types having small concealed infra-basal or with infra-basal completely missing (See Figure 1). Basal plates can be rather small and in Family Holocrinidae they are considerably higher. Radial plates are generally larger without prolongation which can in some cover up the upper part of the column. Articular face of the radials is large with distinct muscular and muscular fossae. Radial plates of Isocrinidae are generally larger with an articular face for arms and with distinct muscular and ligaments. *Metacrinus* (Figure 1) has a small wide cup having concealed

infra-basal plates. The basal plates of *Metacrinus* form the classic basal circlet typical of Articulata and the inter-radial edge covers the uppermost part of the stem. Family Pentacrinitida though not present in the Cenozoic was well established during the Jurassic is worth some mention because of its structure and close similarity to Cenozoic Isocrinida. It has a low bowl shaped cup with concealed infra-basal plates but basal plates that can be very prominent with large radial plates with a large medial ridge (See Figure 10). *Raymondicrinus oregonensis* (Figure 8) is similar in cup design a small dorsal cup and arm structure that resembles other Isocrinida. Moore and Teichert 1978, Moore and Vokes 1951, Hess 1999).

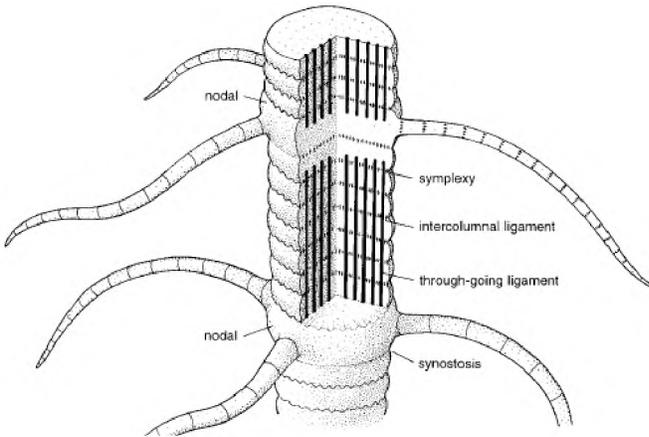


Figure 11. Isocrinida stem with nodal segments with cirri (Hess 1999).

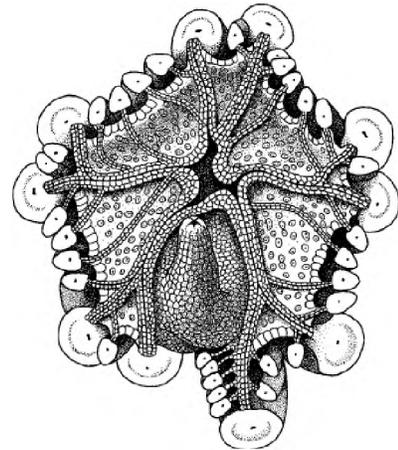


Figure 12. Isocrinida *Metacrinus angulatus* oral view of tegmen (Hess 1999).

Arms generally divided once or more isotomously usually at the primibrachs and further divisions possible. Pentacrinitidae arms divide twice and further divide in intervals of four brachials. Endoxocrinus arms divide at the primibrachs and secundibrachs and will further divide in intervals of 2 or 3 brachials, but divisions after the primibrachs tend to heterotomous. Endoxocrinus and Teleiocrinus both modern crinoids appear to make the most division of arms. Generally it can be assumed the arms of Isocrinida both past and present are long as compared to the size of the cup divide enough times to form a fairly large parabolic fan as shown by the modern crinoids *Endoxocrinus* and *Cenocrinus* (See Figures 7 and 9). This does appear to be a feature that has persisted from the Jurassic to present. Tegmens are plated with a flexible oral opening in which the height may be variable (Moore and Teichert 1978, Hess 1999) (See Figure 12).

Baumiller 1996 found some unique traits that Isocrinida have articulations that allowed them to shed certain appendages in times of environmental stress but also cause disarticulation easier upon the organism's death. Columns are composed of pentalobate, pentagonal, or circular sections with long stems. Columnals have nodes with cirri attached at the nodes of the stem with new nodes and cirri growing as the crinoid lengthens (See Figure 11). *Seirocrinus* of the Jurassic of Holzmaden Germany in the bituminous shales has had stem lengths recorded up to sixteen meters. This probably indicates deeper water environment allowing very long stem growth with gentle currents. A potential theory is that the long stem if broken would allow reattachment on logs or find something else to cling to (Hess 1999, Moore Teichert 1978). Modern Isocrinida have been found in deep water environments in depths up to 600 meters (Hess 1999).

Tauriniocrinus a genus of Isocrinida has been found in the Lower Triassic with this genus being reported in the Oligocene and Miocene of Europe. Excellent specimens exist from the Triassic of China with insufficient material for good descriptions from Cenozoic European deposits reported by (Moore and Teichert 1978).

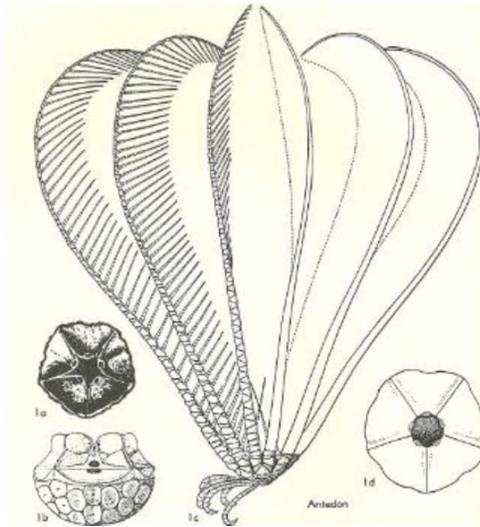


Figure 13. Order Comatulida (Moore and Teichert 1978).

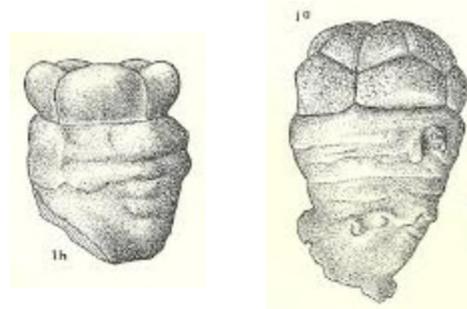


Figure 14. Cyrtocrinida Holopidae, *Cyathidium* showing shield shaped bowl cup (Moore and Teichert 1978).



Figure 15. Cyrtocrinida *Holopus aldis* side view of complete with arms closed in making a fist shape Lohanute islands (Hess 1999).



Figure 16. Cyrtocrinida *Gymnocrinus richeri* complete specimen with arms curled up (Hess 1999).

Order Comatulida (Figure 13) first appeared in the lower Jurassic and are still present and well represented in modern oceans. The most distinguishing feature is the lack of a column, except for the upper most cirri which is where the attachment to the surface or other organisms occurs. Recent Comatulida can change their position by slow crawling along if the environment indicates a change for the organism should occur. With Jurassic and Cretaceous Paracomatulidae "...the conical centrodorsal is composed of a series of closely joined, very low columnals separated by distinct sutures" (Moore and Teichert 1978) (See Figures 2, 13, and 20). Describing what could be described as a true crinoid cup with this group is a bit difficult in Comatulida. This appears to be another feature that really doesn't exist with the oldest members of this group having a central stellate circlet formed from five basal plates which are joined centrally and articulated (Moore and Teichert 1978) (See Figures 13 and 20). In recent forms, basal plates form a ring of large plates which sometimes shrink with age and growth and this is not a feature and trait present in stalked crinoids. Basal plates in some forms grow into a larger plates forming a circlet with radial plates attached other groups the radials form an inter-radial rod structure. These structures do not follow the typical model of a structure that could be called a true crinoid cup. A question arises here: Does this group of crinoids belong with the Subclass Articulata or should they be in another Subclass? Arms are generally undivided but can be divided at the primibrachs and sometimes divide further up in some genera (Moore and Teichert 1978). There is little question when one looks at Comatulida crinoids you see mostly arms attached to something with cirri and no cup appears to be present. Today Comatulida are diverse in reef communities however, they do not preserve well in the fossil record because of what appears to be disarticulating extremely easily (Moore and Teichert 1978).

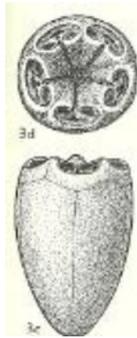


Figure 17. Bourgueticrinida *Conocrinus* (Moore and Teichert 1978).

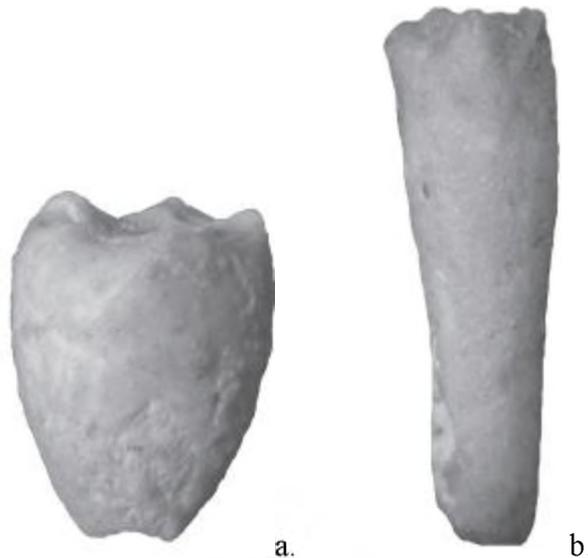


Figure 18. Bourgueticrinida a *Conocrinus pyriformis* and b. *Conocrinus thorenti* (Manni 2008).

Order Cyrtocrinida (Figures 3 and 14-16) have a different orientation and are crinoids that have been described as living similar to barnacles in the environment with many members of this order going extinct at the end of the Cretaceous. Fossil cups have been described as composed of radial plates with no apparent basal plates which sometimes is interpreted as a fused basal circle radials and

a dorsal element that was probably fused without sutures and are asymmetrical. Sub Order Holopodidae (Figure 14) is one group that survived the Cretaceous and the modern Cyrtocrinida *Holopus aldis* (Figure 15) is commonly describes as fists (Hess 1999). It is believed in most Cyrtocrinida, the cup may be formed by a modified columnal or fused columnals where it attaches to the column. In Holopodidae, the cup attaches directly to the substrate and was limited to hard grounds in which to attach itself so this suborder did not have a stalk. Other Cups of this group have also been described as shield bowl or conical shaped composed of fused radials with no sutures present only an articular face for the arms. Columnals when present are cylindrical to barrel shape with the cup attached in an oblique to the stalk. Ventrally there is an inter-radial projection or a proximal brachial which, form a cover of sorts for the cup as a protective measure. Arms are divided at the primibrachs and have sometimes been described as fused primibrachs and when retracted can cover the ventral side of the theca (Moore and Teichert 1978, Hess 1999).

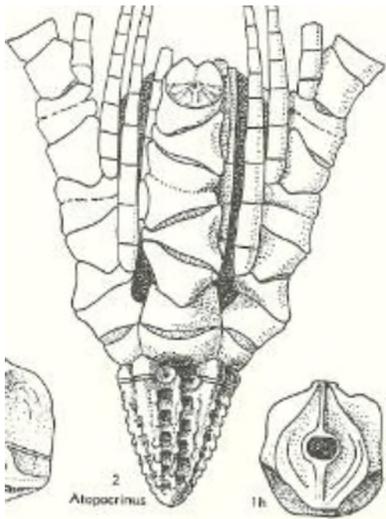


Figure 19. Comatulida Paracomatulidae *Atopocrinus* (Moore and Teichert 1978).

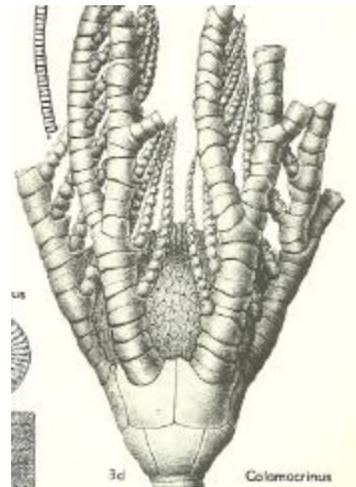


Figure 20. Hyocrinina *Calamocrinus* (Moore and Teichert 1978).

Cyrtocrinida has been known to grow on top of or attached of other organisms such as coral, bryozoans and other objects present. Fossilized forms appear to be limited to the photic zone and requiring sheltered areas (Moore and Teichert 1978). Overall, structure of these crinoids is believed to have been to protect them in shallower water from wave action. *Cyathidium holopus* from the Eocene which is in suborder Holopodidae does not show too many differences from its Cretaceous counterparts. This crinoid had a dorsal cup of fused radials attached directly to hard grounds a crinoid without a stalk. Found in the shallow water deposits of the La Mesta formation deposits was an extremely important find in paleontology which provided specimens that could be described for ecological environment niches (Baumiller 1996, Hess 1999).

However, *Holopus* (Figure 15) and *Gymnocrinus* (Figure 16) both of which are recent forms have been found at depths of 300 to 500 meters in sheltered environments attached to hard substrates. Others crinoids of this group have been discovered at depths up to 900 meters. Arms of these crinoids are found curled up around the asymmetrical arm design which may be a defensive measure. Oral extensions of the primabrachs used as covers help protect the tegmen and other softer interior

parts of the cup. Arms of Cyrtocrinida from Jurassic and Lower could be enclosed inside a cavity for protection. *Holopus*, described as a fist (Figure 15), can roll itself into a ball structure to protect itself and *Gymnocrinus* (Figure 16) has been found curling its arms up over softer areas that require protection. This insight from modern crinoids and past forms shows how other forms Jurassic and Cretaceous adapted. It can be assumed that Cenozoic which aren't well described used these designs for survival (Moore and Teichert 1978, Hess 1999).

