CONTRIBUTIONS IN MARINE MAMMAL PALEONTOLOGY HONORING FRANK C. WHITMORE, JR.

Edited by

Annalisa Berta and Thomas A. Deméré

Incorporating the Proceedings of the Marine Mammal Symposium
of the Society of Vertebrate Paleontology
51st Annual Meeting
Held at the San Diego Natural History Museum
San Diego, California
26 October 1991

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PROCEEDINGS

of the

San Diego Society of Natural History

Founded 1874

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Preface

On 26 October 1991 a symposium on marine mammal evolution was held at the 51st Annual Meeting of the Society of Vertebrate Paleontology in San Diego, California. It was the first symposium on this topic since the one in 1975 held at the American Institute of Biological Sciences meetings in Corvallis, Oregon. The proceedings of that symposium were published as a special issue of *Systematic Zoology* (1976, volume 25:301–446) edited by Charles A. Repenning. Ten years after the Corvallis symposium three of the original participants, Lawrence G. Barnes, Daryl P. Domning, and Clayton E. Ray, published an article in *Marine Mammal Science* (1985, volume 1:15–53) that highlighted notable paleontological discoveries in the intervening years. Since that publication nine years ago, new fossil discoveries, new techniques for investigating evolutionary relationships, and an increase in the number of interested researchers have contributed important new data. The San Diego symposium was organized to bring together many of these researchers and to present a synthesis of our current knowledge of the evolution, systematics, and biogeography of marine mammals (pinnipeds, cetaceans, and sirenians) and marine mammal faunas. The symposium benefited from an international group of participating scientists representing France, Mexico, New Zealand, Russia, and the United States.

Thirteen of the current articles are based on papers presented in San Diego; two additional reports were solicited afterward because of their close relationship to the general theme of the symposium. In the volume, we have arranged the articles into two broad groups, one covering the taxonomy, systematics, and comparative anatomy of specific taxa, the other dealing with the biogeography and biostratigraphy of marine mammal faunas.

One of the participants at the symposium, Frank C. Whitmore, Jr., is widely recognized for his contributions to fossil cetacean systematics and biogeography and for his role as a mentor to many marine mammal paleontologists. Accordingly, we have chosen to recognize Frank's past achievements and continuing research by dedicating this volume to him.

The editors gratefully acknowledge the following individuals who, in addition to most contributors, provided critical reviews of manuscripts: J. David Archibald, Jon A. Baskin, Mario A. Cozzuol, Francis H. Fay, John J. Flynn, John E. Heyning, Richard Hulbert, Samuel A. McLeod, James G. Mead, Jeheskel Shoshani, Michael J. Novacek, Donald R. Prothero, and Charles A. Repenning. We are especially indebted to Clayton E. Ray for his advice and encouragement. Philip Unitt, managing editor of the San Diego Society of Natural History's scientific publications, provided skillful editing of the volume. For funding of this publication we also express our appreciation to the National Science Foundation, National Geographic Society, San Diego State University College of Sciences, and the Kellogg fund of the Smithsonian Institution.

Annalisa Berta and Thomas A. Deméré

Tribute to Frank Clifford Whitmore, Jr.

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With this volume, we pay tribute to our mentor and colleague the "good doctor" Frank Clifford Whitmore, Jr., whose gracious humor, interest in people, and curiosity about the world have meant so much to so many within the field of paleontology and far beyond it. We are pleased to have this opportunity to share our respect and admiration for Dr. Whitmore the scientist, the teacher, and the friend.

Frank was born at home in Cambridge, Massachusetts, on November 17, 1915, to Marion Gertrude (Mason) and Frank Clifford Whitmore, a graduate student at Harvard University. When Frank Jr. was two, the growing family began a series of moves occasioned by his father's burgeoning career in organic chemistry: to Houston and the Rice Institute, to Minneapolis and the University of Minnesota, to Evanston and Northwestern University, to Washington, D. C. and the National Research Council.

Frank, his two younger brothers, and younger sister grew up in a lively family, which included their Irish grandmother and, as often as not, a variety of students who rented rooms in their house. Ideas, adventures, and experiments were encouraged. From these grew their later devotion to science, literature, medicine, dance, business, theater, and art.

Frank completed his intermediate schooling in Evanston before the family relocated, one last time, to State College, Pennsylvania, and Pennsylvania State College. There his life blossomed with friendship, studies, and sports. His three high-school buddies have remained close friends throughout his life. The reporting he did on the high-school paper and *Center Daily Times* marks his early work as a writer, one of the important skills of his career.

In 1933, Frank enrolled as an English major at Amherst College in Massachusetts. However, Frank eventually changed his major to something completely different. The change came about in an unusual way.

"We had to take a science, and somebody said, 'take geology.' So I took geology and I was kind of bored by it and I got a C. But the guy who'd advised me to take it said, 'I know the first course isn't very good, but you ought to take historical geology. That's really interesting." So I signed up for historical geology and nobody else did. This was with F. B. Loomis. . . . Although I was the only person who had registered for the course, [Loomis] agreed to give it. So I had a one-year course in what was not historical geology [but] vertebrate evolution, because that was what Loomis was interested in, and we just sat around three days a week for a year talking about vertebrate evolution. By the end of that year, I decided I wanted to be a vertebrate paleontologist" (Cain 1989).

Within his first week at Amherst, Frank was rushed by the fraternity Phi Kappa Psi. At the end of an exhausting day, he sank into a couch and remarked, quoting a character from the Barney Google comic strip, "Moosenose hurt in feet!" One of his new "brothers" immediately nicknamed him Moose, which remains his name to many friends and relatives to this day.

In January of 1934, in his freshman year, another fateful event occurred. While taking his date on a sleigh ride with a group of other students, the Smith girl seated on his other side got something in her eye. Frank gallantly helped remove it and life for him was never the same afterwards; he dated Martha Burling Kremers of Niagara Falls, New York, until their graduation and engagement. They were married in 1939, after she'd had a year of business school and he had earned his master's degree at Pennsylvania State University.

Although Frank's B. S. *cum laude* with honorable mention in geology from Amherst centered on vertebrate paleontology, his M. S. in paleontology and stratigraphy dealt instead with invertebrates. Frank M. Swartz was the only resident paleontologist at Penn State; his specialty was ostracodes and so Frank studied ostracodes. That year also provided a good background in sedimentology from Paul Dimitri Kryrine.

Frank continued his education at Harvard University, studying under one of the world's foremost vertebrate paleontologists, Alfred Sherwood Romer. Frank was Romer's first student from the geology department; all previous students had been from biology. Romer referred to himself as a zoologist. Frank recalls, "I had quite a battle with Romer to be allowed to take structural geology because he thought that would be a waste of time. I felt it would be a way to get a job, which it turned out to be. . . . I remember as a student, I got to know C. B. Schultz pretty early, and Morris Skinner and Lloyd Tanner and Mylan Stout, the Nebraska folks, and thinking how strange and rather dull that they were always worrying about stratigraphic correlation. They were talking about the Valentine problem, the Marsland Formation, and so on. In a way, they certainly were more geological than we easterners were" (Cain 1989). Thanks to his training at Amherst and Penn State, Frank himself proved to be an exception to this generalization.

A particular admonition of Romer's has in turn been heard by Frank's own children and young colleagues, probably because it fit so well his own proclivities: "Learn to write while you're a student—you can always learn geology later."

Frank's first real field experience in vertebrate paleontology came during the summer of 1940. The Harvard field crew headed west toward the Unita Basin of Utah to collect fossil mammals in a used pie truck purchased for $85. "I can remember . . . when we heard that France had fallen, sitting around the campfire, all of us wondering where we'd be a year from then" (Cain 1989). While in the field, Frank became the father of twins, Geoffrey Mason and John Kremers, and their birth kept him out of the army long enough to complete his doctorate. To support his family, Frank served as a teaching fellow and university fellow in paleontology.

Harvard was the right place and 1940 the right time to witness an exciting event, the founding meeting of the Society of Vertebrate Paleontology. Frank recalled, "of the starving graduate students, only those on the premises, like me, could afford to attend. And we couldn't exactly go overboard socially; the cocktail party at the founding meeting cost $1.00. My wife Marty and I took stock of our finances and decided I really should go but that she couldn't afford to (we would have had to get a sitter for our 6-month-old twins)" (Whitmore 1989).