Order Millericrinida has a general range as first appearing in the Middle Triassic to the Holocene. Most of Millericrinida suborders were extinct prior to Cenozoic. However, Suborder Hyocrinina (Figure 20) was reported geologically in the Lower Tertiary to the Holocene, so there so if one of the other suborders of this group survived the Cretaceous there is a gap in its ancestor at least to this point. Unlike many of the previously described specimens this group has a thin walled large cup which is composed generally of five basal plates, five radials, with the infrabasals generally not present in this group. Hyocrinina, however, can have as few as three basal plates fused to form a base circlet. The tegmen is made up of multiple small polygonal shaped plates that may continue into the inter-brachial plates (See Figure 20). Arms of this group are usually undivided except *Calamocrinus* that has irregular distal branching. The cup is attached to a column that is long, smooth and slender without nodes or cirri. This is a distinct difference from the other stalked crinoids of the Articulata. This distal part of the column is attached to the substrate by an expanded disc with no radix. Something interesting in exploring the Treatise is that *Calamocrinus* appears to be the only representative until the Holocene where there are many more representatives. So is this just a lack of representation in the fossil record or is it a case allowing *Calamocrinus* to branch off to new forms (Moore and Teichert 1978, Hess 1999)?

Cenozoic Deposits

Forms appear to be present but complete specimens from the geologic record is not as complete as past assemblages. Stems and fragments of crinoids appear to be common all across the globe in marine sediments; this at least provides a record of specimens. *Metacrinus* has been found in sediments that appear to have been deposited in shallow water from the Paleocene to the Oligocene in New Zealand and Antarctica. *Isselicrinus* from the Eocene of Denmark and in Southeast England both specimens found in a clay which is a deep water deposit. However, modern forms of this type of crinoid have been found associated with drift wood including palm wood. Jurassic assemblages have been found with crinoids attaching to drift wood that has sunk to the bottom or possibly pseudo pelagic existence floating from logs in the ocean. So there are some questions for some of the crinoids more closely related to *Pentacrinites* of the Jurassic as to potential life style (Moore and Teichert Hess 1999).

The Keasey formation Lower Oligocene from Northwest Oregon reveals complete specimens of Isocrinida *Raymondicrinus oregonensis* (Hess 1999). Crinoids found there are some of the best preserved and in particular for the Tertiary. These crinoids were found in a massive tuffaceous siltstone and some layers of ashy tuff. Other organisms found with these crinoids indicate this was an offshore environment but sediments deposited were of volcanic origin and close enough to the shore to be effected by volcanic eruptions (Moore and Vokes 1950, Hess 1999). *Raymondicrinus* is an unusually tall crinoid with a small discoid dorsal cup with rays that bifurcate isotomously three

times to the point as to form up to forty arms. The cup from the holotype is only about 10 mm with the outstretched arms being almost 210 mm across at their widest point. Length of some of the specimens in the Oregon deposit have been up to an impressive 90 mm. Arms of some specimens were described as, "...spreading out like spokes from a wheel" (Moore and Vokes 1950, Hess 1999).

Raymondicrinus oregonensis was found to have a muscular articulation and muscular articulations have been found in the modern Isocrinida, *Metacrinus* and *Saracrinus*. An ophiuroid, preserved was also found on some arm fragments and another on a bivalve. From the level of preservation of the Oregon fauna a very rapid burial is probable given the type of the deposits and the massive bedding indicates that volcanic activity had a prominent factor in this well preserved deposit. Other fauna also was present indicates this environment below the wave base and combined with the type of sediments helped allow for spectacular preservation. As is common along the west coast of the United States offshore geology is access to colder water upwelling to fauna's, so as it appears this deposit was linked to an area where cold water upwelling area from a deeper area. Modern crinoid beds today can be linked in the Pacific and Atlantic oceans seek out similar environmental niches for survival (Moore and Vokes 1950, Hess 1999).

The La Mesta Formation mostly Eocene and possibly the Lower Oligocene are considered shallow marine estuary water deposits comprised of 800 meters of sandstones and siltstones of the La Meseta Formation of the Antarctic Peninsula. *Metacrinus fossilis* and *Eometacrinus australis* (Isocrinida), *Notocrinus rasmusseni* and *Notocrinus seymorensis* (Comatulid), and *Cyathidium holopus* (Cyrtocrinida) have been found at Seymour Island of the Antarctic Peninsula. *Eometacrinus australis* and *Cyathidium holopus* are preserved in diverse fauna would found in a transgressive sequence in crinoids were present but not dominant in the lower part of the La Mesta formation sequence. This environment contained a rich fauna including bryozoans that formed colonies as well as numerous corals, brachiopods, gastropods, polychaete worms, echinoids, fish and shark remains. Fossil penguins and polydolopid marsupial mammals have also been found which also supports a shallower environment and also brings some question as to the actual age of the deposit which could make it early Oligocene. Diversity and the type of organisms present and sedimentary features found indicate a shallow normal marine environment for some parts of the sequence. Overall, these crinoids appear to examples with the ability to survive in cooler temperature waters ranging 10-15°C an important ecological note (Baumiller 1996, Hess 1999).

Tertiary deposits of Europe yield crinoids from various countries. Northern Italy collected by Michelotti resulted in about two hundred crinoid specimens being deposited in a collection some of which were destroyed during WWII. Order Bourgueticrinida and *Conocrinus pyriformus* (Figures 17 and 18) are pear shaped cup with high basals and low radial plates and is found in the Eocene and Miocene of Europe. *Conocrinus thorenti* (Figure 18) has an oblong cup with radials within distinct sutures between the plates, and *Conocrinus senguenzai* is known but there are only poor specimens known. Both are known from Italy and other localities in Europe. Other members of this order noted are *Bourgueticrinus italicus* and *Bourgueticrinus zignoi* are identified in this collection from poorly worn specimens. Order Cyrtocrinida is represented in Tertiary of Europe by *Cyathidium holopus* is described as a small oblique tubular cup with an irregular underside and slender radial plates. *Cyathidium gastaldii* is described as low pentagonal oblique cup with five fairly long radial plates.

Living specimens of Cyrtocrinida have been found living encrusted to the hard sea bottom and on the walls of submarine caves 100 meters to 900 meters deep (Manni 2008).

Modern Isocrinidae are typically found in deep water environments starting around 100 meters and deeper and are not found in shallow waters. However, *Endoxocrinus* in the Caribbean has been found in shallower areas and shows evidence of predation since arms are not regenerated as frequently as other crinoids. Oji has theorized crinoids moved to deeper waters to escape predation by modern fish which many of the Mesozoic crinoid assemblages are deeper water environments. Stalked Isocrinida have been found in waters 200- 300 meters deep with the most common crinoid found being *Cenocrinus asterius*. *Cenocrinus* has more than fifty arms that can be spread out in fan shaped described as a “wilted flower posture” (See Figure 9). The cirri are postured extending out from the columnals and cirri are used in attachment to the substrate. Study of modern crinoids show that they prefer moderate current with density increasing in these areas. The Straits of Florida has shown crinoids at depths of 500 - 700 meters attaching to hardgrounds on the flanks of the lithoherms. *Endoxocrinus parrae* (Figure 7) were found attached to hard ground areas with whorls of cirri with arms in a “parabolic filtration fan oral side down current.” Crinoids were found in unconsolidated sediment when an object or a low outcrop was available for attachment, however, no crinoids were found in unconsolidated sediment without some object to attach to (Hess 1999).

Stemless Cyrtocrinida thought to have been extinct since the late Cretaceous were found in 1967 and 1971 attached to boulders at depths of 380-900 meters. Others have since been discovered since 1971 but there is still large gaps in the Cenozoic with limited numbers of specimens being reported in the geologic record of this time frame. The Eocene specimens appear to be similar to those of the Jurassic and early Cretaceous. Is this because of lack of preservation possibly there were only one or two survivors after the Cretaceous and since a possible repopulation in the later part of the Cenozoic (Baumiller 1996, Hess 1999)?

Conclusion

As a matter of fact I do give a lot of belief to the geologic principal of uniformitarianism proposed by James Hutton. In preparing this article and reading the publications, articulate crinoids is a group of crinoids where we can take a look at the key to the past by examining the present. Since lots of orders of articulate crinoids are still alive in our oceans studying these animals and how they are living will give us insight into how crinoids existed in the past.

Examination of the Treatise and the available publications does reveal many gaps in the geologic record. There are many individual species present in oceans today so there are specimens yet to be discovered as potential paleontology links to these current organisms. From the specimens that are present to examine it is evident that crinoids were present in the Cenozoic and potentially in good numbers. Crinoids just don't appear to be present in rocks is it a matter of preservation as suggested by Hess 1999 or are there other factors such as predation, or could we just not be looking in the right places to this point. Quick disarticulation is definitely an issue with articulates suggesting that the good deposits in the Cenozoic represent very quick burials. Another possibility is that some of the real good deposits are in not easily accessible places such as the Antarctica deposit.

Some perspective on classification some of these groups may be the only thing they have in common is that they are crinoids and should be in different groups not all lumped in together as Articulata. Orders Comatulida, Uintacrinida, Roveacrinida, and Cyrtocrinida may very well belong in a completely different groupings as least in general appearance they don't bear much resemblance to others in this group. One group Cyrtocrinida looking not really like crinoids as we knew them at all. Comatulida certainly look like crinoids but don't but there not in resemblance to some of the other Articulata which is the same with Uintacrinida. Crinoids are currently being looked at in reclassification should these groups be part of articulates or their own groups. When you look at some articulates especially you actually see traits of Inadunates a crinoid that has its beginning in the Ordovician. Some articulates, especially stalked Articulata such as *Dunnicrinus mississippiensis* a Cretaceous crinoid from Mississippi, appear similar in appearance to Cladid Inadunates crinoids of the Paleozoic, with the main difference being the lack of a true anal plate. *Dunnicrinus* also has a long slender elongate design with little or no branching in the arms appears to a return to simplicity. Is this just an evolutionary step forward of Cladids or is it truly a new Subclass of Crinoids that is currently in place? Some may suggest that Cladid crinoids are still with us, it is going to take a looking at the entire line of these types of crinoids to tell. There is some discussion that the anal plate in adult forms in the late Paleozoic was beginning to disappear which adds to the discussion. So if this is true when do Articulata actually arise in the Paleozoic or the Triassic has it has previously been suggested or are some of the Articulata actually part of Cladids? If Articulata originate earlier than previously suggested reclassification of all crinoids at the Subclass and Order level may really be required to explain the similarities between Cladids and Articulata. Order Millericrinida, Suborder Hyocrinina, show similarities but some very significant differences especially in the stalked column. This group has no nodes or cirri and uses a large disc for attachment and even may only have three basal plates forming the circlet. This Suborder also appears to be significantly different at least in general appearance from many of the other forms in this Order and somewhat more primitive in general structure than other stalked articulates.

It now seems that the lack of revision as mentioned by Sims and Savastopulo (1993) is beginning to catch up to this entire group of extremely interesting crinoids. The discoveries of crinoids deep in the oceans is giving paleontologists lots of good information and definite leads as to how these organisms previously existed and an eventual new classification scheme of articulates which may very well tie some articulates closer to their Paleozoic ancestors. Environmental niches occupied by crinoids have shifted in depths of the oceans to shallow shelf areas as seen in the Mississippian such as Crawfordsville and were warmer tropical waters.

During the middle Mesozoic and into the Cenozoic a fundamental change from shallow environments to deeper water environments especially for stalked crinoids such as Isocrinida takes place. During the Jurassic world-wide sea levels did begin to rise and this would continue well into the late Cretaceous. Causes in environmental preference has taken place for a number of reasons, but deep water environments during times of stress seems to be a bit of a safe haven especially during significant sea level drops or was it simply a gradual adjustment to the natural rise in sea level. Another possible reason is predation by fish, echinoids, bryozoans, gastropods, and possibly even ammonites which were all prevalent especially in shallow environments. Echinoids dramatically increased their numbers in the Mesozoic and are known predators of crinoids in today's environments. There have been events of extinction that would have definitely helped this transition

take place that would have favored deeper water forms over shallow water forms. Also, during the Cretaceous sea level was the highest the world has seen with 65 % of the world covered by water.

As the Cretaceous progressed overall sea level began to recede as seen in the Pierre Sea way in central North America. The Tethys Sea once stretched from what is now the Indian Ocean to today's Atlantic Ocean and was large, deep and rich in life diversity. Today all that is left is the Mediterranean Sea which is much shallower than its ancestral ocean. This does correspond to a general rise of the continental land masses world-wide. Baumiller 1996 has suggested that the shift from shallow to deeper water began in the early Cretaceous and was completed in the Eocene especially with stalked crinoids. However, the lower part of the La Mesta in the Eocene clearly shows a shallow environment where stalked crinoids existed so a complete transfer of a preferred environment. During the Pleistocene world-wide glaciation lowered sea levels 100 meters or approximately 300 feet, exposing what is now most of the continental shelf. However, Comatulida do thrive in more shallow environments where as Isocrinida tend to prefer deeper environments. Comatulida with their ability to at least creep along using cirri were able to move to depths of water. It is possible that some shallow forms of crinoids just plain and simply weren't able to keep up so those that were able to adjust to deeper water had a better chance of survival. Another pattern that does appear to have taken place is crinoid's ability to thrive in cooler temperatures between 10 to 15 degrees Celsius and this could be tied into especially stalked crinoids movement into deeper cooler water with access to even deeper water with up welling currents. Crinoids or at least some of them throughout geologic time have shifted their preference to deeper cooler waters. This move may have actually began in the Permian when global temperatures were have suspected to have risen substantially, so forms that could shift from shallower water to deeper waters probably one or more possible Cladid ancestor. As Earth's temperatures cooled some crinoids definitely moved back into shallower environments especially as sea level rose in the Cretaceous. But it is obvious that many stalked crinoids over time have found a environmental niche in much deeper cooler waters to their liking. This would have definitely been a survival advantage during the Pleistocene when sea levels fell some 300 feet and subjecting these crinoids to fewer potential changes.

Many Articulata are still present today and in larger numbers from previous time periods of the Cenozoic. Miocene deposits from Japan discovered the Isocrinida, *Teleiocrinus springier* which is still present in the Indian Ocean showing survival through the Pleistocene ice age extinction. Crinoids of the Order Bourgueticrinida and Millericrinida have been noted in abyssal plain using branching dendroid roots for attachment in the soft sediment. *Endoxocrinus* and *Cenocrinus*, two recent stalked Isocrinida crinoids, show definite resemblance to crinoids of old and give us an insight to how and where crinoids living in deep water exist.