Frank's doctoral study, suggested by Romer, was the cranial morphology of three Oligocene artiodactyls. Frank wrote, "It is the purpose of this study to examine in detail the cranial anatomy of some of these extinct genera, because endocranial characteristics are probably nonadaptive, that is, unlikely to be influenced by the

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
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Figure 1. Frank C. Whitmore, Jr., while professor at Rhode Island State College, Kingston, Rhode Island (now the University of Rhode Island), ca. 1943.

environment, and therefore useful in determining the taxonomic position of groups of animals" (Whitmore 1953:117). For this study, a serial sectioning apparatus was designed and built by F. Russell Olsen of Harvard's Museum of Comparative Zoology. This sectioning technique, perfected for paleobotany with cellulose acetate peels, was adapted for vertebrates and described in a paper by Olsen and Whitmore (1944). It was a pioneering achievement in its approach and formed the basis of later work by others, in which details of cranial anatomy such as blood circulation, ear morphology, and brain conformation have been used in phylogenetic studies of fossil mammals.

Frank's first postgraduate job was a teaching position at Rhode Island State College (now the University of Rhode Island) from 1942 to 1944. "I was the entire geology department. I got to teach a lot of things I'd never studied before, such as specimen petrology and engineering geology, which I made up myself" (*Paleo News* 1990). When the Army Specialized Training Program came to the college, he also taught economic and political geography. Preparation for these courses aided him most in the next phase of his career.

During this time, Frank Sr. asked his son, "If you could talk to any paleontologist you wanted to, whom would you choose?" Frank named W. B. Scott, and his father offered to pay his way to Princeton for a visit. Frank remembers, "With some qualms, I wrote to Scott and asked if I could come and see him, and he said yes. So I got on the train and went down . . . to Princeton, and Dr. Scott met me. He showed me around the lab. I remember he was then about 80. . . . He had me to lunch at the faculty club. . . . Then Scott showed me the Eocene mammals in the Princeton collection. I had spent the previous summer in Utah . . . so I was interested. At the end of the day Scott asked me if I would like to collaborate with him in the study of Eocene mammals in the Princeton collection" (Cain 1989).

Unfortunately, the war intervened, and Frank was unable to take up the opportunity. His observations about Dr. Scott that day, however, presaged Frank's own support of young people in his field. "I probably never would have done it on my own. . . . But it does give you an idea of what a really decent person Scott was and how he would give up a whole day to an unknown" young instructor (Cain 1989).

Frank joined the honorary scientific fraternities, Gamma Alpha and Phi Sigma, and he conducted short field trips while in Rhode Island. But his life was not all science; the war was on, and he had to take his turn up in the college tower as an airplane spotter, minimally trained in the silhouettes of domestic and enemy aircraft.

In March of 1944, Frank was hired by the U. S. Geological Survey to edit classified reports in the one-year-old Military Geology Unit. By September of 1945, he had become chief editor, supervising four geologists and 15 typists and draftsmen.

Not long after the birth of their first daughter, Katherine Burling, Frank and Marty prepared for his assignment to the Engineer Intelligence Division, Southwest Pacific Area, by moving the family to a small house near Niagara Falls.

Frank's position as scientific consultant on terrain intelligence took him first to Manila, where he organized the Natural Resources Section of the General Headquarters of the Supreme Commander for the Allied Powers, in preparation for the occupation of Japan. After two months, he relocated to Tokyo, where he served as chief of the Engineering Geology Unit, Natural Resources Section. He supervised the field checking of terrain intelligence reports and consulted with the U. S. Army on foundation conditions, location of construction materials, and selection of airfield and port sites.

Frank became a commodity specialist in precious metals, compiling data on gold and silver production in Japan. As Frank tells it, "Since I was the paleontologist and didn't know much, they looked around for the least harmful thing for me to do. That's how I was put in charge of the precious metals. My job was mainly to hold audience with Japanese gold and silver mine operators and tell them 'no,' they could not mine gold. It was the perfect bureaucrat's job, sitting there all day saying 'no.' I was also in charge of the vaults of Japan, where I saw more money than I will ever see again, with piles of sheet gold one meter on a side" (*Paleo News* 1990). There were also stacks of platinum crucibles and "buckets of diamonds." The temptations might have been great, except that the military officer from whom Frank took over the vaults was later arrested for trying to re-enter the United States with a pocket full of diamonds.

When asked to join the Geological Survey, Frank knew it was likely to mean an overseas assignment, possibly in a war zone. But he could not know that his work, and that of his colleagues, would help directly in saving the lives of Allied troops and hastening the conclusion both of World War II and the Korean War. In 1946, the U. S. Army recognized his work with the highest civilian award the United States bestows, the Medal of Freedom. One would think a tribute of this magnitude would involve a personal presentation if not a public ceremony, but the medal was simply sent to his home with a two-sentence cover letter.

One event during Frank's duty in Japan created enough controversy that its echoes can still be heard, and so we cannot exclude it from this account. The story of the Peking Man fossils involved bones of *Sinanthropus pekingensis* and other relics, which the Japanese had earlier stolen from China. Frank, as part of his duties, was to take custody of these objects, pending their return to the National Geological Survey of China. But there has always been disagreement over the actual location of the objects and the sequence of events prior to Frank's arrival on the scene. According to one story, in 1941 the specimens were packed in three cases marked "secret" and turned over to U. S. marines who were evacuating Chinwangtao, China, aboard the Dollar Liner *President Harrison*. The liner ran aground in the Yangtze River near Shanghai on December 8, and the marines were captured. There is documentary evidence that scientists from the Tokyo Imperial University visited Peking in August, 1942, at the request of the Japanese North China Army and took the collection to Tokyo. After the surrender of Japan to the Allied powers, a letter from the Central Liaison Office of Japan alerted the Allies to the collection's existence. The Natural Resources Section was directed to take action to return the specimens, and the section chief dispatched Frank to examine the collection. In his memo, Frank stated he could "find no traces of *Sinanthropus*" (Lamp and Huang 1990). Many, including Frank, believe the fossils rest at the bottom of the Yangtze River, but he has been accused of keeping secret information on their whereabouts. To this day, the original fossils have never been recovered, but good casts exist and excavations at the Peking Man site have turned up additional specimens.

Frank's overseas work did not end in Tokyo. He spent the spring of 1946 assigned to the 24th Corps, U. S. Army, in Korea to survey and map railroads, major highways, landing beaches and ports, including Inchon, which played an important part in the later U. S. invasion. While in Korea, Frank was promoted to chief of the Military Geology Unit.

His return to Washington, D. C., did not mean an immediate end to the family's separation. The government had mushroomed during the war, with little or no increase in housing, and Frank spent months trying to buy or rent a house in the area. Eventually he found one in West Hyattsville, Maryland, and moved the family south from Niagara Falls. Frank and Marty's last child, Susan Hale, was born in 1948, during their ten years in that house.

With the end of war-related work, it was assumed that the Military Geology Unit would be shut down, and Frank was looking forward to joining the Paleontology and Stratigraphy Branch and returning to his fossil vertebrates. But the war had demonstrated to the U. S. military how little it knew about foreign geology, and so the unit was transformed into a regular branch of the Geological Survey. Frank stayed on as chief until 1959.

His management skills and abilities, in part acquired in Asia, enabled Frank to develop and direct the worldwide activities of the branch, which employed about 120 scientists and support personnel, with headquarters in Washington and field offices in Tokyo, Heidelberg, and Salzburg. Frank organized interdisciplinary field-mapping programs involving the study of geology, soils, vegetation, hydrology, and topography.

Frank's leadership was increasingly recognized and put to use. He chaired numerous groups including the U. S. Geological Survey's Geologic Division Staffing Committee and the committee to compile permafrost terms for the first and second editions of the American Geological Institute's *Glossary of Geology*. He also served as security officer for the Geologic Division between 1948 and 1956.

In recognition of the International Geophysical Year in 1958, the Lake Peters Research Station (renamed the G. William Holmes Research Station in 1970) was established in the northeastern part of the Brooks Range of Alaska. Frank was on the team that conducted the initial reconnaissance at this offshoot of the Arctic Research Laboratory at Point Barrow and formulated plans for continuing research in the area.

Finally, after 15 years of administration, Frank joined the Paleontology and Stratigraphy Branch of the Geological Survey as a senior specialist in vertebrate paleontology. He was assigned an office at the National Museum of Natural History. "When I came back to paleontology . . . I was, for all intents and purposes, fresh out of graduate school, although I'd had my Ph.D. for seventeen years" (Cain 1989). Frank became the informal chief of the survey's vertebrate paleontology staff, which included Charles Repenning at the Menlo Park, California, office and Ed Lewis at the Denver office.

He launched a series of diverse investigations. In 1959 and 1960, he collected and studied Miocene and Pleistocene vertebrates from Martha's Vineyard, Massachusetts, as part of the work done by the Engineering Geology Branch. His biostratigraphy of that complexly deformed area helped determine the history of Pleistocene deformation on the island.

From 1959 through 1965, Frank conducted biostratigraphic studies of Paleozoic and Mesozoic fish and Tertiary mammals from Wyoming and Montana, to aid ongoing geologic mapping there. He was principal investigator for field and laboratory studies of Miocene mammals from Panama between 1962 and 1965. This resulted in a biostratigraphic correlation with faunas in Texas and Florida, established that the Miocene mammal fauna of Panama was entirely of North American affinity, and helped to define a circum-Caribbean Miocene zoogeographic province and to delineate the southern extent of the North American land mass. These results were published in *Science*.

At about the same time, Frank began collaborating with Bertrand Schultz and Lloyd Tanner of the University of Nebraska on work at Big Bone Lick, Kentucky. This important Pleistocene site is the type locality of *Mammut americanum*, the American mastodon, and *Bootherium bombifrons*, an extinct musk ox. It is also the site where, on Thomas Jefferson's orders, explorers Lewis and Clark collected bones for shipment back to the amateur scientist and president of the United States.

The team's field and lab studies, from 1962 through 1970, of the late Pleistocene mammals and stratigraphy of Kentucky contributed to the geomorphic history and paleoclimatology of the Ohio valley. After five summers of field work, their results helped convince the state of Kentucky to create Big Bone Lick State Park, ensuring preservation of the site. For his efforts, Frank was anointed an Honorable Kentucky Colonel by the state.

Meanwhile, Frank was also being exposed to fossil marine mammals, thanks to his close association with Remington Kellogg, world-renowned expert, who worked in the Paleobiology Department of the museum. It was Dr. Kellogg who made the west side of the Chesapeake Bay a permanent fixture in Frank's life as Frank increasingly helped the elder paleontologist and, after his death in 1969, took over some of his work.

During the late 1960s and early 1970s, Frank was principal investigator for the Calvert Cliffs Paleontology Project on Chesapeake Bay. This project entailed detailed interdisciplinary paleoecological and stratigraphic studies during excavation for the Calvert Cliffs nuclear power plant. Funding for this work came from the Ford Foundation and National Geographic Society.

The Calvert Cliffs Paleontology Project opened the door to Frank's association with the National Geographic Society. In 1971, he was asked to join the prestigious Committee for Research and Exploration, serving as Dr. Kellogg's replacement. The committee grants millions of dollars each year for research projects throughout the world, some of which are later described in the society's magazine.

In 1972, Frank returned to Alaska, this time to Amchitka Island, where he collected fossils of the historically extinct Steller's sea cow (*Hydrodamalis gigas*). He and others worked on the rate and

Figure 2. Frank C. Whitmore, Jr., 1965, holding skull of fossil musk ox collected in 1807 by William Clark (of Lewis and Clark fame) and exhibited in the White House in the same year.

mode of Pleistocene uplift of the island, as indicated by beach deposits, which were critical to the prediction of the effects of nuclear testing.

Work on Oligocene whales from South Carolina resulted in two publications in 1975 and 1976. Since 1976, Frank has been principal investigator on the study of Paleocene vertebrates from Saudi Arabia. Paleoecologic studies of this estuarine fauna established the geographical position of part of the ancient Tethys Sea, and contributed to the delineation of lime deposits needed for cement manufacture.

Like that of the other research scientists at the Geological Survey, part of Frank's job involved handling "examination and report" (E & R) requests. Some were submitted by colleagues in other disciplines whose investigations turned up pieces of what might be bone. Others came in via USGS public-relations people from citizens who wanted to know something about their backyard digs or vacation treasures.

One E & R stands out above all others, both for its unusual nature and because it landed on the desk of a man whose knowledge of historical time is as acute as his understanding of geologic time. This was "The Case of the Papal Proboscidean."

Sylvio Bedini, then deputy director of the National Museum of History and Technology (now the National Museum of American History) asked Frank to identify, from photographs, some bones dug up during the air-conditioning of the papal apartments in the Vatican. Everyone was puzzled when Frank identified at least one bone as that of an elephant. Further research revealed that in 1514, when Pope Leo X had a stranglehold on the spice trade to the Far East, King Emmanuel the Great of Portugal wanted a share of the action. To get on the good side of the pope, Emmanuel presented him with a young elephant. No elephant had been seen in Rome since the time of Hannibal, and it proved to be a great curiosity—especially as it had been trained to genuflect whenever the pope appeared. It also held water in its trunk and squirted designated victims on the command of its trainer. One day, the elephant's keepers decided they would gild the elephant from head to toe as a surprise for the pope. The unexpected surprise was that the gilding killed the elephant. The devastated pope directed the papal painter, who happened to be Raphael, to paint a life-size mural of the elephant; Raphael felt this was beneath him and ordered an apprentice to complete the mural on the palace wall. The elephant was subsequently buried beneath the painting. The mural is now gone but the bones remain (Whitmore 1978).

This and many others stories have been shared gleefully over lunch at the museum, whose collegiality is perfectly suited to Frank's temperament. For years, he took a bag lunch to the office of his longtime friend Harry Ladd. As the other members of the lunch mess would appear, they would array themselves around the desk with their sandwiches and the talk would begin. Here, one might say, is an example of the cross-fertilization that takes place in a great museum—scholars engaged in the exchange of ideas. Ideas certainly were exchanged—on politics, reminiscences of fieldwork, stories of questionable taste, the Washington Redskins; innumerable small bets were made, usually on sports or politics, and duly recorded on Harry's desk calendar (Whitmore and Tracey 1984).

A story Frank tells on himself concerns a day, decades past, when he was collecting a fossil whale along the shores of Chesapeake Bay. Typically, there were a few helpers along that day—amateur collectors and aspiring young scientists. In the course of the long day, one of these youths said to Frank—surely out of the greatest respect—"You must be one of the last of the old-time collectors!" And so he is.

Perhaps it is Frank's memory of W. B. Scott and that day at Princeton, or perhaps it is simply Frank's openness and interest in people that cause him to be so generous with his time and his knowledge. He frequently gives tours behind the scenes at the museum to school and college groups, out-of-town visitors, and amateur collectors. In the 1950s, Washington-area school children watched him on the early WETA television science series *Time for Science*. And school children nationwide now see him on one segment of PBS's 26-segment story *The Voyage of the Mimi* when the young protagonist visits Frank at the museum to learn about whales and paleontologists.

Frank retired from the United States Geological Survey in 1984, but he continues his work as a research associate and curator emeritus of the Smithsonian Institution in his old office there. His current studies include the taxonomy and description of fossil Pliocene whales and terrestrial mammals from the Lee Creek phosphate mine at Aurora, North Carolina, and description of Miocene marine mammals from the Pisco Formation of Peru. Many of his papers and publications have been deposited in the Smithsonian Institution archives.

While Frank came late to his life's research, his colleagues and employers valued highly the management and leadership he brought with him to the museum. His ability to listen, to draw others out, and to mediate discussion of touchy subjects has often been tested.

Frank was appointed chair of the joint U. S. Geological Survey/Smithsonian Institution committees for the design of new labs and for decisions regarding the paleontology collections. In 1971, he was general chair of the Geological Society of America meetings in Washington, with 4300 people attending. For the American Association for the Advancement of Science and the Mexican Science Council, he chaired a symposium on land connections between North and South America.

Figure 3. Frank C. Whitmore, Jr., studying fossil whales at the University of Otago, Dunedin, New Zealand, 1988.

The list of institutions on whose panels and committees he has served is long and varied. It includes the Department of Defense, American Geological Institute, National Research Council, and the Center for the Study of the First Americans. He has provided scientific guidance to the Schoelkopf Geological Museum in Niagara Falls, New York, and to exhibit specialists at the National Museum of Natural History and the state of South Carolina.

In 1979, he served as general chair of the International Centennial Symposium of the USGS on "Resources for the 21st Century." Brought together were some 500 scientists, corporate executives, and government officials from 48 countries. Frank spent five years planning the agenda, booking speakers, and editing and rewriting many of the foreign papers to make them publishable in English.

Professional societies have provided Frank with a continuous thread throughout his varied career. And they have all benefited by his membership. He's at home both at small, convivial monthly meetings and at huge national conventions. His wit at the dinner table is as valuable to many as his chairing of committees and symposia.