Comatulida are typically found in recent shallow water assemblages and can be dominant with as many as twenty individuals in a square meter as reported by Macurda and Meyer. The crinoids Paracomatulida had up to 300 individuals in a square meter preserved in a fossil assemblage in the Jurassic Klingnau formation in Switzerland. Today Comatulida live routinely attached to other organisms such as coral in coral reefs. This is definitely revealing and gives evidence to crinoid's life style and environmental preference past and present. There is absolutely no reason to think when we look at crinoids in oceans today that we are not looking at crinoids of the past, and James Hutton's ideas are not at work today!

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Cenozoic Nautiloids

John A. Catalani

Introduction

Cephalopods have had a long and tortuous history since they evolved in the Late Cambrian, some 490 million years ago. The earliest cephalopods were the externally-shelled nautiloids. They gave rise to arguably the most popular cephalopods, the ammonites (more correctly ammonoids) also with external shells (as well as coleoids). The two groups coexisted from the Devonian Period to the end of the Cretaceous Period when ammonites (last group of ammonoids) became extinct at the Cretaceous-Paleogene (K-Pg) boundary (or did they?). Whatever the circumstances and timing of the ammonite extinction, nautiloids were the only externally shelled cephalopods to successfully survive the K-Pg Extinction. Two genera of nautiloids (*Nautilus*, *Allonautilus*) are still alive today residing in the depths of the southwestern Pacific/eastern Indian Oceans, and, due to geographically isolated populations, may in fact be diversifying once again.

Classification of Cephalopods

The classification of cephalopods has undergone many changes in recent years with some orders yet to be confirmed as valid. The following is a simplified classification that outlines the diversity of cephalopods:

Phylum MOLLUSCA

Class CEPHALOPODA

Subclass NAUTILOIDEA (external shells)

Extinct nautiloids

Extant *Nautilus* and *Allonautilus*

Subclass BACTRITOIDEA (external shells)

Extinct bactritids

Subclass AMMONOIDEA (external shells)

Extinct goniatites

Extinct ceratites

Extinct ammonites

Subclass COLEOIDEA (internal or no shells)

Extinct belemnites

Extant decapods (squids and cuttlefishes)

Extant octopods

Extant *Argonauta* ("Paper Nautilus")

Cephalopods--A Brief Geologic History

It appears that the first true cephalopod evolved from a septate monoplacophoran that developed a siphuncle. The earliest externally shelled cephalopod was the Late Cambrian nautiloid *Plectronoceras*. Extensive field work in China has revealed that Late Cambrian nautiloids diversified into 4 orders, 34 genera, and about 130 species. As shown in Fig. 1, nautiloids and ammonoids experienced several periods of stress when their taxonomic numbers were severely reduced. For nautiloids, the first of these taxonomic bottlenecks occurred near the end of the Cambrian when only one order, Ellesmerocerida, and two genera, *Clarkoceras* and *Ectenolites*, crossed the Cambrian-Ordovician boundary. This severely depleted fauna once again diversified during the Ordovician. After the Ordovician, however, nautiloids decreased both in taxonomic diversity and shell-form morphology. During a second bottleneck near the end of the Triassic, nautiloid diversity was reduced to one genus, *Cenoceras*, which crossed into the Jurassic allowing the nautiloids to once again diversify (although the discovery of an Early Cretaceous orthocerid indicates more crossed the boundary than just *Cenoceras*).

All Late Cretaceous nautiloids so far known were, as are *Nautilus* and *Allonautilus*, members of one order, the Nautilida. Of the nautiloids present at the end of the Cretaceous, at least three families and at least five (a number subject to certain inconsistencies, see below) genera crossed into the Paleogene Period. Today, nautiloids are experiencing a third bottleneck that has decreased their diversity to two genera. However, several genetic studies reveal that the separate *Nautilus* populations in the Pacific (isolated by extreme ocean depths that form barriers to migration) are genetically variable and a new diversification event may be beginning. Surprisingly, major mass extinctions at the end of the Permian and Cretaceous Periods did not appreciably affect the nautiloids.

Ammonoids and coleoids (octopods, squid, cuttlefish) appeared in the Early Devonian, both having evolved from the bactritids. What sets the bactritids apart from their orthocerid ancestors and links them to the ammonoids and coleoids is their reproductive strategy--bactritids produced large numbers of tiny eggs resulting in very small hatchlings. Of the nine (more or less) ammonoid orders, four were pretty much confined to the Paleozoic. Of these, by far the most important and diverse group was the order Goniatitida, the goniatites. Although their morphologies varied, the shells of most goniatites were small, relatively smooth, and involutely coiled. In addition, it appears that, based on a deep hyponomic sinus, the goniatites were good swimmers. Another order, the Prolecanitida, was morphologically more diverse than the goniatites and gave rise to the "transitional" order Ceratitida, the ceratites, in the latest Early Permian.

Ceratites displayed a wide variety of shell coiling and ornamentation as well as more complex sutures than the goniatites. Although ceratites evolved during the Permian, the vast majority are found in Triassic rocks having survived the Permian extinction. The Early Triassic diversification continued until the total standing ammonoid diversity was actually higher than that of both the Permian and the rest of the Triassic. In contrast, recovery of many benthic groups, such as snails and clams, was delayed until well into the Middle Triassic. Although exact details are lacking, the order

Phylloceratida arose in the Early Triassic and was the only order that survived the Late Triassic extinction giving rise to all post-Triassic ammonoids.

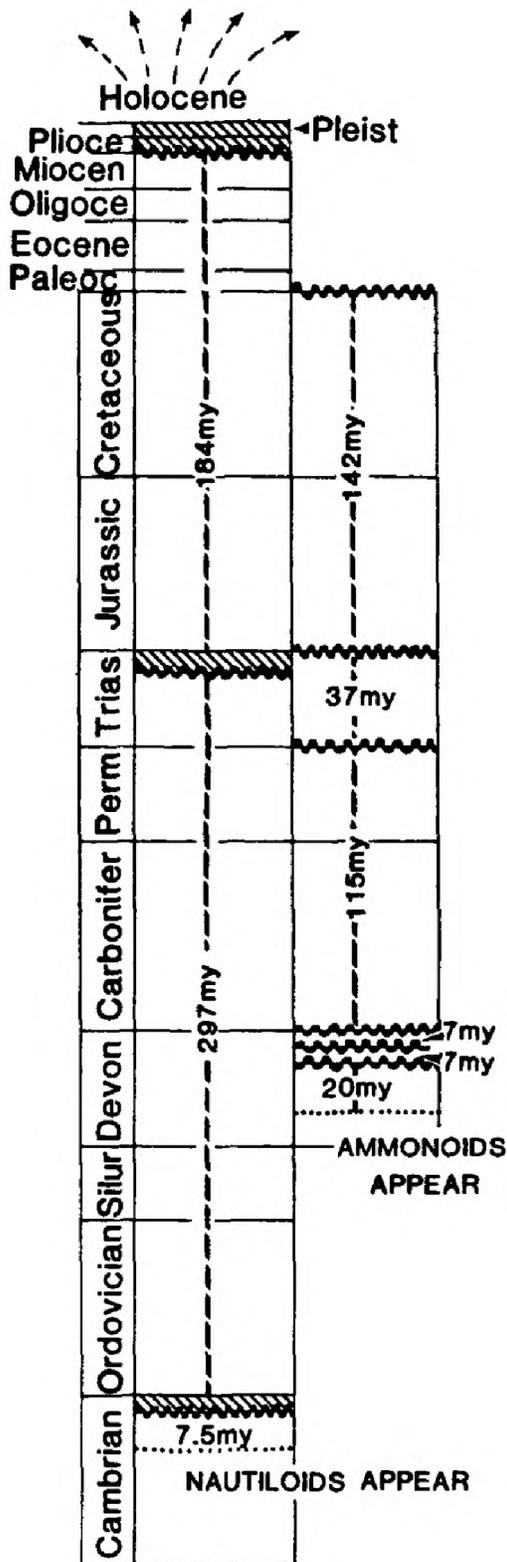


Fig. 1. Geologic time scale showing significant events in the evolution of both nautiloids and ammonoids. Crises are indicated by jagged lines while severe “outages” or bottlenecks are identified by hatching. (From Teichert 1988, Fig. 31.)

There were four orders of ammonoids in the Jurassic and Cretaceous Periods. The Phylloceratida and the Lytoceratida were possibly the only true deep-water ammonoid groups. The third order, the Ancyloceratida, contained most of the heteromorphs. The last and the most diverse ammonoid order was the Ammonitida, true ammonites that displayed regular coiling. These ammonites diversified into a large number of specialized species that were often limited in geographic range.

The ammonoids experienced crises near the end of the Devonian (actually three separate events with only two to four genera surviving each event), the end of the Permian (essentially only ceratites survived), the end of the Triassic (the only crisis affecting both nautiloids and ammonoids), and, of course, at the end of the Cretaceous when they completely disappeared (see Fig. 1).

The Extinction

It has been argued that both the taxonomic diversity and abundance of Cretaceous ammonites declined through time and that the perceived mass extinction of the ammonites at the end of the Cretaceous was just the last gasp of a dying group. However, much of the drop in diversity had been noted for the shallow-water taxa when, in reality, many ammonites added heavy shell ornamentation and started to inhabit deeper waters in response to the increased numbers of shell-crushing predators. In fact, the decline in diversity of these ammonites was compensated for by the increased diversity of the heteromorphs. More recently, studies of Masstrichtian (last stage of the Cretaceous) rocks indicate fairly consistent ammonite diversity, albeit reduced from the previous stage, right to the end of the period (Ward 1997, Witts et al. 2015, Fig. 2).

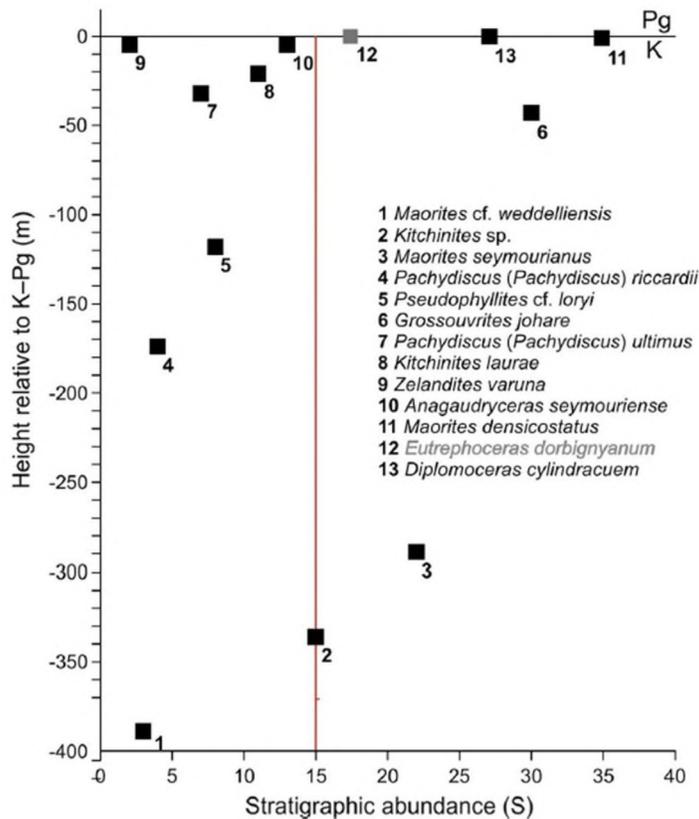


Fig. 2. Distribution of ammonites and one nautiloid (*Eutrephoceras*) at the K-Pg boundary in sections at Seymour Island, Antarctic Peninsula. (Modified from Witts et al. 2015.)

When considering the demise of one group and the survival of a closely related group one must attempt to find some advantage the surviving group had over the disappearing group. Therefore, speculations on why the ammonites went extinct at the K-Pg boundary while the nautiloids “survived these environmental disturbances relatively unscathed” (Stilwell and Grebneff 1996, p. 83), have focused on specific differences between the two groups. Many differences have been cited, such as shell design or short-lived and geographically-restricted ammonite species, but the most logical explanation is based on the difference in the reproductive strategies between ammonites and nautiloids.

Ammonites grew fast and many died young, perhaps within one year as many coleoids do today. To compensate for this short lifespan, thousands of extremely small eggs were laid in mass spawning events followed by post-mating adult mass mortality. The 1 mm-or-so hatchlings would have spent growth-time in the plankton since they were positively buoyant and were not able to reach neutral buoyancy for some time. This made them susceptible to the end-Cretaceous collapse of the planktonic ecosystem (Holland 1987; Gallagher 1991). It appears that the impact of an asteroid-sized body on Mexico’s Yucatán Peninsula (Chicxulub crater) tapped subsurface sulfur-rich rocks resulting in prolonged acid rain and acidification of ocean surface waters.

Nautiloids, on the other hand, laid only a dozen-or-so, very large eggs each season (*Nautilus* has a life span of 20-30 years). These eggs were not only laid in deeper waters but also took up to a year to hatch. Juveniles hatched with fully-functional shells that allowed them to actively negotiate the water column, to assume an adult lifestyle, and be able to swim to deeper water to avoid predators. Fossil evidence indicates that extinct nautiloids experienced a similar reproductive cycle. For example, preserved morphologic features indicate that the juveniles of the Cretaceous nautiloid *Eutrephoceras* had four chambers in place upon hatching. Additionally, evidence from oxygen isotopes indicates that the eggs were laid in relatively warm water at depths of around 100-200 meters. Therefore, even if the end-Cretaceous event killed all of the adult nautiloids and ammonites, as some have suggested, as well as the ammonite progeny in the plankton, the nautiloids were able to outlast the severe environmental effects of the K-Pg event because of the slow development of their large eggs nestled on the ocean floor (Fig. 3).