Frank was a founding member of the Society of Vertebrate Paleontology in 1940; he later served on its executive board and is an honorary life member. He's been a member of the Paleontological Society of America since 1942. In 1944, he joined the Paleontological Society of Washington, later serving as vice-president and president. That same year, he joined the Geological Society of Washington, becoming councillor, secretary, first vice-president, and then president. In 1945, perhaps to show that he couldn't live without meetings wherever he might be stationed, he helped found the Geological Society of the Philippines.

He became a fellow of the Geological Society of America in 1947, and has served on its Penrose Medal Committee and as its Penrose citationist. Three years later, he became a fellow of the American Association for the Advancement of Science, eventually serving as section secretary and chairman, councillor, and chair of the Newcomb Cleveland Prize Committee.

Although not of the highest scientific significance, one membership gave Frank a wider forum for his well-known humorous talents. In 1944, he joined other young U. S. Geological Survey types as a member of the Pick and Hammer Club. Begun in 1894 as the Association of Aspiring Assistants, it was originally an offshoot of the Geological Society of Washington. By the mid-twentieth century, this platform for talks by unestablished geologists was best known for its annual show, which spoofs the stuffed shirts of the geologic bureaucracy. Frank participated fully in writing songs and dialogue, acting in minor and major roles, singing lustily, and dancing, among other things, the academic gavotte in cap and gown.

In 1967, he was invited to be a guest on the television program *To Tell the Truth*. He was, in fact, the "true" vertebrate paleontologist, but got himself in hot water by misunderstanding one of the questions. Instead of answering "dinosaur" to the query, "What was the largest carnivore in the world?" he replied, "bear." Consequently, the panel was led astray and guessed the wrong contestant. Immediately following the show, Kitty Carlisle lit into him, "Imagine, a bear! How ridiculous!" And when Frank returned to his office at the museum, there in his chair sat a huge femur of a meat-eating dinosaur.

In 1981, Frank was traveling in China when he was awarded the Meritorious Service Award by the Interior Department. This got him out of shaking hands, on stage, with then-secretary James G. Watt, not one of his heroes. When it was Frank's time to receive his 40-year service scroll and pin, a representative came to his office, stated something to the effect that he knew Frank wouldn't want a lot of pomp and ceremony, discovered he didn't have the award in his pocket, and left saying it would be sent in the mail.

There is a type of honor frequently bestowed by his colleagues that has been harder to receive. Because of his friendship, respect for biography, and skill as a writer, over the years Frank has been asked to prepare memorials to several fellow scientists. As a result, his bibliography includes memorials to Alfred Romer, Remington Kellogg, Harry Ladd, Willy Postel, Louis Ray, John Huddle, and Charley Johnson. They are graceful tributes to men whose work and character he admired.

In addition to his own writing, Frank has reviewed many books and papers. One stands out from all the rest, and we quote it here as an example of the good doctor's breadth of knowledge, attention to detail, and mellow humor. From his review of the sixth edition of "*Eoornis pterovelox gobiensis*" Whitmore stated, "Far ahead of his time, Fotheringham thoughtfully melded together every aspect of the natural history of his subject: the occurrence of its fossil ancestors, references to it in Egyptian hieroglyphics, its appearance in Cro-Magnon cave paintings, and at the other extreme of scientific inquiry, the most painstaking physiologic studies of wing-beat frequency and of the pH cycle of the bird's beak fluid, observed under the most difficult conditions over an entire year. The author's discovery that each dumbbell-shaped egg contains a male and a female, and his analysis of the part played by parthenogenesis in the evolution of the genus, makes the mind boggle" (Whitmore 1967).

But a truer indication of a person's worldliness and erudition may be the letter to the editor, of which Frank has written many. Here we quote from a joint response by Whitmore and Hotton to a 1972 article in *Smithsonian Magazine* entitled "Fantastic Animals Proved Tall Timber of our Mythology." "The taxonomy of the sidehill gouger (*Membriinequales declivitatis*) is more complicated than Carson suspects. There are subspecies, not yet formally named but recognized by local inhabitants, and there is more than a scintilla of evidence that the morphology and habits of these taxa can be correlated. Among many examples we can cite is the sidehill dodger, which inhabits the Driftless Area of Wisconsin; the dextrosinistral limb ratio approaches unity although the metapodials on the downhill side are noticeably stouter. The sidehill gouger is the common Pennsylvanian species, but it has been speculated (Hotton, *in litt.* 1972) that all of the different varieties spring from the little-known strike-runner (*Crestophilus ambiguus*) in which the right front and the left rear limbs are short and the left front and right rear are long, or vice versa. These animals ran the long Tennessee ridges in late Pleistocene time but became extinct during the Pleistocene epoch, perhaps because of trauma resulting from attempts to run ridges of newly formed glacial cirques" (Hotton and Whitmore 1972).

A professional life as busy as Frank's might leave the impression that he has little activity outside his career, but his nonscientific interests are many. When their family was young, he and Marty took their children on many day trips, to Rock Creek Park and the zoo, on picnics, to Civil War battlefields, and the like (mysteriously, after he began working at the museum, Saturday trips to the Smithsonian decreased markedly). Drives to the country, and longer trips to visit relatives, invariably involved a stop along the road so he could give a brief lesson on an especially noteworthy outcrop.

Despite the financial strains of a growing family, the Whitmores made sure to attend an occasional play and took the children along at a young age. This meant Saturday matinees at the National Theater, where dramas and musicals tried out on the way to Broadway, and a brand-new local group, Arena Stage, put on productions at the Hippodrome and the Old Vat. The Whitmores have had season tickets to Arena Stage since the 1960s.

Certain aspects of Frank's work have intersected with his and Marty's other interests, especially their love of travel. Field trips to Martha's Vineyard took them back to the New England of their student years. Frank's membership on the Committee for Research and Exploration means their joining the National Geographic Society's triennial tours of current research projects; hence their trips to South America, Africa, Europe, Asia, and Australia.

At home, alongside mementoes of their long life and many travels together, the Whitmores display tokens of affection from friends and family. Half of the pictures, statuettes, and trinkets depict the moose, Frank's long-time alter ego. The other half are whales, in honor of the marine-mammal paleontologist. In addition, he has accumulated a veritable wardrobe of whale neckties, in colors suitable for every occasion—from Christmas to St. Patrick's Day to a meeting at the National Geographic Society.

Frank continues to serve as vice-chair of the National Geographic Society's Committee for Research and Exploration. He attends to his mail and his research at the museum. When in town, Frank and Marty still frequent the Tuesday Lunch Group of museum denizens, at the Beeffeeders on Tenth Street. They continue to travel extensively, in part to keep up with the four children, now scattered across the country. There are five grandsons, three stepgrandchildren, and great-grands may soon be on the way.

Many of us owe some measure of our professional progress to this man who took time to listen, teach, and put up with the ignorance of budding scientists and up-and-coming collectors. While working with Frank in the late 1960s, we used to refer to him as "the good doc," a nickname we still use with reverence and respect for a man who means that and more. To us, he will always be "the good doc."

ACKNOWLEDGMENTS

We are first and foremost thankful to Martha Kremers Whitmore, who was generous in her assistance. When Ralph Eshelman called Marty at home (knowing Frank was safely downtown in his office) to tell her of this tribute, he told her he had something secret to discuss concerning her husband. In typical Marty fashion she responded in a happy, friendly voice, "How mysterious and exciting! What is it?" She immediately offered a file she has kept on Frank from early in their marriage, including newspaper clippings, programs, personal notes, letters, photographs, certificates, and more. Without this material, our tribute to Frank would be woefully incomplete. But just as revealing were the little notes she has frequently written him, supporting his work and commending his achievements. They illustrate her admiration for, and devotion to, her husband. For this love he is most fortunate.

Many of Frank's friends and co-workers added to this tribute. Everyone approached was enthusiastic and supportive, making our job all the easier. It is obvious from these contacts that Frank has many friends who wish him well. Among them are Edwin Snider, Joshua Tracey, Ellis Yochelson, Barry Bishop, Tom Dutro, Richard and Mary Ellen Williams, Pamela Henson, Clayton Ray, David Bohaska, Nicholas Hotton, Warren Blow, and Joseph Cain.

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The Early Miocene Littoral Ursoid Carnivoran *Kolponomos*: Systematics and Mode of Life

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ABSTRACT.—Species of the large extinct early Miocene carnivoran *Kolponomos* Stirton, 1960, are known from a few fossils found in marine rocks along the northeastern margin of the Pacific Ocean in Oregon and Washington, U.S.A. These animals are notable for their massive skulls with markedly deflected rostra and broad, crushing cheek teeth like those of a sea otter. Originally based on an incompletely preserved snout from the marine lower Miocene Clallam Formation at Clallam Bay, Clallam County, Washington, and questionably assigned by Stirton to the Procyonidae, the taxon has until recently remained enigmatic and not certainly assigned to any particular carnivoran family. Additional specimens from the type locality, including a nearly complete cranium with some teeth, provide new data on the cranial morphology of the species. Another specimen, consisting of a nearly complete cranium, mandible with dentition, and some postcranial bones, from the lower Miocene Nye Mudstone on the Oregon Coast, represents a new species, *Kolponomos newportensis*.

The new material demonstrates that *Kolponomos* is an ursoid most closely related to members of the paraphyletic family Amphicynodontidae. Similar phylogenetic roots have been postulated for the pinnipeds as a whole, and cladistic analysis implies a sister-taxon relationship of *Kolponomos* with the Pinnipedimorpha. The few postcranial bones available demonstrate that *Kolponomos* was amphibious but not a strong swimmer.

Kolponomos was probably littoral in distribution, all specimens having been discovered in nearshore marine rocks. The crushing cheek teeth would have been suited to a diet of hard-shelled marine invertebrates. The anteriorly directed eyes and narrow snout indicate that *Kolponomos* could view objects directly in front of its head, of benefit to an animal that would selectively eat epifaunal marine invertebrates. The elongated upper canine and third incisor teeth clustered in thickened bone at the anterior end of the down-turned snout and the posteriorly retracted nasal opening are adaptations that would allow the animal to pry organisms from rocks while keeping its nostrils away from the substrate. Large paroccipital and mastoid processes indicate strong neck muscles that could provide powerful downward movements of the head. These features indicate that *Kolponomos* probably fed on marine invertebrates living on rocky substrates, prying them off with the incisors and canines, crushing their shells, and extracting the soft parts, as do sea otters.

Kolponomos represents an unique aquatic adaptation for marine carnivorans, whose mode of living and ecological niche are approached only by modern sea otters.

INTRODUCTION

The early Miocene carnivoran genus *Kolponomos* Stirton, 1960, is known from a few fossils found in marine rocks along the northeastern margin of the Pacific Ocean in Oregon and Washington. *Kolponomos* was originally based on an incompletely preserved snout from the marine lower Miocene Clallam Formation at Clallam Bay, Clallam County, Washington. The relationships and morphology of the type species of the genus, *K. clallamensis* Stirton, 1960, have remained problematic, and for many years the animal was not assigned with certainty to any particular carnivoran family. Stirton (1960) questionably assigned it to the Procyonidae, and was followed by Piveteau (1961), Romer (1966), and Thenius (1969). Carroll (1988) classified the taxon as Carnivora, *incertae sedis*, and Ray (in Barnes et al. 1985:43) regarded it as an enaliarctine pinniped.

Additional specimens, including a nearly complete cranium with some teeth, have now been collected from the Clallam Formation near the type locality of *Kolponomos clallamensis* at Clallam Bay. These provide additional data on the cranial morphology of the type species. Barnes et al. (1985) announced the discovery of a nearly complete cranium and mandible with some postcranial bones of *Kolponomos* from the lower Miocene Nye Mudstone on the Oregon coast. This specimen represents a new species of *Kolponomos*. The purpose of this study is to describe and illustrate all known specimens of *Kolponomos*, to redescribe and rediagnose *K. clallamensis*, to describe a new species from Oregon, to comment on the relationships and taxonomy of the genus, and to discuss implications for its functional morphology and behavior.

METHODS AND MATERIALS

All specimens were in hard concretionary sandstone matrix. Those from Washington were prepared by use of pneumatic chisels and formic acid; those from Oregon were prepared by mechanical and air abrasive methods.

Geologic ages cited herein are modified according to the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout et al. (1983). The acronyms for institutions are as follows: AMNH, American Museum of Natural History, New York, New York; BM(NH), British Museum (Natural History), London, England; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; UCMP, University of California Museum of Paleontology, Berkeley, California; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Casts of the crania have been placed in AMNH, USNM, UCMP, LACM, and the University of Nebraska State Museum. Measurements, in millimeters, of the crania, dentitions, and mandible of the

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species of *Kolponomos* have been provided in Tables 1 and 2. Cranial restorations of *Kolponomos clallamensis* are based on all available specimens.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Infraorder Arctoidea Flower, 1869

Parvorder Ursida Tedford, 1976

Superfamily Ursoidea (Gray), 1825

Family Amphicynodontidae (Simpson), 1945

Included genera.—This paraphyletic family includes *Amphicynodon* Filhol, 1882, *Pachycynodon* Schlosser, 1887 (including *Paracynodon* Schlosser, 1899), *Allocyon* Merriam, 1930, and *Kolponomos* Stirton, 1960.

Kolponomos Stirton, 1960

Kolponomos Stirton, 1960:346.
Kolponomus Carroll, 1988:635, 672.

Emended diagnosis of genus.—Stirton's diagnosis was based solely on the holotype of *K. clallamensis* and amounted to a description of that specimen. New material allows a refinement of that diagnosis. The characters noted are all derived with respect to other Carnivora: I^3 with large root; I_1 vestigial or missing; cheek teeth with strongly inflated principal cusps; P^{1-3} and P_{1-3} with anterior and posterior cingular cusps, P_4 also with prominent posterolingual cingular cusp; P^4 molariform with large protocone; M^1 with large conules, lingual cingulum only between principal cusps; M^2 markedly smaller than and lying posterolingual to M^1 with posterolingually placed metaconule; M_1 quadrate in occlusal outline; M_2 triangular with reduced talonid; M_3 absent.

Facial region of skull markedly flexed downward relative to basicranial plane; muzzle deep; nasal retracted to above P^1 or P^2, its sutural contact with frontal wide, slightly wider anteriorly than posteriorly; long process of premaxilla nearly meeting corresponding processes from frontal along nasal suture; palate highly vaulted anteriorly; infraorbital foramen greatly enlarged and opening into shallow fossa in maxilla; infraorbital canal very short; orbit facing forward and relatively small; zygomatic arch widely flaring with strong postorbital process and variably developed masseteric process; postorbital process of frontal lacking; lacrimal foramen small, variably present; sphenopalatine foramen large and closely associated with posterior palatine foramen; optic foramen small, nearly same size as ethmoid foramen; anterior process of alisphenoid forming strut bracing palate against braincase; mastoid process hypertrophied into long column extending laterally and ventrally; posterior carotid foramen well anterior to posterior lacerate foramen; foramina for venous occipital sinus in foramen magnum; lambdoidal crest strongly extended posteriorly on either side of midline.

Type species.—By original designation, *Kolponomos clallamensis* Stirton, 1960.

Included species.—*Kolponomos clallamensis* Stirton, 1960, late Early Miocene, Washington; *Kolponomos newportensis*, new species, Early Miocene, Oregon.

Kolponomos clallamensis Stirton, 1960

Figures 1–7, 13–14

Kolponomos clallamensis Stirton, 1960:347, figs. 1–4.

Diagnosis of species.—A species of *Kolponomos* differing from *K. newportensis*, new species, by the following derived features: cranium with anterior part of palate more highly vaulted; infraorbital foramen larger, approximately twice the diameter, opening into prominent fossa; large masseteric process on ventral surface of zygomatic arch at jugal/maxillary suture; maxilla rather than jugal forming anterior rim of orbit; paroccipital process larger, oriented vertically rather than posteroventrally; basioccipital narrower, especially posteriorly between posterior lacerate foramina; narrow, prominent vertical crest on occiput dorsal to foramen magnum lacking; zygomatic arch more strongly arched dorsally. In addition, *K. clallamensis* is distinguished by the following primitive features: rostrum narrower, with anterolateral margin of snout around canine and I^3 not flaring laterally, nearly vertical; hamular process of pterygoid straighter, smaller, not extending so far ventrally; mastoid process shorter, straighter, and oriented vertically rather than being twisted and projecting anteroventrally beneath the external auditory meatus; intercondylar notch present and deep.

Holotype.—UCMP 50056, anterior part of cranium with roots of left I^3 and both M^1's, collected in 1957 by Mrs. Betty Willison.

Type locality.—UCMP V5761, 250 yards east of Slip Point lighthouse near section line, NW 1/4 NE 1/4, Sec. 21, T. 32N, R. 12W, and LACM 5933, Slip Point, Clallam Bay, Clallam County, Washington.

Referred specimens.—LACM 131148, from the type locality, a nearly complete cranium with parts of the left I^2 and I^3 and right and left P^2 and M^1, collected by Albin Zukofsky, II, February 1988; LACM 123547, from Merrick's Bay, Clallam Co., Washington, a fragment of tooth (M_2?) collected by William Buchanan, May 1983.