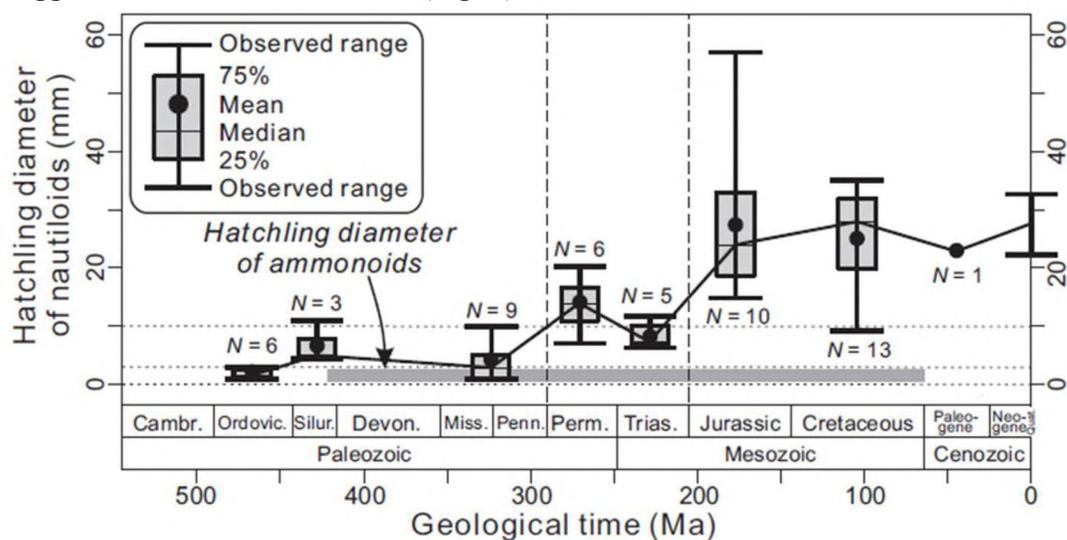


Fig. 3. Graphic display of nautiloid and ammonoid hatching size through time. 37
(Modified from Wani 2011, Figure 1.)

There has been, however, evidence presented that suggests ammonites may have survived for a time into the Paleogene. As usual when dealing with a stratigraphic boundary, it is based on a degree of resolution so that the uncertainty in exact timing of the boundary affects the placement of the fossil specimens. However, since the K-Pg boundary is taken to be the Iridium layer, placement of the ammonite fossils in question is more certain. Also to be considered, of course, is the question of reworking of Cretaceous fossils into Paleogene sediments.

Short-term (~200000 years) survival of ammonites has been proposed for several locations. Machalski and Heinberg (2005) report two genera/species preserved in Danian (lowest stage of the Paleogene) rocks Stevns Klint, Denmark. Evidence that these are not reworked Cretaceous fossils includes infilling of the conch that is “indistinguishable from the surrounding limestone” and conch infill that contains “*Operculodinella operculata*, a calcareous dinocyst typical of the Danian” (p. 97). They admit, however, that “none of the presented arguments for ammonite survival into the Danian is unequivocal” (p. 109). Other sites at which presumably non-reworked Danian ammonites occur include the Netherlands and New Jersey, USA.

Based on this, admittedly, meager evidence, Paleogene ammonites would suggest that, although the K-Pg event decimated both adults and progeny, some were able to survive briefly in isolated areas. Unfortunately, assuming ammonites actually did survive for a time, it appears that too few survived to mount a viable recovery effort and they eventually went extinct.

Cretaceous Nautiloids

Cretaceous nautiloids that passed through the K-Pg boundary were the root-stock of all post-Cretaceous nautiloids. Late Cretaceous nautiloids were characterized by low diversity. However, the taxa that were present were stratigraphically much longer-ranging than coexisting ammonites. As stated above, several nautiloid genera/species crossed the K-Pg boundary, others did not. One genus that did cross the boundary was *Eutrephoceras* (U. Jurassic-Miocene, Fig. 4). This is one of the most cosmopolitan of nautiloid genera. The large number of taxa that have been assigned to this genus has required many of them to be relegated to sub-species or varieties as a way of distinguishing morphotypes. Additionally, *Eutrephoceras* was exceptionally widespread in geographic range during both the Late Cretaceous and Early Paleogene and is therefore found in numerous exposures worldwide.

Post-Cretaceous Nautiloids

Although, as mentioned previously, nautiloids were not severely affected by the K-Pg extinction event, that does not mean to imply that they were not affected at all. Recent evidence suggests that nautiloids were indeed challenged by the changing environmental conditions. Responses included migration out of certain locations and into others as well as extinction of isolated local species. Survivability appears to have been directly related to the size of the area inhabited by individual nautiloid species.

Of the dozen-or-so nautiloid genera that were present at the end of the Cretaceous, five continued into the Paleocene Epoch (oldest Epoch of the Paleogene Period). Then, beginning at the onset of the Paleocene, there was an increase in both the diversity and abundance of nautiloids. In addition to the surviving genera, at least three additional genera appeared during both the Paleocene and the Eocene-Oligocene Epochs. Therefore, at any one time during the Paleogene period, ten-or-so Cenozoic nautiloid genera were alive (Figs. 5-9). Subsequently, diversity of nautiloids decreased until there were only two genera present during the Miocene. There then occurs a gap of six million years (Pliocene-Pleistocene) during which only one fragmentary specimen of *Nautilus* has been collected. Therefore, the ancestry of present-day nautiloids (*Nautilus* and *Allonautilus* with five to six species/subspecies, Fig. 10) has remained uncertain (but see below) even though the genus *Nautilus* appears to have evolved in the late Eocene-early Oligocene. The evidence for this, however, is restricted to only a few specimens of one species, *Nautilus praepompilius*, found in a single area of Kazakhstan.

Cenozoic nautiloids are found world-wide including SE USA, NW USA, Italy, India, Japan, Australia/New Zealand, and the Vienna Basin among other localities. As with several Cretaceous taxa, stratigraphically and geographically wide-ranging Cenozoic genera (such as *Eutrephoceras*, *Cymatoceras*, *Aturia*, etc.) are in need of taxonomic revision.



Fig. 4. Examples of the Late Cretaceous nautiloid *Eutrephoceras dekayi* from Montana. The left specimen is from the Bear Paw Fm and the right specimen is from the Pierre Shale Fm.



Fig. 5. Example of the Paleocene nautiloid *Cimomia vaughani* from the Midway Group Kaufman County, Texas.



Fig. 6. Example of the Eocene nautiloid *Eutrephoceras carolinense* from the Castle Hayne Fm of North Carolina.



Fig. 7. *Aturia* sp. from the Paleocene Clayton Fm Wilcox Co., Alabama.



Fig. 8. Three views of a specimen of *Aturia aturi* from the Miocene of Puglia, Italy. (From Wikimedia Commons)



Fig. 9. *Deltoidonautilus sp.* from the Eocene of Salzburg.



Fig. 10. Present-day nautiloids. Left: *Nautilus pompilius*; Right: *Allonautilus perforatus*.

As far as can be determined, Cenozoic nautiloids had essentially the same lifestyle as today's *Nautilus*--relatively deep-water (200-300 meters) reef habitats with daily vertical migrations in search of food. Although 300 m appears to be the maximum depth attained by the living animal, the *Nautilus* shell has an implosion depth of 600 m, indicating that the animal observes a safety margin during life--confirming the obvious intelligence of *Nautilus*. The occurrence of some fossil genera, such as *Aturia*, in relatively deep-water sediments suggests that these nautiloids could tolerate low-oxygen waters. If this proves to be the environment of choice for a substantial number of genera, it may account for the lack of Cretaceous-Paleogene nautiloids preserved in shallow-water shelf sediments representing well-oxygenated conditions (Schlögl et al. 2011).

Aturia is one of the most diverse, abundant, and geographically wide-ranging Cenozoic nautiloid genera. Therefore, it has been studied intensely. The distribution of any nautiloid species (genus) is always under scrutiny as to the true paleogeographic origin of the specimens: are they preserved more-or-less in place or is their distribution a result of post-mortem drift due to floating shells. Analysis of the preservation of *Aturia* shells in several localities have revealed that the shells, including the living chambers, are intact and free of micro-boring organisms. This suggests that the shells could not have drifted very far if at all. Analysis of internal structures of *Aturia* and *Nautilus* has uncovered several differences. The siphuncular tube of *Aturia* is double walled while that of *Nautilus* is single walled suggesting that *Aturia* was more efficient in regulating buoyancy. Also, studies of the embryonic development of *Aturia* have shown that, while incubation was relatively long (several months?), the hatchlings were smaller with only three-or-so chambers formed whereas *Nautilus* eggs incubate for about a year and juveniles emerge with six to seven chambers formed. Additionally, the sutures (septa) of *Aturia* are more complex than the simple, somewhat sinuous sutures of *Nautilus* and resemble in form those of Paleozoic goniatites (Ward 1987, Nielsen et al. 2009).

Phylogenetic analysis of *Nautilus* and *Allonautilus* “readily separates *Nautilus* species from the two species assigned to *Allonautilus*, as well as from all other taxa in the analysis” (Ward and Saunders 1987, p. 1057). The position of the *Allonautilus* species in the analysis suggests “that they are *ancestral* to the *Nautilus* species, rather than being *derived* from *Nautilus*” (p. 1057) although this is by no means unequivocal (see below). Even though the genus *Nautilus* is generally regarded by most researchers as the last evolved nautiloid, Ward and Saunders (1987) “suggest that *Nautilus* may be one of the *earliest* evolved of post-Triassic nautilaceans” (p. 1057). Ward and Saunders further propose that the first species of *Nautilus* may be directly descendant from *Cenoceras*, the single nautilid genus to survive the end-Triassic bottleneck. This would contradict the phylogenetic analysis presented above that suggested *Nautilus* was derived from *Allonautilus*, indicating just the opposite. Supporting this alternative hypothesis is the morphological similarity of *Allonautilus* to both *Cenoceras* and *Nautilus* hatchlings suggesting that *Allonautilus* evolved from *Nautilus* in the mid-Tertiary by the process of paedomorphosis (resemblance of adult animals to the young of their *ancestors*).

Nautiloids were a major component of Paleozoic faunas but the subsequent decline in diversity has limited the present-day group to only two genera and five to six species. But such bottlenecks have occurred before and, unlike ammonites, nautiloids have survived and diversified after each outage incident. Bonacum and colleagues (2011) “suggest that the present-day nautilids are undergoing a period of evolutionary radiation throughout the Indo-Pacific region” (p. 87) that will hopefully ensure the survivability of such a marvelously engineered animal.

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The McAbee Fossil Beds Heritage Site

Rick Poropat

Introduction

The Cenozoic fossil record of British Columbia is dominated by deposits of Eocene age yielding fossils preserved in ancient lake sediments. The McAbee Fossil Beds Heritage Site is one of the most significant places in British Columbia for the study of Eocene fossils. The site is composed of two parcels of Crown land located just north of Highway 1/97, approximately 13 kilometers east of Cache Creek in British Columbia. (Figure 1) It is part of an ancient lake bed which was deposited approximately 51 million years ago and is known worldwide for an incredible abundance, taxonomic diversity and quality of Eocene fossils. The heritage site includes the known extent of the fossil beds at two separate locations: McAbee-Battle Creek (east parcel) and Perry Ranch (west parcel); a total of approximately 548.23 Hectares. (1,355 acres.)

The McAbee site has great value to paleontology because it contains the greatest diversity and clearest record of insects such as ants, bees, and wasps as well as delicate flower and plant parts in the province. It represents a significant and irreplaceable record of the biological history of this time period on earth. The McAbee Fossil Beds site is also valued as an educational resource for teaching people of all ages about the principles and practices of paleontology. The fossil collections from this site are an important resource for scientific study and many new species have been discovered in the past decade.



Figure 1. View of McAbee site from highway showing lacustrine sediment exposures. (Modified from McAfee Site Assessment Report; Wilson, M.V.H. 2009.)

Geology

The McAbee Fossil Beds consist of approximately 30 m of bedded, siliceous sediments within a 550 m sequence of reworked pyroclastic (volcaniclastic) rocks. (Mustoe, 2005) The sediments are informally named the McAbee beds but are considered to be part of a yet unnamed formation within the late to early Eocene Kamloops Group. (Ewing, 1981) Farther to the east, the Kamloops Group contains lacustrine sediments of a similar age that are named the Tranquille Formation, however, the McAbee beds are not known to be continuous with that formation and are not included in it by most authorities. The fossil beds themselves are interpreted to be diatomaceous, lacustrine deposits within a regional drainage basin, although the diatoms are highly altered and are not visible in the sediments. This interpretation is based upon the fine preservation of at least five families of freshwater fish (Wilson, 1980) along with insects and terrestrial plant remains. The damming of a paleo-valley by a volcanic flow created a relatively deep lake with apparent annual bedding, most likely deposited as deep-water flows and from the water column. (Hebda, 2014) Sediment deposition and thermal and physical deformation occurred in the upper part of the sequence and the fossiliferous shale was deposited in quiescent intervals. The shale deposits lie on an ash-flow tuff and are capped by flow breccias. Mega fossils, along with fossil pollen, were used to link the McAbee site with 15 other Eocene lacustrine sites distributed in western British Columbia and near Republic in the state of Washington. (Dillhoff, et al, 2005) This lacustrine system is referred to as the Middle Eocene Okanagan Highlands.

The lowest, well-exposed 25-60 m is composed of three stratigraphic zones which vary with respect to volcanic input, texture and alteration. (Hebda, 2014) The basal 12 m thick zone of shales interbedded with volcanic ash consists of five definable sedimentary units. Chocolate brown fissile shales in the middle of the zone contain the best preserved fossils. In the second zone, 12-20 m above the base, brown crumbly to blocky fine sandstones are interbedded with thin shales and massive basal sandstone. Fossils are poorly preserved in this zone. The third zone, 20-60 m above the base, contains progressively deformed and altered beds composed of chalky, reddish, deformed shales interbedded with massive brown sandstones. The shale and sandstone units are individually thick. (3.5-7.5 m) The silicified shale is rarely fissile, but is fossiliferous. Above 60 m, limited exposures reveal that beds extend >100 m above the base and are fossiliferous, but highly altered. Volcanic breccias disrupt and truncate the lake sediments at thicknesses varying from 30 m to >100 m and have thermally and physically altered the underlying lake sediments.