Formation and age.—Extensive marine sedimentary deposits are exposed on the north side of the Olympic Peninsula in Washington. The lower Miocene Clallam Formation and underlying Eocene and Oligocene deposits are exposed in wave-cut cliffs and terraces and in man-made excavations for more than 70 miles (112 km) along the south shore of the Strait of Juan de Fuca. The stratigraphy and invertebrate paleontology of this thick sedimentary sequence are well known (e.g., Addicott 1976a,b,c; Armentrout et al. 1983; Feldman et al. 1991; Rau 1964; Snavely 1983; Snavely et al. 1980; Tabor and Cady 1978), but only a very few fossil vertebrates have been recorded [Stirton 1960 (carnivore); Olson 1980 (bird); Domning et al. 1986, and Ray et al. 1994, this volume (desmostylian); Barnes 1987, 1989 (whale)]. Specimens of *Kolponomos clallamensis* are from the Clallam Formation, deposited during the Pillarian Molluscan Stage (Addicott 1976a; Moore and Addicott 1987) of the early Miocene. A measured section at Slip Point (Addicott 1976b: fig. 4) shows that the rocks exposed there belong to the lower part of the Clallam Formation. The lower part of the Pillarian Molluscan Stage containing *K. clallamensis* includes an interval of time correlative with the late Arikareean North American Mammal Age.

Skull.—The nearly complete referred skull (LACM 131148) has parts of the left I^2 and I^3 and both P^2's and M^1's, but is missing the right zygoma and the anterolateral margin of the right premaxilla and maxilla, much of the ascending ramus of the right maxilla, the right nasal, the dorsal surface of the interorbital region, the sagittal crest, much of the roof of the braincase on the right side, and the lambdoidal crest (Figs. 1–4). Structures of the right orbit are fully exposed.

The skull of *Kolponomos clallamensis* is roughly triangular in dorsal aspect, with a broad occipital region and a narrow snout (Figs. 5–7). The dorsal profile is arched, and the zygomatic arches are prominent. At its anterior extremity, the rostrum is thick and ventrally deflected. In anterior view, the narial opening is elongated dorsoventrally and tapered ventrally. A considerable thickness of the premaxillae anterior to the narial opening separates the incisors from the anterior margin of the naris. There is a rather prominent vertically oriented premaxillary protuberance. On either side of it, the anterior surface of the premaxilla slopes abruptly anteroventrally. On either side in this area, the distal part of the root for I^3 forms a bulge in the premaxilla. Otherwise, the bone surface in this area is depressed. The vertical premaxillary eminence extends posterodorsally and is continuous with the relatively narrow and sharp margins of the naris. Immediately anterior to the naris, the bone surface is rugose and punctured by many small foramina.

The maxilla–premaxilla suture is fused and obliterated anteriorly on both the holotype and the referred cranium, but on both specimens the sutures bounding the premaxilla lateral to the naris and the nasal bone are discernable. The ascending process of the premaxilla extends posteriorly to about mid-length on the nasal. It does not meet the anterior process of the frontal as in living bears but stops approximately 2 to 3 mm from the frontal. Along the lateral margin of the naris, the premaxilla forms a nearly vertical lateral surface. It is almost horizontal adjacent to the nasal bone, however. The lateral surface of the snout is dorsoventrally high and flat. Between the canine and the zygomatic arch it is concave.

There is a nasolabialis fossa on the dorsal part of the ascending ramus of the maxilla immediately anterior to the orbital margin. This fossa is broad and shallow, and is bordered anterodorsally by a slight protuberance, dorsally by a faint horizontal ridge, and posteriorly by the orbital margin, which has a vertically elongated antorbital process. The infraorbital foramen has a large anterior opening, 18 to 21 mm high by 10 to 11 mm wide. The foramen opens into a broad fossa, strongly emarginated ventrally, and extending anteriorly nearly to the P^2.

The nasal bones are elongated, nearly parallel-sided, with rounded posterior borders. Where they join posteriorly they are not separated by the frontals. They slope anteroventrally and are nearly flat transversely. On the holotype they are approximately 74 mm long; on the referred cranium, although incomplete, the left nasal is 69 mm long as preserved. The nasals are narrowest just anterior to their mid-length and are wider both anteriorly and posteriorly. Their anterior margin is thick and slightly up-turned, especially near the sagittal line. They expand laterally at the anterior margin.

The posterior part of the nasals is at the highest part of the cranium, which has a smooth, domelike profile. The low supraorbital ridges of the frontals extend posterodorsomedially from just lateral to the posterior ends of the nasals. Posteriorly the interorbital constriction tapers uniformly toward the braincase, to its narrowest point in the intertemporal region. The top surface of the interorbital region on the referred cranium is weathered away, but on the holotype cranium a low crest extends posteromedially from each supraorbital process toward the sagittal plane. These crests lap anteriorly onto the frontals, and where they merge posteriorly on the midline they form a slight V-shaped sulcus. Posteriorly from this point there is a low, broad sagittal ridge on the holotype, but the cranium is missing posterior to the intertemporal region. The mid-sagittal region posterior to this area is broken on the referred cranium also.

The braincase is elongated and tapers anteriorly toward the interorbital constriction. Its dorsal surface slopes laterally toward the temporal fossa and flares posterodorsolaterally to the nuchal crest, which is, however, almost entirely lost on the referred cranium. The surface of the bone is slightly undulating but not strongly rugose or pitted. The frontal–parietal suture ascends the anterolateral wall of the braincase from the back of the orbital region, approaches the midline, then bends posteriorly over the dorsal surface of the braincase to extend posteromedially toward the midline. The squamosal fossa, forming the floor of the temporal fossa over the squamosal, is broad and shallow, does not slope anteriorly, and extends posteriorly into a broad sulcus in the lateral part of the nuchal crest.

The occipital shield is in the shape of a broad isosceles triangle, with the apical part broken away. A broad median crest extends dorsally from the foramen magnum toward the nuchal crest. This crest is flanked by a pair of broad fossae. In turn, each fossa is flanked laterally by a broad eminence, preserved on the left side and in part on the right of the referred cranium, that extends dorsolaterally to merge with the posterior side of the nuchal crest. From this point, the nuchal crest becomes narrower ventrolaterally and curls posteriorly in the area posterior to the temporal fossa. Dorsal to each condyle is a prominent transversely oriented fossa that is continuous with a large fossa lying dorsal to the paroccipital process and below the nuchal crest. The paroccipital process curves posteroventrally almost as far ventrally as do the occipital condyles. It has a vertical posterior swelling that extends dorsally into the lateral fossa. The foramen magnum is wide and compressed dorsoventrally. Its dorsal margin is a broad arch, only slightly peaked medially.

The occipital condyles are relatively small, canted dorsolaterally, with sharp edges around the lateral and ventral margins of the articular facets. The medial side of each is slightly excavated and has a small condyloid foramen. The condyles are separated ventrally by a broad U-shaped intercondylar notch. Their articular surfaces are not continuous ventrally but separated by a fossa that is a continuation of the intercondylar notch and aligned anteroposteriorly with the median ridge on the basioccipital. The condyles are positioned relatively ventrally in relationship to the basicranium. At the anterior margin of each condyle, immediately posterior to the hypoglossal foramen, is a recess in the margin of the articular surface.

The orbit is of rather small diameter, measuring approximately 33 mm transversely in the referred cranium. At the anterior margin of the orbit, immediately ventral to the antorbital process, is a small (3 mm diameter) lacrimal foramen. The anterior part of the orbit has a convex medial wall that protrudes into the orbit in the area posterior to the infraorbital foramen. Immediately posterior to this area is a large (9 mm diameter), round sphenopalatine foramen that is immediately dorsal to and very close to the slightly smaller (6 mm) orbital aperture of the posterior palatine foramen. The tract for the optic nerve is elongated and relatively deep, leading posteroventrally from the ethmoidal to the optic foramen and into the orbital fissure; these foramina are approximately equal in size. The anterior lacerate foramen (orbital fissure) and foramen rotundum lie in a large fossa as in pinnipeds, although a partition of bone separates them. As in other caniform carnivorans, the anterior aperture of the alisphenoid canal opens into the ventral wall of the anterior lacerate foramen and does not have a separate opening into the orbit.