The discovery that McAbee fossils were originally preserved in diatomite explains the outstanding preservation of fine detail. The presence of diatomite may also suggest the depositional environment was a deep water deposition. Wilson (1980) used the taphonomy of fish, insect and plant remains to establish depth and distance from shore at other sites in the Highlands. His model also seems to indicate a deep-water deposition at McAbee, however, abundant bionid flies and taxodiaceous leaf remains may be more consistent with a near-shore deposition.

Paleontology

Fossil plants from the McAbee fossil beds were first described by the Geological Survey of Canada, (Dawson, 1890; Penhallow, 1908) however these studies were more concerned with the value of the plants for stratigraphic comparison than for their value to paleontology. Hills and Baadsgaard (1967) radiometric dating work contained the first published mention of the McAbee beds. Serious scientific study of the McAfee bed fossils did not occur until Dr. Len Hills (and his University of Calgary students) work on palynology and leaf fossils in the 1960s and early 1970s; the Dr. Mark Wilson (University of Alberta, 1977) study of Middle Eocene fish from British Columbia and the Richard M. Dillhoff, et al, (2005) work comparing Okanogan Highlands flora at several localities. Significant published work on the fossil plants and insects has only occurred since the 1980s and a comprehensive study of the McAbee flora and fauna has yet to be published.



Figure 2. Laurel oak?: *Quercus sp.*



Figure 3. Flower: *Florissantia quilchenensis*.

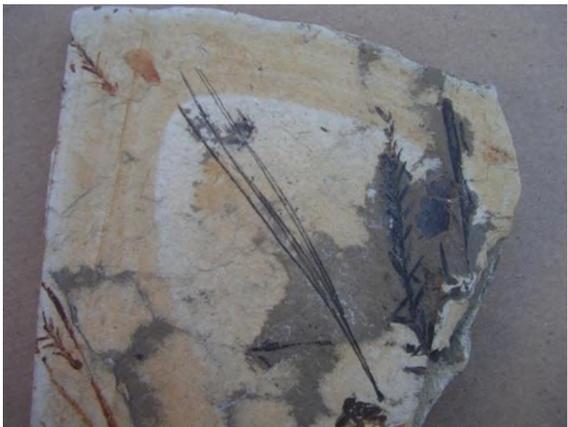


Figure 4. *Pinus sp.* needles and the dawn redwood: *Metasequoia sp.*



Figure 5. *Sequoia sp.* branch tip.

At McAbee, fossils are typically preserved as impressions or carbonized films. Highly detailed leaf (Figure 2), shoot, fruit, nut, flower (Figure 3), seed (Figure 8) and cone specimens are abundant and represent at least 87 taxa. Some represent the first known occurrence of extant species, providing valuable data for the study of plant evolution and Eocene paleoenvironments. Angiosperms seem to be predominant with at least 55 broadleaf types identified. Also common are Gymnosperms which include at least 20 conifers (Figure 4 & Figure 5) and two ginkgos. (Figure 6) Many additional specimens of both types have yet to be described.



Figure 6. *Ginkgo dissecta*.



Figure 7. Fly: *Plecia sp.*



Figure 8. Maple seed: *Acer rousei*.



Figure 9. Freshwater fish: *Eohiodon rosei*.

The McAbee Fossil Beds are best known for the abundant, well preserved insect (Figure 7) and fish (Figure 9) fossils. Birds, spiders and a new species of freshwater crayfish, *Aenigmastacus crandalli*, have also been found. The particularly diverse and well preserved insect fossils are comparable to insects of modern tropical forests.

The Heritage Designation

Active mineral claims in the McAbee area raised concern from paleontologists that scientifically important fossils, and potentially valuable scientific information might be lost as a result of mining activities. In response to those concerns, the Province hired Dr. Mark Wilson, a professor in the Department of Biological Sciences at the University of Alberta in 2007, to assess the significance of the McAbee fossil beds. Dr. Wilson reviewed available literature, obtained factual information from experts, conducted a field inspection, and provided an independent professional opinion on the scientific significance of the site in relation to other comparable sites in British Columbia. He concluded that the McAbee site is one of the two or three most significant sites in B.C. containing Eocene fossils, and is the most diverse site known in Canada for fossils of this era. Dr. Wilson identified the site's key advantages as high species diversity, excellent fossil preservation, abundant, recognizable fossils and site accessibility.

In order to ensure that significant fossils are made available for research and to the people of British Columbia, the Province reached a voluntary agreement in 2008 with tenures holders and other stakeholders outlining a strategy for the preservation of significant fossils at the site. A provincially funded geological and paleontological survey of the McAbee fossil beds was completed in December 2009. The survey report presented new scientific information on the importance of the site, its geology and the accessibility, quality, diversity and abundance of fossils. Based on the survey, the British Columbia government determined that the site warranted heritage designation, given the significance of the McAbee fossil resource and the fact that the voluntary agreement did not adequately protect the site.

The McAbee fossil beds were officially granted Heritage Site protection by the B.C. Ministry of Forests, Land and Natural Resource Operations on July 19, 2012. The designation prevents damage to the fossil beds by restricting certain activities and authorizing others through permits. Its scope includes the known extent of the fossil beds as well as key ecological and landform features and deposits of the Eocene volcanic complex of interior British Columbia. The heritage designation will ensure the fossil resource is managed to provide research, education and recreational opportunities.

An important goal of the heritage site is to conserve the heritage values of McAbee, including providing information on how to interpret common fossils and significant fossils, conveying site-safety and site-conduct messaging, and educating the public about the many values of the site. A Conservation Management Plan is currently under development which will provide information on how to access the site, which parts of the site are accessible to the public and guidelines with respect to practices at the site. Day-to-day permitting responsibility will be handled by the regional office of the Ministry of Forests, Lands and Natural Resource Operations.

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Florida's Plio-Pleistocene and the Caloosahatchee Formation of South Florida

Irene Broede

The Pliocene Epoch began 5.3 million years ago (Mya) and ended 1.8 Mya. The Pleistocene began 1.8 Mya and ended at 0.01 Mya (10,000 ya). In Plio-Pleistocene time glaciers formed, then melted, and sea levels rose and fell. In Florida when the glaciers melted, the ocean probably came up only 15 to 20 feet above today's level. As the glaciers formed, sea levels dropped to 300 feet below its present level. This did not happen only four times, the sea advanced and retreated thirty times from the late Miocene through the Pleistocene. When the ice masses melted, seas covered all the low coastal parts of Florida. During glacial times the sea retreated doubling the land mass of Florida. This fluctuating shoreline explains why terrestrial fossils are found many miles out in the Gulf of Mexico, and why marine deposits are found inland.



Diagram of Florida from Brown, R.C. 1988.

During glacial periods, temperatures dropped over most of the world and parts of North America were uninhabitable. Florida fared well during these temperature extremes. The glaciers never got any closer than southern Illinois. In Florida, interglacial temperatures were a little warmer than present day temperatures and in glacial times only slightly colder. The sea around Florida acted as a temperature buffer.

Between glacial periods, the terrain and vegetation were probably much like the unaltered areas of Florida today. Glacial intervals were considerably drier. When sea level was low, a wide savanna extended from the Florida west coast along the Gulf of Mexico to the Caribbean coast of Mexico and the Yucatan and on to South America. Animal dispersal occurred in both directions along this corridor to and from South America. It is known as the Great American Faunal Interchange. The

interchange began in the late Pliocene and has recurred during glacial intervals. This coastal plain also provided an avenue of migration into Florida for animals of western North America.

When sea level was high, the coastal corridor was flooded and animals could enter Florida only from the north. North America was linked to Eurasia during the glacial periods when sea level was low, but this land bridge could only be crossed by animals that were adapted to cold.

Life was abundant in the Plio-Pleistocene seas. Fossils of sharks, rays, and bony fishes are found in Plio-Pleistocene marine deposits, and closely resemble extant species. Marine mammals such as the long-beaked dolphins disappeared in the Pliocene, and toothed whales similar to the sperm whale grew more common. Manatees replaced the dugongs in the Pliocene to the present day.

Plio-Pleistocene reptiles were basically the same as those of the present day. The crocodile, *Gavialosuchus* became extinct and there were no more crocodiles in Florida until recent times. The large land tortoise *Geochelone* was present in the Pliocene and disappeared in the late Pleistocene.

Birds are represented by increasing numbers of present day species. Florida's most remarkable Pliocene bird was *Titanis walleri*, a predatory flightless bird about 10 feet tall. Its closest relatives were in South America.

In Plio-Pleistocene times, the edentates arrived in Florida from South America. They include sloths, armadillos and glyptodonts. The ground sloth, *Glossotherium* appeared in the Pliocene, and the giant ground sloth, *Eremotherium* came in the Pleistocene. *Eremotherium* grew to 20 feet in length and was the largest land animal ever to live in Florida. The armored glyptodonts reached Florida in the Pliocene. Other edentates include a big armadillo twice the size of the extant armadillo, and *Holmesina* an armadillo-like animal that was six feet long.

Florida was home to a giant beaver, *Castoroides ohioensis* during the Plio-Pleistocene. The carnivore *Boraphagus*, a Pliocene dog, and *Canis lepophagus*, a Pliocene coyote also lived in Florida during this time.

The short-faced bear, *Arctodus* and *Tremarctos* evolved in the new world and inhabited Florida in both the Pliocene and Pleistocene. *Tremarctos floridanus* was a massive bear and was probably herbivorous. *Smilodon gracilis*, a smaller saber-cat first appeared in the Pliocene. The late Pleistocene saber-cat *Smilodon floridanus* grew to the size of a modern lion. *Felis atrox*, a giant Pleistocene lion, was 50% larger than any living lion.

The gomphothere *Cuvieronius* spread into South America in the late Pliocene after having most of its evolution in Florida. During the Pleistocene the American mastodon, *Mammut*, lived in Florida and became extinct at the end of the Pleistocene. Mammoths, *Mammuthus*, were present in Florida only during the Pleistocene. Some mammoths grew to 13 feet tall at the shoulder. Both mammoths and mastodons survived until about 10,000 years ago.

The gazelle-horse *Nannippus* survived to the end of the Pliocene. *Equus* first appeared in the Pliocene and flourished for 4 million years. The teeth of *Equus* are found in almost every Pleistocene fossil deposit in Florida. *Equus* disappeared from North America at the end of the Pleistocene.

Tapirs with down-curved noses lived in Florida from the late Miocene through the Pleistocene. Two genera of peccaries, *Platygonus* and *Mylohyus* were common in Florida during the Pliocene-Pleistocene.

North America is the home continent for camels. *Hemiauchenia*, a camel, survived through the Pleistocene and *Palaeolama* appeared in Florida from South America in the early Pleistocene. By the end of the Pleistocene, no camels remained in North America.

Primitive deer appeared in the earliest Pliocene, and by late Pliocene the most common deer was *Odocoileus*, indistinguishable from the modern white-tailed deer.

The only bovid to spread extensively into Florida was the genus *Bison*. *Bison latifrons* had horns spanning 6 feet.

Climate change probably caused many extinctions at the end of the Pleistocene, about 10,000 years ago, when over 40 genera became extinct. At about 10,000 years ago *Homo sapiens* invaded Florida. Aggressive hunting may also be a cause of the extinctions. The cause or causes of the Pleistocene extinction is still under debate.

The Caloosahatchee Formation of South Florida

The deposits of the Caloosahatchee Formation of South Florida have been world famous because of the wide range of invertebrate fossil fauna found there. Over the past century there has been much debate about the age of the Caloosahatchee Formation. The marine deposits along the Caloosahatchee River were first studied scientifically by Professor Angelo Heilprin in 1887. Professor Heilprin and Mr. Joseph Wilcox explored the river banks in the winter months of 1885-86. Their exploration was sponsored by the Wagner Institute and the Academy of Natural Sciences of Philadelphia. The results of their exploration were published in the Transactions of the Wagner Institute. In describing these beds, Heilprin noted that the freshness and beauty of preservation of the fossils might indicate a younger age. Closer inspection of the Caloosahatchee fossils revealed a good number of extinct forms, such as *Siphocypraea problematica*, *Vasum horridum*, and *Liochlamys bulbosa*. Out of 89 species collected, 48 were the same as recent forms.

In the winter months of 1886-87, Mr. Wilcox and Dr. William H. Dall explored the Caloosahatchee region and made large collections of fossil mollusks. Dr. Dall accepted the task of describing these collections which took a number of years. His work on the fossil collections became a monograph of the entire East Coast Tertiary fauna. From the Florida Pliocene, Dall listed 639 species, of these 48% were of recent forms and 28% were restricted to the Caloosahatchee Formation.



Siphocypraea problematica
and 2 examples of *Vasum*
horridum, collected by
author.



Liochlamys bulbosa example
from Peterson, 2008.

In recent years, the study of the Pliocene mollusks was enhanced by collecting the spoil banks of various canals and dredging projects in southern Florida. The deepening of the Caloosahatchee River produced spoil banks that were gone over by Mr. Maxwell Smith and Mr. Thomas L. McGinty. This resulted in the discovery of many new species. These new species were described in the “Nautilus”, a publication by Smith and McGinty. The spoil banks between Ortona Locks and La Belle are the type area of the Caloosahatchee Formation.

The Pliocene mollusks of southern Florida consist of about 776 named forms. Marine mollusk shells are the most common macro-fossils of South Florida. They are excavated from quarries (shell pits) for road fill and mined for aggregate to make concrete. The number and diversity of Florida’s

fossil mollusks was much greater than that of living shells. This fauna is a shallow-water assemblage that lived at a depth of 100 fathoms or less.



Shell Pit in Arcadia, Florida. Top: Long view. Bottom: Close-up showing shells.

In 1958 the Formation was studied by Dubar and thought to be Pleistocene because of the presence of the fossil horse *Equus cf. leidy* and the armadillo *Chlyamytherium septentrionalis*. These two species indicated a Middle Pleistocene age. Horace Richards objected to the placement of the Caloosahatchee Formation in the Pleistocene on the basis of the large number of extinct mollusks. When the Pleistocene was extended back about 2 million years, it was conceded that part of it might be very early Pleistocene. The problems of the age of the Caloosahatchee Formation were discussed in two field conferences held in Florida in 1968 and 1969. More recently some samples of corals were dated by the helium-uranium method, and yielded dates between 1.8 and 1.9 million years.



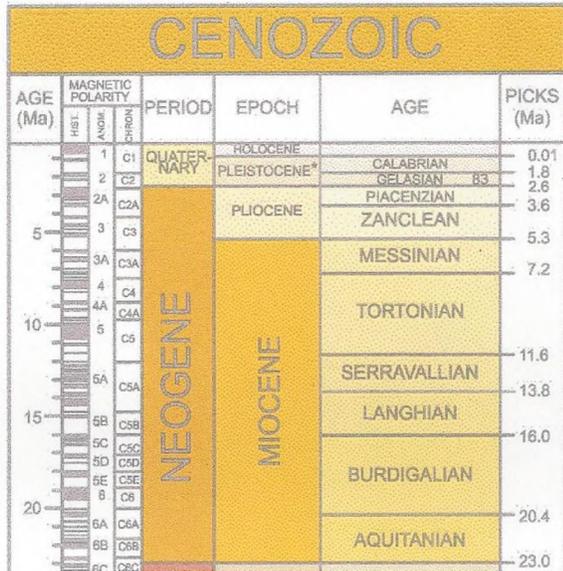
Extinct Fossil shells collected by author.

Top row, left to right: *Strombus leidy*, *Terebraspira scalarina*, *Arca wagneriana*

Middle row, left to right: *Mitra compsa*, *Echinofulgur echinatum*

Bottom row, left to right: *Nodipecten collierensis*, *Ecphora quadricostata*,
Anadara rustica (2 shells)

Additionally, based on the presence of the remains of a Gomphothere (*Cuvieronius sp.*) and a primitive mammoth (*Mammuthus haroldcooki*) the Caloosahatchee Formation dates to about the time of the Plio-Pleistocene boundary. The most recent chronostratigraphic studies by Missimer (2002) have placed the Caloosahatchee Formation of South Florida in the Pleistocene. The bulk of the age data on this formation has it straddling the Calabrian and Gelasian stages.



← Date of Caloosahatchee Formation From the Geological Society of America.

Acknowledgement

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DETAILED STRATIGRAPHY OF A CLASSIC PLIO-PLEISTOCENE MARINE EXPOSURE IN SARASOTA, FLORIDA

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Introduction

The former Ashland Petroleum and Asphalt Corporation (APAC) shell pits (=Warren Bros pit of Puri *in* Weisbord, 1972; MacAsphalt pits of Petuch, 1982) were directly west of I-75, just north of its junction with State Rt. 780 (Fruitville Road), 9 km east of Sarasota, in Sarasota County, Florida (sec. 13, T 36 S, R 18 E). This locality (Figure 1) and its exposed Plio-Pleistocene section and fossil biota have been described by a number of authors. These include Puri, *in* Weisbord (1972); Hunter, *in* Weisbord (1981); Petuch (1982, 2004); Geary and Allmon (1990), Jones *et al.* (1991); Lyons (1992); Zullo and Harris (1992), and Allmon (1992, 1993). Petuch and Roberts (2007) designated the exposed section at this locality as the “standard reference section for the Pliocene of Florida and the Atlantic Coastal Plain”. Plio-Pleistocene outcrops are typically very short-lived and incompletely exposed in the Atlantic Coastal Plain and peninsular Florida areas. The APAC site was unique for the continuous pumping of the pits which led to continuous exposure of from 10 to 20 m of Plio-Pleistocene section during the 1980’s and early 1990’s. Unfortunately, the APAC pits are now flooded and are the site of a 600-acre lake at the Nathan Benderson Park and are surrounded by residential and commercial developments (Petuch and Roberts, 2007; Portell *et al.*, 2012). The former shell pits and spoils piles are now inaccessible. However, some of the described stratigraphic units are currently exposed 2-3 km to the east in the adjacent operational Schroeder Manatee Ranch (SMR) (formerly Quality) Aggregates pits, east of I-75 and south of University Parkway (Allmon, 1992, 1993; Zullo and Harris, 1992; Petuch, 2004; Portell *et al.*, 2012; observations of the author, 2004 and 2009).

Previous Work

Measured sections from the APAC pits and descriptions of the stratigraphic units exposed and their faunas have been provided previously by Hunter, *in* Weisbord (1981) and Petuch (1982). Hunter described over two meters of an upper clean quartz sand, underlain by slightly more than six meters of shelly sand, and nearly two meters of phosphatic, fossiliferous sandy clay. She recognized 14 distinct faunal/stratigraphic subdivisions within the strata exposed at the site. Petuch (1982), describing the section on the east side of the pits, measured 20 m of exposed strata and also identified 12 well-defined stratigraphic/faunal “units” that were traceable throughout the quarry operations. He described an uppermost 4.6 m of unfossiliferous yellow sand (Unit 0), underlain by 12 m of very fossiliferous shelly sand (Units 1-10), and a basal 1.8+ m thick gray fossiliferous muddy sand that was partially lithified and contained abundant marine vertebrate remains (Unit 11). Subsequent authors have largely affirmed the stratigraphic units described by Hunter and Petuch as occurring throughout the shell pits (Lyons, 1991, 1992; Allmon, 1992, 1993).

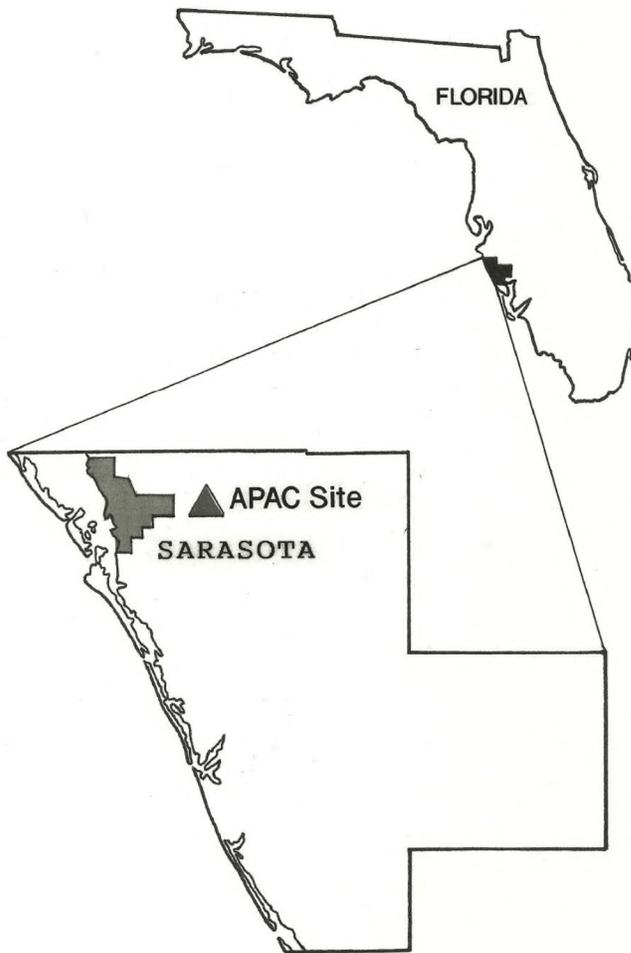


Figure 1. Location of the former APAC shell pits, east of Sarasota, in Sarasota County, southwest Florida.

The author extensively studied the exposures at the APAC site in 1987, 1989, and 1992. The studied portion of the operation was located nearly 1 km west of Petuch's sections (1982, Figure 1). In the late 1980's, the site was roughly divided into three pits aligned in a north-south array (Figure 2). The South Pit was inactive, partially flooded, and heavily vegetated. Good, fresh, in-place sections were exposed in the Central Pit, especially along its western wall (Localities #1 and #2) and along a shallow drainage ditch running east-west along the northern wall of the Central Pit (Locality #3). Additional exposures were along the south and west walls of the North Pit (Localities #4, #5 and #6). These sections were measured, lithologies and faunas collected and noted, and a composite section was constructed for this portion of the site (Figure 3). A detailed description and analysis of this section in terms of its facies, faunas, and environments is provided in the succeeding discussion.

Approximately 10 m of strata were measured along the west wall of the Central Pit, generally corresponding to Units 0-10 as described by Petuch (1982). Rapid facies changes are typical, particularly in the upper 4 m of the exposed section. The measured section consists of 1.2 – 2.5 m of cross-bedded, well-sorted quartz sand, largely barren of fossils (Unit 0); a 2-m thick complex of interfingering dark, organic-rich terrestrial paleosols, peaty beds, and thin marine shell beds (Unit 1); underlain by 5.5 m of primarily shelly marine quartz sand (Units 2-10) (Figure 3). This section has also been described in some detail by Lyons (1991) and Lyons, *in* Scott and Allmon (1992).

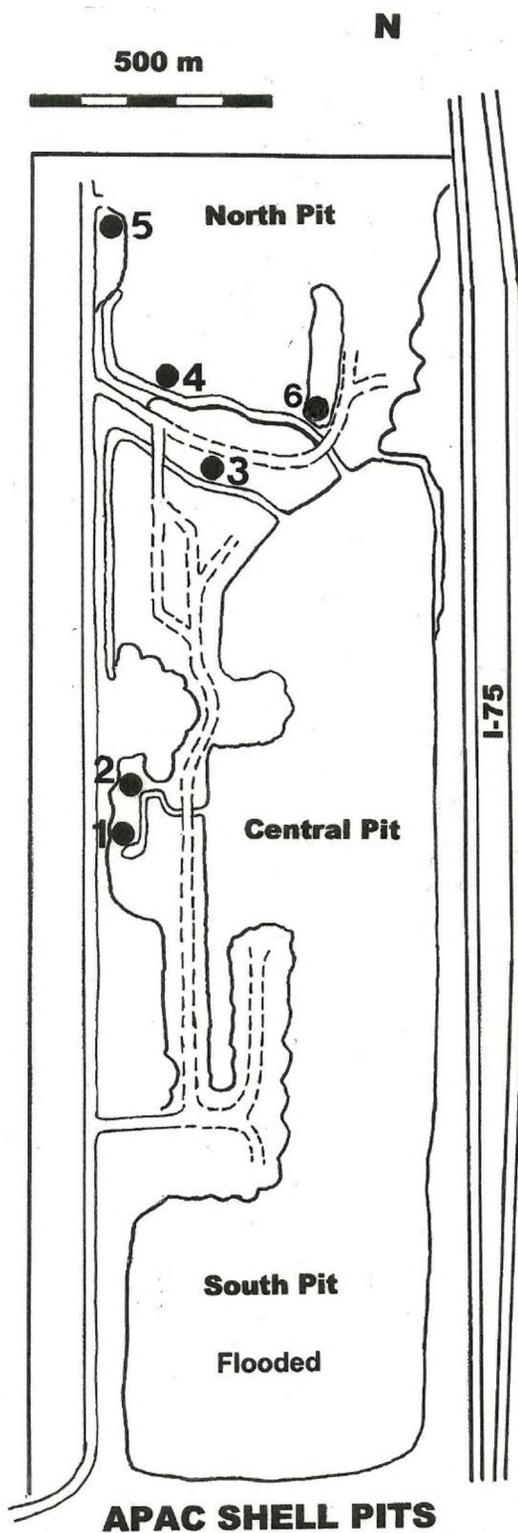


Figure 2. Sketch diagram (modified from Geary and Allmon, 1990) showing the locations of the sections measured by the writer along the west edge of the APAC shell mining operation as it existed in 1987 and 1989.

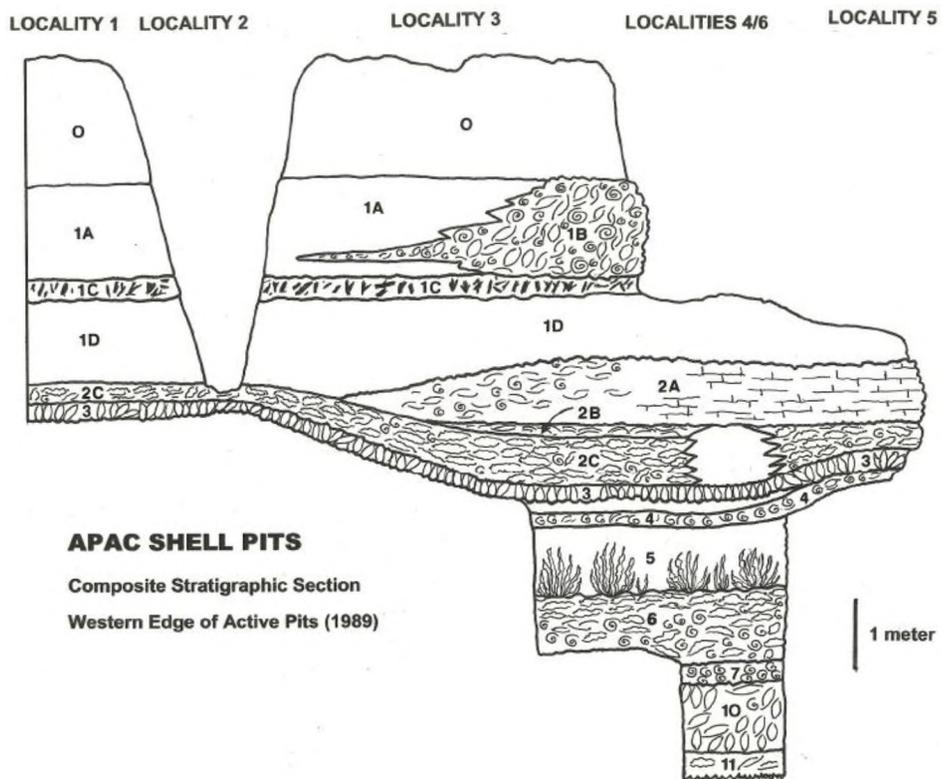


Figure 3. A composite stratigraphic section of the Plio-Pleistocene strata exposed along the western edge of the APAC shell mining operation in 1987 and 1989. Numbers refer to the informal faunal units identified and used by Petuch (1982) and others at the APAC and SMR shell pits east of Sarasota. See text for detailed descriptions of these “units”.