The zygomatic arch is stout and curves uniformly outward from the orbit. The zygomatic process of the squamosal increases only slightly in thickness posteriorly, and the posterior extremity of the jugal diminishes equally in diameter as it extends posteriorly. The zygomatic arch is not straight in its middle but curves both laterally and dorsally. At its anterior end, it is massive, forming thick dorsal and ventral margins around the infraorbital foramen. The ventral root of the zygomatic arch is very stout and descends vertically to form a buttress dorsal to the M^1. This buttress forms a vertical component to the anterior end of the zygomatic arch that continues dorsally through the dorsal margin of the infraorbital foramen.

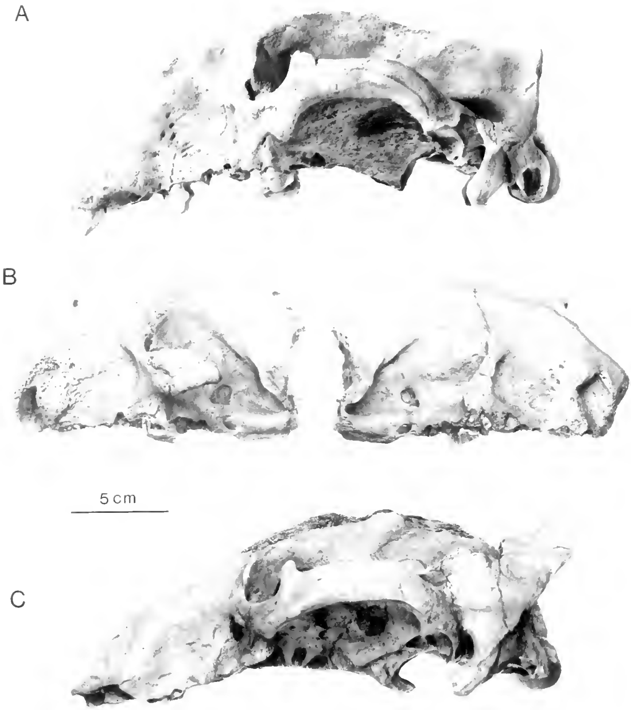

Figure 1. Lateral views of the crania of species of *Kolponomos*. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148, left side; B, *K. clallamensis*, holotype, UCMP 50056, left and right sides; C, *K. newportensis* n. sp., holotype, USNM 215070, right side reversed to left for comparison. All specimens to same scale.

From this point, the zygomatic arch flares posterolaterally to form the lateral margin of the orbit. The jugal bone extends anteromedially over the maxilla, forming a partially mortised joint. The jugal does not form the anterior rim of the orbit. Ventral to the orbit, the maxilla flares where it meets the jugal, and together they form a prominent masseteric process. This process projects ventrolaterally, and a crest extends posteriorly from it along the ventrolateral border of the jugal. The postorbital process of the jugal is stout, broad anteroposteriorly, and its apex is located anteriorly. The anterior extremity of the zygomatic process of the squamosal abuts the posterior side of the postorbital process and is dorsoventrally expanded and slightly up-turned. From this point the zygomatic process curves uniformly posteroventrally to the glenoid fossa. At the glenoid fossa, the zygomatic process curves medially to form the dorsal surface of the glenoid fossa.

The glenoid fossa is elongated transversely, narrow anteroposteriorly, and has a smoothly curved articular surface. In contrast to that of typical Ursinae, the glenoid fossa is situated in a plane dorsal to the basioccipital plane. In ursines, the glenoid fossa is ventral to the plane of the basioccipital. As is typical of the Ursidae, the postglenoid process is well developed medially, projecting anteroventrally to the glenoid fossa, and diminishes laterally. The postglenoid process is thin anteroposteriorly and does not form an anteroposteriorly thickened buttress as in the Ursinae. There is a low preglenoid process laterally.

On the dorsal surface of the zygomatic process of the squamosal,

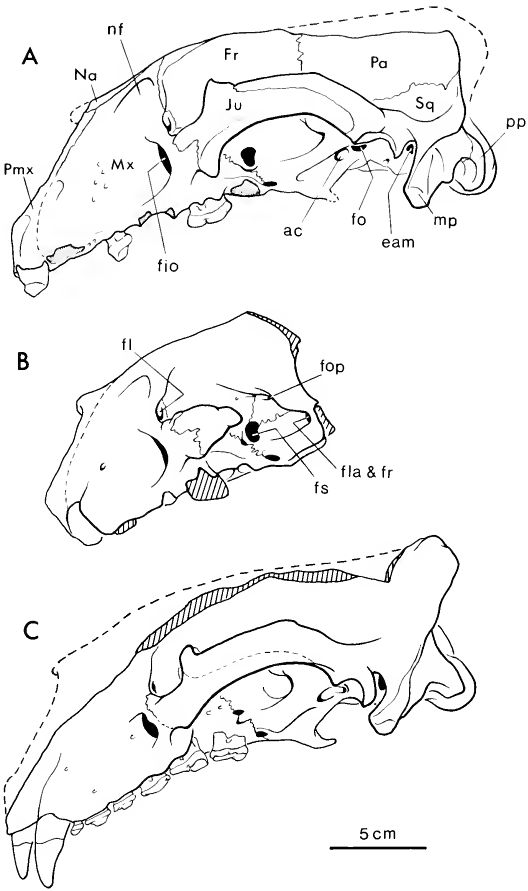

Figure 2. Outline drawings of restored crania of *Kolponomos* species viewed from the left and oriented so that the basicranial plane is horizontal. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype; UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070 with tooth row restored. All drawings to same scale. Symbols for anatomical features: ac, alisphenoid canal (posterior aperture); eam, external acoustic meatus; fio, infraorbital foramen; fl, lacrimal foramen; fla, anterior lacerate foramen; fo, foramen ovale; fop, optic foramen; Fr, frontal; fr, foramen rotundum; fs, sphenopalatine foramen; Ju, jugal; mp, mastoid process; Mx, maxilla; Na, nasal; nf, nasolabialis fossa; Pa, parietal; Pmx, premaxilla; pp, paroccipital (= jugular) process; Sq, squamosal.

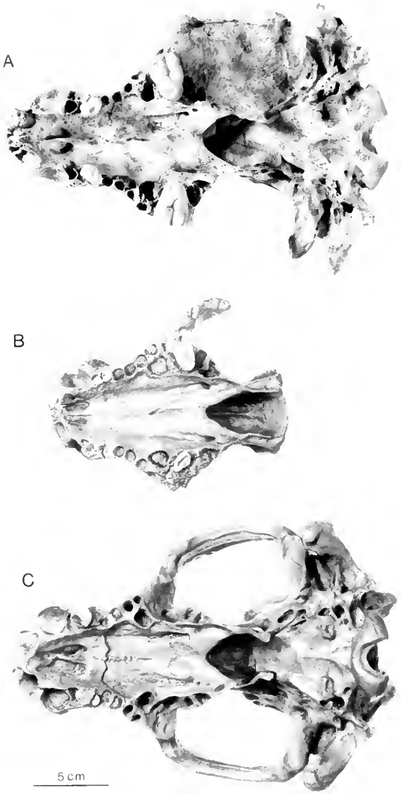

Figure 3. Ventral views of the crania of species of *Kolponomos*. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.

where the zygomatic arch meets the squamosal fossa, there is a prominent tuberosity. This tuberosity also is at the anterolateral edge of the shelf dorsal to the external auditory meatus. This shelf slopes posteroventrally and expands dorsoventrally as it merges with the base of the mastoid process.

The palate is elongated and concave both anteroposteriorly and transversely. On either side of the midline the palate is subplanar, essentially flat transversely and gently arched anteroposteriorly, from the incisive foramina to the palatal notch. Anteriorly and laterally the palate descends abruptly to the inner margin of the dental arcade. The anterior end of the palate is deflected ventrally, so that the alveolar margins of the canines and incisors are positioned more ventrally than those of the cheek teeth.