Stratigraphy and Age

Three major fossiliferous marine units are traditionally recognized as comprising the Plio-Pleistocene section in south Florida (Olsson, 1968). These include, in ascending order, the Tamiami Formation of Mansfield (1939), the Pinecrest Beds of Olsson (1964), and the Caloosahatchee Formation of Dall (1887). Due to the highly variable lithologies associated with these units across the south Florida area and the distinctiveness of their enclosed molluscan faunas, these units have been more often differentiated on the basis of these faunas rather than their respective lithologies, so that they are used more in a biostratigraphic rather than lithostratigraphic sense. Descriptions and discussions of the nomenclature of the Plio-Pleistocene stratigraphy in south Florida can be found in Olsson (1964, 1968); Hunter (1968, 1978); Brooks (1968); Dubar (1974); Petuch (1986, 2004, 2007); Lyons (1991); Allmon (1993); and Scott (1990, 2001).

Petuch (1982) initially described the stratigraphy of the strata exposed on the east side of the APAC pits, adjacent to I-75. He identified basal “Chesapeake Miocene” beds (Units 11 and 10) as facies within the Tamiami Formation that were overlain by the fossiliferous quartz sands of the

Pliocene Pinecrest Beds (Units 9-2), and capped by an upper sand (Unit 1) with highly fragmented molluscan shells that had affinities to the Plio-Pleistocene Caloosahatchee Formation.

Lyons (1991, 1992), studying the stratigraphy along the western margin of the shell mining operation, followed suite, placing Petuch's Units 8-2 in the Middle Pliocene Pinecrest beds which he believed were a sandy facies of the Tamiami Formation. He also described an expanded, lithologically complex Unit 1 that included peaty, non-marine beds interspersed with shelly marine sands with an abundant Caloosahatchee molluscan fauna.

Using a combination of ostracode biostratigraphy, terrestrial mammalian biostratigraphy, strontium isotope dating, and magnetostratigraphy, Jones *et al.* (1991) arrived at a Middle Pliocene age for Units 10-5 of Petuch (3.5-2.5 mya) and a Late Pliocene age for Units 4-2 (2.5-2.0 mya). Stanley (1991), using a different interpretation of the terrestrial mammalian and paleomagnetic data, has argued that most of the exposed section (Units 10-2) at the APAC site is Middle Pliocene (3.5-3.05 mya) in age.

Zullo and Harris (1992) and Harris and Zullo (1993), discussing the sections exposed at the APAC and Quality Aggregates sites in Sarasota, used a combination of sequence stratigraphy and biostratigraphy to place the Murdock Station Formation and the overlying lower Pinecrest Beds (Units 11-5) in their Coastal Onlap TB3-6 Cycle and the overlying upper Pinecrest Beds (Units 4-2) in their TB3-7 Cycle. These Cycles were thought to correspond to the N19/20 Foram Zones of Blow (1969), roughly Middle Pliocene in age.

Allmon (1993) summarizing all of the available data at that time, indicated that the lower part of the Pinecrest Sand at the APAC site (Units 10-5) was early to mid-Late Pliocene in age (3.5-3.0 mya) with the upper part of the Pinecrest (Units 4-2) being Late Pliocene in age (2.5-2.0 mya). He suggested that the entire Pinecrest section exposed at the APAC site spanned 0.5 – 1.5 million years.

In 1998, the Pliocene Series was formally divided into a Lower Pliocene Zanclean Stage, a Middle Pliocene Piacenzian Stage, and an Upper Pliocene Gelasian Stage (Rio *et al.*, 1998). On this basis, Unit 11 at APAC would be placed in the Early Pliocene Zanclean Stage; Units 10-5 would be placed in the Middle Pliocene Piacenzian Stage; and Units 4-2 at the APAC site would be placed in the Late Pliocene Gelasian Stage.

Petuch (2004) and Petuch and Roberts (2007, Figure 4.3) further refined the stratigraphy of the fossil-bearing strata originally described from the APAC pits, placing Petuch's Unit 11 in the Sarasota Member of the Murdock Station Formation (Early Pliocene, late Zanclean); Unit 10 in the Buckingham Member of the Tamiami Formation (earliest Piacenzian Pliocene); Units 9-5 in the Pinecrest Member of the Tamiami Formation (mid-Piacenzian Pliocene); Units 4-2 in the Fruitville Member of the Tamiami Formation (late Piacenzian Pliocene); and Unit 1 in the Fordville Member of the Caloosahatchee Formation (latest Piacenzian Pliocene).

In 2009, the IUGS formally designated the Gelasian Stage to be the earliest subdivision of the Pleistocene and went back to a two-fold subdivision of the Pliocene with an Early Pliocene Zanclean Stage and a Late Pliocene Piacenzian Stage (Gibbard and Head, 2010).

Following up on these shifts in the age of these respective units, Missimer (2012) placed the Pliocene-Pleistocene boundary as currently defined within the Pinecrest section exposed at Sarasota, with the lower Pinecrest Sand (Units 9-5) being placed in the Late Pliocene Piacenzian and the upper Pinecrest beds (Units 4-2) being placed in the Early Pleistocene Gelasian Stage. The contact between the earliest Pleistocene Gelasian and the succeeding early Pleistocene Calabrian was placed within the overlying Caloosahatchee beds (Unit 1). A suggested stratigraphic nomenclature and the respective ages for the strata exposed at the APAC site is presented in Table 1.

TABLE 1 – Stratigraphic Nomenclature and Ages of the Respective Lithologic and Faunal Units formerly exposed at the APAC Shell Pits site, Sarasota, Florida

Formation	Member	Faunal Unit	Series	Stage	Age
Bermont/Ft. Thompson	?	Unit 0 <i>Mammuthus</i> sp.	Pleistocene	?Aftonian	<0.8
Caloosahatchee	“Fordville”	Unit 1 <i>Macrocallista/Dinocardium</i> Beds	Pleistocene	Gelasian-Calabrian	2.0-0.8
Upper Tamiami	Fruitville	Unit 2 Upper <i>Hytissa</i> Beds Unit 3 <i>Perna incurva</i> Bed Unit 4 “Black Bed”	Pleistocene	Gelasian	2.5-2.0
Lower Tamiami	Pinecrest	Unit 5 Upper <i>Vermicularia</i> Bed Unit 6 Lower <i>Hytissa</i> Beds Unit 7 <i>Strombus</i> Beds	Pliocene	Piacenzian	3.5-2.5
Tamiami	“Buckingham”	Unit 10 <i>Mercenaria tridacnoides</i> Bed	Pliocene	Earliest Piacenzian	3.6-3.5
Murdock Station	“Sarasota”	Unit 11 <i>Chesapecten-Chesaconcaus</i> Beds	Pliocene	Zanclean	5.3-3.6

Facies, Faunas, and Environments at the APAC site

Big Picture Overview

Petuch (1982, 2004) and Petuch and Roberts (2007) reconstructed the Tamiami section exposed in the Sarasota, Florida area as being deposited under a variety of environments developed in a semi-protected series of lagoons that were part of what they termed the “Myakka Lagoon System”,

marginal to the so-called “Tamiami Subsea” that occupied most of the Okeechobee Basin or the “Everglades Pseudoatoll” in the Plio-Pleistocene. Water depths and environments inferred for the various faunal units described by Petuch (1982, 2004) at the APAC site ranged from lower-energy, deeper subtidal marine habitats with depths of at least 10m for the basal Zanclean Murdock Station Formation (Unit 11) to high-energy beach environments for the capping Pleistocene sand deposits (Unit 0). The intervening Tamiami strata included a mosaic of various lagoonal facies, ranging from deeper water subtidal parts of lagoons (10-100 m in depth) through shallower water seagrass and sand flats (0-5 m deep) for portions of the Buckingham and Pinecrest Members (Units 10 and 7); and intertidal and shallow subtidal oyster bars 0-2 m deep (Units 9,6, and 2), shallow subtidal mussel beds (Unit 3), and estuarine mudflat and mangrove swamp environments (Unit 4) in the Fruitville Member.

Jones *et al.* (1991) indicated that the Pinecrest/Tamiami section exposed at the APAC site represented at least one transgressive-regressive cycle. Units 10-5 were deposited during a sea-level rise in the Middle Pliocene. The occurrence of Late Blancan terrestrial vertebrates in Unit 4 and brackish water ostracodes in Units 4 and 3 indicated the initiation of a regressive event near the base of Unit 4. These authors speculated that this regressive event was associated with the initial growth of large ice sheets in the Northern Hemisphere, beginning 2.4 mya. The overlying units at APAC were deposited during subsequent sea-level rises.

Stanley (2014) has proposed that the bulk of the strata exposed at the former APAC shells pits are Late Pliocene in age and were formed as part of a transgressive barrier island-lagoon complex and all accumulated within at most a few thousand years. He postulates a lagoonal seagrass habitat with banks of *Hyotissa* oysters bordering the lagoon subtidally and flanking intertidal colonies of *Vermicularia* gastropods. The “Black Bed” facies formed in a marsh along the back of the barrier island with distal tidal channels draped with *Perna* mussels.

Detailed Stratigraphy, west side of the Central Pit, APAC site, 1987

UNIT 11 = *CHESAPECTEN-CHESAONCAVUS* BEDS (Murdock Station Member, Tamiami Formation; Early Pliocene, Zanclean)

Lithology: 32 cm exposed on the floor of the North Pit. Dark gray, muddy quartz sand, typically partially lithified. Medium-grained, subrounded quartz with lesser amounts of subrounded black phosphatic grains, with appreciable amounts of dark gray calcareous clay coating grains and filling interstitial spaces between grains. Large calcitic molluscan shells and cemented masses of giant barnacles floating in a muddy quartz sand matrix. Weathering a buff color.

Fauna: Molluscan fauna dominated by taxa with calcite shells including the large plicate scallops *Chesapecten jeffersonius* (Say) and *C. septenarius* (Say) plus the oyster *Ostrea compressirostra* Say, whose shells serve as substrate for clusters of the giant balanid barnacle *Chesaoncavus tamiamiensis* (Ross). Associated species include the bay scallop *Argopecten comparilis* (Tuomey and Holmes) and small aragonitic bivalves including *Mulinia congesta* (Conrad) and *Astarte undulata* Say. The extinct ribbed muricid gastropod *Ecphora quadricostata* (Say) and abundant marine vertebrate remains are also locally common. Along with the molluscan fauna in the succeeding Unit 10, the Unit 11 molluscan fauna has affinities to the Pliocene Yorktown Formation

in Virginia (Petuch, 1982, 2004). Illustrations of the fossils from this unit and the others described here can be found in Petuch (2004) and Portell, Means, and Hulbert (2012).

Environment: Nutrient-rich, up-welling influenced, deeper water sound or inner shelf facies.

UNIT 10 = *MERCENARIA TRIDACNOIDES* BED (Buckingham Member, Tamiami Formation; early Late Pliocene, Piacenzian)

Lithology: 80-85 cm at the south end of the North Pit. Tightly-packed masses of whole shells, aragonitic and calcitic, with equal numbers of articulated and disarticulated bivalves, in a matrix of buff-brown, sand-size angular shell fragments, black phosphatic grains, and subangular to subrounded, medium-grained quartz sand and minor amounts of silt and clay. Sediments often partially cemented with calcite.

Fauna: Dominated by large “hard-shelled” infaunal venerid clams with Yorktown affinities, including the distinctive corrugated form *Mercenaria tridacnoides* (Lamarck), plus *M. rileyi* (Conrad), *Macrocallista reposta* (Conrad), *Lirophora latilirata* (Conrad), and *L. ulocyma* (Dall). Less common are in-situ specimens of the siphonate burrower *Panope reflexa* (Say), the elongate arcid *Granoarca propatula* (Conrad), the fluted anomiid *Placuanomia plicata* (Tuomey and Holmes), *Marvacrassatella meridionalis* (Dall), and the carditid *Carditamera vaughani* (Dall). Other than fragments of large turritellids, gastropods are curiously absent from this bed at the northern end of the APAC site.

Environment: Nutrient-rich shallow marine sandy bay bottom facies.

UNIT 7 = *STROMBUS* BED (Pinecrest Sand Member, Tamiami Formation; Late Pliocene, Piacenzian)

Lithology: 40+ cm thick in the north wall of the Central Pit. Well-sorted, gray, medium-grained, subangular to subrounded quartz sand with numerous whole, complete aragonite and calcitic molluscan shells, with most of bivalves articulated. Locally dense masses of the shells of the gastropod *Strombus*, tightly packed together in jumbled clusters.

Fauna: Typically dominated by numerous individuals of the small “fighting conch” *Strombus floridamus* Mansfield variety, 55-65 mm in length. Associated molluscan fauna very diverse, including characteristic “Pinecrest” bivalves *Carolinapecten eboreus* (Conrad), *Miltha disciformis* (Heilprin), *Archinella cornuta* (Conrad), *Trachycardium acelinensis* Tucker and Wilson, and *Chione procancellata* Mansfield; plus the gastropods *Eichwaldiella pontoni* (Mansfield), *Lobatus hertwerkorum* (Petuch), *Akleistostoma floridana* (Mansfield), *Sconsia hodgii* (Conrad), *Calophos wilsoni* Allmon, *Cymatophos lindae* Petuch, *Terebraspira sparrowi* (Emmons), *Heilprinia carolinensis* (Dall), *Pleioptygma carolinensis* (Conrad), *Turbinella streami* Petuch, *Cymatosyrinx acclinica* Tucker and Wilson, and *Contraconus adversarius* (Conrad).

Environment: Shallow marine bay or lagoonal grassflats environment.

UNIT 6 = LOWER *HYOTISSA HAITENSIS* BEDS (Pinecrest Sand Member, Tamiami Formation; Late Pliocene, Piacenzian)

Lithology: 60-100 cm thick at the north wall of the Central Pit. Patchy clusters of tightly-packed, whole, usually articulated and cemented large pycnodontine oysters occurring in masses interspersed with medium-grained, subrounded quartz sand with coarse, angular shell fragments and numerous whole shells.

Fauna: Diverse molluscan fauna dominated by typical “Pinecrest” taxa, especially the large pycnodont oyster *Hyotissa haitensis* (Sowerby), and a diverse set of encrusters, including *Spondylus rotundus* Heilprin, *Chama crassa* Heilprin, *Plicatula hunteri* Shaak and Nicol, and byssally-attached bivalves including *Arcoptera* cf. *A. wagneriana* Dall, *Anadara lienosa* (Say), and *Caloosarca floridanus* Vokes. Also a diverse set of predatory gastropods, including the large muricids *Chicoreus floridanus* Vokes, *Hexaplex hertwerkorum* Petuch, and *Phyllonotus globosus* (Emmons), the large, knobless Horse Conch *Triplofusus duplinensis* (Smith), and the spiny vase *Hystrivasum locklini* (Olsson and Harbison); plus isolated large coralla of the compound corals *Solenastrea bournoni* Edward and Haime and *S. hyades* (Dana).

Environment: Oyster bioherms interspersed with seagrass meadows.

UNIT 5 = UPPER *VERMICULARIA RECTA* BED (Pinecrest Sand Member, Tamiami Formation; Late Pliocene, Piacenzian)

Lithology: 55 to 70 cm thick. Lower 15-25 cm consisting of dense, large, in-situ colonies of tubular vermiculiform gastropods, oriented vertical to the bedding with tubes extending upward a maximum distance of about 25-30 cm. Upper 40 cm consisting of barren or shell-poor, clean quartz sand.

Fauna: Dominated by large colonies (30+ cm in diameter) of the sessile vermicularid gastropod *Vermicularia recta* Olsson and Harbison. Exposed portions of tubes locally encrusted by small balanid barnacles.

Environment: Shallow subtidal sponge or macroalgal “gardens” encrusting shelly substrates and supporting large clusters of sessile suspension-feeding turrnellid gastropods.

UNIT 4 = THE BLACK BED (Fruitville Member, Tamiami Formation; Early Pleistocene, Gelasian)

Lithology: 12 to 40 cm of dark, olive-gray muddy sand, moderately well-sorted, fine to medium-grained, subrounded quartz sand with a mix of silt and clay and shell fragments.

Fauna: Very fossiliferous with shells stained a peculiar dark blue-black or maroon color. Distinctive molluscan fauna of numerous, small, thin-shelled infaunal filter-feeding bivalves including *Mulina sapotilla* (Dall), *Tagelus divisus* (Spengler), and *Eurytellina alternata* (Say), and an abundance of the

gastropods *Pyrazisinus* spp., *Melongena draperi* Petuch, *Echinofulgur jonesi* Petuch, *E. helenae* Olsson, *Pyruella laevis* Petuch, and *Hystrivasum squamosum* (Hollister). Also locally common are the fresh-water snails *Helisoma disstoni* (Dall) and *Viviparus georgianus* (Lea). Occasional Late Blancan terrestrial vertebrate remains.

Environment: Estuarine mudflats flanked by mangrove thickets adjacent to mouth of a major river.

UNIT 3 = *PERNA INCURVA* SHELL BED (Fruitville Member, Tamiami Formation; Early Pleistocene, Gelasian)

Lithology: 11 to 40 cm thick. Typically tightly-packed clusters of whole, articulated, usually up-right in-situ mussels in a matrix of clean, medium-grained, subangular quartz sand with minor shell fragments and clay. Grading below into barren quartz sand 1-20 cm thick. Sharp upper contact with Unit 2 with pycnodontine oysters directly colonizing the upper surfaces of these mussel beds.

Fauna: Dominated by large, articulated, in-place specimens of the mytilid mussel *Perna incurva* (Conrad) and an attached epifauna of crepidulid gastropods and balanid barnacles. Associated with a diverse but low-density benthic fauna of the infaunal clams *Florimetus magnoliana* (Dall), *Macrocallista greeni* Ward and Blackwelder, and *Stewardia anodonta* (Say), and the predatory neogastropods *Chicoreus judeae* Petuch, *Solenosteira mulepenensis* Petuch, *Pyruella federicoae* Petuch, and *Cinctura* cf. *C. sarasotaensis* Petuch.

Environment: Patchy mussel beds comprised of large, byssally-attached filter-feeding mussels associated with grassflat beds on a shallow subtidal, low-energy marine sandy bay bottom.

UNIT 2C = UPPER *HYOTISSA HAITENSIS* BED (Fruitville Member, Tamiami Formation; Early Pleistocene, Gelasian)

Lithology: 35-75 cm thick, thickening to the north. Tightly-packed, whole, mostly articulated pycnodontine oyster shells, some cemented together, in a sparse matrix of medium-grained, subangular quartz sand with minor shelly detritus. Entire unit often stained an orange-red rust color due to iron oxide staining. At Localities #1, #2, and #3 to the south, abrupt contact with underlying *Perna* Bed. Unit 2C is absent at Locality #4 in the North Pit, replaced by barren sand.

Fauna: Dominated by in-place, articulated specimens of the large pycnodontine oyster *Hyotissa haitensis* (Sowerby), forming local biostromes with accessory encrusters including compound corals *Diploria* and *Siderastrea*, cemented and byssally-attached bivalves including *Chama emmonsii* Nicol and *Arcoptera* cf. *A. wagneriana* (Dall), and vermetid gastropods. Interspersed with a grassflat fauna including the infaunal clams *Chione erosa* (Dall), *Macrocallista greeni* Ward and Blackwelder, *Mercenaria carolinensis* (Conrad), and *Linga pensylvanica* (Linne) and the gastropods *Strombus floridamus* Mansfield variety, *Phyllonotus globosus* (Emmons), *Calophos wilsoni* Allmon, *Cymatophos lindae* Petuch, *Pleioptygma carolinensis* (Conrad), and *Cymatosyrinx acclinica* Tucker and Wilson.

Environment: Oyster bioherms interspersed with grassflats.

UNIT 2B = SCALLOP BED (Fruitville Member, Tamiami Formation; Early Pleistocene, Gelasian)

Lithology: 40 cm thick at Locality #3. Intermittent clusters of tightly-packed stacks of mostly disarticulated large (80-160 mm in diameter), fan-shaped scallop valves, oriented convex-up, in a matrix of clean, medium-grained quartz sand. Sharp contact with 2A – marked by an iron oxide-coated surface.

Fauna: Dominated by large fan-shaped scallops, including abundant *Carolinapecten eboreus* (Conrad) and less common specimens of *Amusium mortoni* (Ravenel), nearly to the exclusion of all other organisms. Few disarticulated valves of *Hyotissa haitensis* (Sowerby) with in-situ specimens of the mussel *Perna incurva* (Conrad) and rare large specimens of melongenid gastropod *Melongena* sp.

Environment: Storm-reworked deeper-water bay facies or wash-over fan debris layers.

UNIT 2A = “TRANSITIONAL” BED (?Fruitville Member, Tamiami Formation; Early Pleistocene, Gelasian?)

Lithology: 0-100 cm thick, thinning to the south. Highly variable in nature, ranging from light-colored, moderately well-sorted, medium-grained, subrounded quartz sand with locally abundant whole, but largely disarticulated shells to the southeast – grading into hard, clinker, dark-gray fossiliferous “limestone” to the northwest. “Limestone” is actually calcite-cemented quartz sands and shell, likely meteoric in origin.

Fauna: A diverse mixture of Tamiami and Caloosahatchee taxa, with the former consisting of *Hyotissa haitensis* (Sowerby), *Perna incurva* (Conrad), *Eichwaldiella pontoni* (Mansfield), and *Calophos wilsoni* Allmon; and the latter including *Anomalocardia caloosana* (Dall), *Chione elevata* (Say), *Phrontis vibex* (Say), *Rexmela* sp., and *Comus “waccamawensis”* Smith. This unit bridges the gap between the previous Tamiami molluscan fauna and the overlying Caloosahatchee molluscan fauna.

Environment: Shallow marine bay facies.

UNIT 1D = PALEOSOL (?Caloosahatchee Formation; Early Pleistocene, Gelasian?)

Lithology: 0-150 cm thick, thinning to the north. Dark brown, organic-rich, moderately well-sorted, medium-fine, subrounded quartz sand, locally peaty with an abundance of fine granular organic material and minor clay. No large-scale sedimentary structures. Texture comparatively homogeneous.

Fauna: No identified fossils were observed.

Environment: Swampy, vegetated, terrestrial lowland marginal to shallow marine bay.

UNIT 1C = “WOODY” BED (?Caloosahatchee Formation; Early Pleistocene, Gelasian?)

Lithology: 50 cm thick across the west end of the Central Pit. Dark brown, organic-rich, well-sorted, medium to fine grained, subrounded quartz sand, locally peaty and with an abundance of in-situ, upright carbonized woody trunks and roots.

Fauna: Associated with the carbonized wood were poorly-preserved carbonized remains of the mastodon *Mammut americanus* (Kerr), represented by limb bones, vertebrae, rib bones, and a mandible and teeth.

Environment: Densely vegetated shrubby thickets bordering a shallow marine bay.

UNIT 1B = MACROCALLISTA-DINOCARDIUM BED (“Ford Member”, Caloosahatchee Formation; Early Pleistocene, Calabrian)

Lithology: 0-155 cm thick, thinning to the south. Clusters of whole, articulated aragonitic shells, some tightly-packed, some preserved in life position, in a matrix of clean, moderately well-sorted, subrounded medium-grained quartz sand with shell fragments. Limonitic and clay-rich to the south and locally becoming cemented and indurated to the north, forming a clinkery, hard, rough, dark-gray “limestone” of probable meteoric origin.

Fauna: A low-diversity molluscan fauna of in-situ, small infaunal clams and small gastropods to the south (*Mulinia lateralis* (Say); *Raeta plicatella* (Lamarck), and *Petricola pholadiformis* (Lamarck), with *Phrontis vibex* (Say) and *Trivia permagna* Johnson). Bed becoming thicker and fauna more diverse to the north (Locality #3) with the large infaunal clams *Macrocallista nimbosa* (Lightfoot), *Dinocardium robustum* (Lightfoot), and *Mercenaria permagna* (Conrad), plus large specimens of the melongenid gastropod *Rexmela* sp. and giant specimens of the busyconid *Sinistrofulgur* sp. and the fascioliid *Triplofusus giganteus* (Kiener). Typical Caloosahatchee species present include the bivalves *Anomalocardia caloosana* (Dall), *Argopecten anteampliocostatus* (Mansfield), *Carolinapecten solaroides* (Heilprin), and *Miltha caloosaensis* (Dall); and the gastropods *Bactrospira perattemuata* (Heilprin), *Lobatus* cf. *L. leidy* (Heilprin); *Siphocypraea problematica* Heilprin, *Pyrazisinus scalatus* (Heilprin), *Busycoarctum rapum* (Heilprin), *Echinofulgur echinatum* (Dall), *Terebraspira scalarina* (Heilprin), *Pleioptygma lineolata* (Heilprin), *Contraconus tyronensis* (Heilprin), and *Conus* “*waccamawensis*” Smith.

Environment: Shallow marine bay that deepened to the north.

UNIT 1A = PALEOSOL (?Caloosahatchee Formation; Early Pleistocene, Calabrian?)

Lithology: 0-150 cm thick, thinning to the north. Dark brown, organic-rich, moderately well-sorted, medium-fine grained, subrounded quartz sand, locally peaty with an abundance of fine granular organic material and minor clays. No large-scale sedimentary structures observed. Texture comparatively homogeneous.

Fauna: No identified fossils were observed.

Environment: Swampy lowland environment marginal to bay or lagoon.

UNIT 0 = BEACH SAND (?Bermont Formation; Middle Pleistocene, Aftonian?)

Lithology: 1.2 to 2.5 m thick, thinning to the north. Clean, well-sorted, well-rounded, medium-grained quartz sand; locally with prominent low-angle cross-bedding. Light buff to white in color; uniform in texture.

Fauna: Largely barren of fossil remains. One isolated, fragmentary molar assignable to the mammoth genus *Mammuthus* from the sand exposed at Locality #3.

Environment: High-energy, coastal beach deposit.

Significance of the Plio-Pleistocene Exposures at the APAC site

The former APAC Shell Pits site in Sarasota, Florida was one of the most extensive and important exposures of Pliocene and early Pleistocene marine strata in North America. Fortunately, due to the continuous pumping of much of the site during its operations in the 1980's and 1990's plus the policies of the management of the shell pits that allowed interested scientists and amateur collectors alike access to the site on weekends and other times when mining operations were shut down, the sections and the fossil faunas exposed were extensively studied and collected prior to the flooding of the site over 15 years ago. As indicated in the above descriptions, the entire Pliocene-Pleistocene section was very fossiliferous with the molluscan fauna incredibly abundant and very diverse. Fossil shells exposed at the site, aragonitic as well as calcitic, are remarkably well-preserved, often preserving color patterns as well as the fine details of the shell's external ornament. Complete growth series of individual species could be easily collected, documenting the ontogenetic changes in shell morphology as well as the complete range of shell variation within species populations. Collections made from the site will continue to be a prime source for the description of many new molluscan taxa well into the 21st century.

Strata and fossils at the APAC site also capture a critical moment in the Earth's recent geologic history – documenting the changing marine environments that accompanied the closure of the Central America Isthmus and the resulting restructuring of the marine biotas in the Caribbean and East Pacific basins and as well as the effects of the concurrent onset continental glaciation in the northern hemisphere on these same faunas (Stanley and Ruddiman, 1995; Allmon *et al.*, 1996). These global changes are reflected in the changing environments and faunas documented in great detail in this 10-20 m Plio-Pleistocene section in west-central Florida. These include the move from cooler water (?), upwelling-influenced marine faunas with Yorktown affinities at the base of the section (Early Pliocene, Zanclean Units 11-10) towards a more tropical molluscan fauna with some Eastern Pacific affinities in the succeeding Piacenzian (Late Pliocene Units 9-5) and Gelasian (Early Pleistocene Units 4-2), followed by a series of likely climate-induced extinction events and faunal

turn-overs in the succeeding Early and Middle Pleistocene (Units 1-0). Continued study of this section and these faunas will likely continue to provide new insights into the complex relationships between Plio-Pleistocene climate change and the evolution and extinction of shallow marine biotas in the Western Atlantic and Caribbean regions.

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