The septum separating the incisive foramina is continuous posteriorly with a slight raised ridge extending more than 30 mm posteriorly along the midline suture of the palate. These foramina are large and reniform. On either side of the palate, at the posterolateral corner just medial to the M^2 alveoli, are the posterior palatine foramina, closely associated with the maxillo–palatine suture. These foramina are variable in size and number. All are large on the holotype. On the referred cranium, the anterior foramina are both of intermediate size, while the posterior foramina are of different

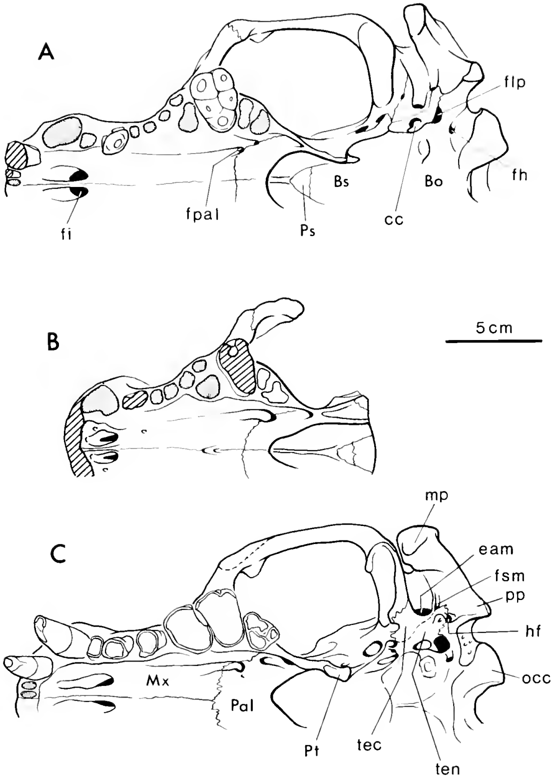

Figure 4. Outline drawings of restored crania of *Kolponomos* species, viewed ventrally. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070, with tooth row restored. All drawings to same scale. Symbols for anatomical features: Bo, basioccipital; Bs, basisphenoid; cc, carotid canal; eam, external acoustic meatus; fh, hypoglossal foramen; fi, incisive foramen (= palatine fissure); flp, posterior lacerate foramen; fpal, palatine foramen; fsm, stylomastoid foramen; hf, tympanohyal pit (= hyoid fossa); mp, mastoid process; Mx, maxilla; occ, occipital condyle; Pal, palatine; pp, paroccipital (= jugular) process; Ps, presphenoid; Pt, pterygoid; tec, ectotympanic; ten, entotympanic.

sizes, intermediate on the left and small on the right. On both crania the anterior foramen is continuous with a prominent anteroposteriorly elongated sulcus that extends anteriorly to a point where it disappears medial to the P^3. Posterior to the palatine foramina and the M^2 the posterolateral palatal margin is formed by a narrow vertically oriented crest pierced by a foramen. This crest is continuous posteriorly with the sharply keeled ventral border of the pterygoid hamulus. On the referred cranium, the hamulus is very thin transversely and concave laterally, as is typical of the Ursinae, but is bent sharply ventrally. The narrow posterior process of the pterygoid hamulus extends posteriorly. The main part of the pterygoid–palatine strut ascends posteriorly, to join the basicranium around the posterior aperture of the alisphenoid canal. The lateral surface of the strut is rounded and convex and continues onto the ventrolat-


A
B
C
509
5cm

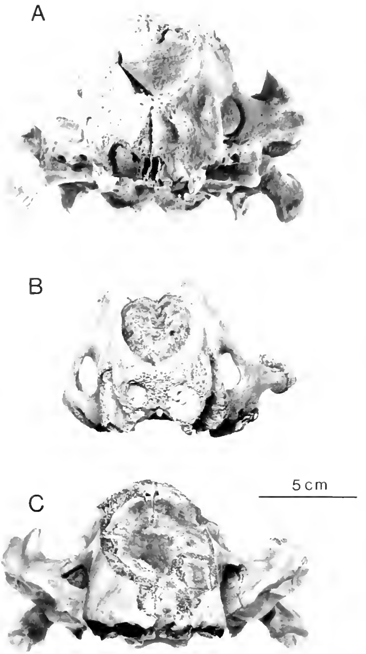

Figure 6. Anterior views of the crania of *Kolponomos* species. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.

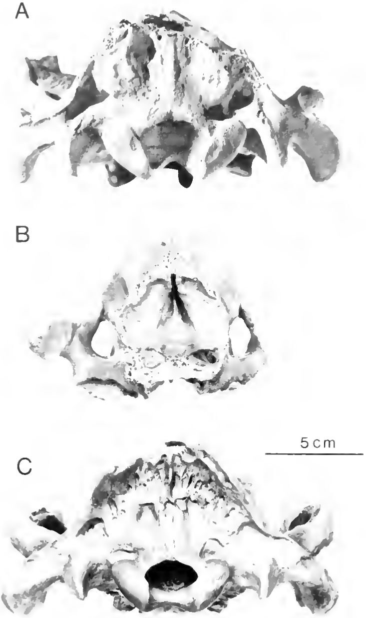

Figure 7. Posterior views of the crania of *Kolponomos* species. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.

eral surface of the braincase wall. From the pterygoid hamulus, a fine ridge extends posteriorly along the medial side of the posterior aperture of the alisphenoid canal and the foramen ovale and continues into the auditory tube of the bulla.

The internal narial opening is highly arched and wide. The palatal notch is broadly rounded in the referred specimen, has a slightly acute apex in the holotype, and extends anteriorly almost to a point between the centers of the M^2's. On either side of the internal narial opening, the palatine–pterygoid struts sweep medially to form a sharp, underhanging border. The roof of the internal narial opening ascends anteriorly and in its anterior part has a medial keel formed by the vomer and presphenoid. The presphenoid–basisphenoid suture is transversely oriented and is not coossified. The basisphenoid is nearly flat where it forms the roof of the internal naris between the pterygoid hamulae. It expands posteriorly and at its lateral edge, dorsal to the pterygoid hamulus, bears a groove that extends posterolaterally into the median lacerate foramen. The median lacerate foramen is elongated anteroposteriorly and is situated at the anteromedial corner of the bulla.

The basioccipital–basisphenoid suture is fused, and its precise location is not visible. The basioccipital has a median crest that widens posteriorly and spreads toward each condyle. On either side are a curved fossa and a rugosity that mark the insertion of the rectus capitis ventralis muscles. Posterolateral to the fossa, between the condyle and the bulla, is the hypoglossal foramen, which is transversely oval and approximately 3 mm in diameter.

The tympanic bulla is small and has a rugose ventral surface. It is fused laterally to the squamosal and the base of the mastoid

Figure 5. Dorsal views of the crania of *Kolponomos* species. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.

process. Posteromedially it is separated from the basioccipital by a sulcus. Anterolaterally it expands posteroventral to the medial part of the glenoid fossa and is broadly appressed to the posteromedial part of the postglenoid process. An oblique crest on the ventral surface of the bulla that extends from the stylomastoid foramen to the anteromedial margin appears to mark the junction between the entotympanic and the ectotympanic. If this is true, the entotympanic contribution to the tympanic bulla is approximately equal to that of the ectotympanic.

There appears to be a small postglenoid foramen located in a fissure where the medial part of the postglenoid process is overlapped by the bulla. The ventral surface of the bulla is retracted posteriorly at the anteromedial corner ventral to the median lacerate foramen. The posterior lacerate foramen lies at the posteromedial corner of the bulla and is semicircular and positioned obliquely. The external auditory meatus is round, approximately 4 mm in diameter, and recessed far beneath a wide shelf formed by the squamosal.

The mastoid process is very long, extending outward from the cranium variably 38 and 44 mm on either side, measured from the notch where it joins the paroccipital process. It projects anteroventrolaterally from the basicranium. The process is basically three-sided; one flattened surface medial, one anterior, and one posterior. The medial surface is concave in contrast to the other two, which are slightly convex. At its distal end, the mastoid process is compressed anteroposteriorly. The concave medial surface expands proximally toward the basicranium and is confluent with a large recess surrounding the hyoid fossa. This same recess extends onto the anterolateral surface of the paroccipital process, which is at this place deeply excavated. The paroccipital process projects posteroventrolaterally from the basicranium and is compressed transversely. Its anteroventral margin is a crest that extends anteromedially toward the bulla, reaching the posterior side of the bulla between the stylomastoid foramen and the posterior lacerate foramen.

As in the Ursinae, the hyoid fossa is separated from the posterior lacerate foramen by a ridge of bone. The hyoid fossa sits within a deep recess. In ursines, the hyoid fossa is widely separated from the external auditory meatus by a wide expanse of the bulla. In *Kolponomos clallamensis*, however, the hyoid fossa is very close to the external auditory meatus. Also, in *K. clallamensis* the stylomastoid foramen lies midway between the hyoid fossa and the external auditory meatus, whereas in the Ursinae the stylomastoid foramen is widely separated from the external acoustic meatus and is within the recess that houses the hyoid fossa.

Dentition.—The upper dentition consists of I$^{1-3}$, canine, P$^{1-4}$, and M$^{1-2}$. The actual teeth present in the referred cranium are the roots of the left I$^{2-3}$ and the complete left and right P^2's and M^1's. On the left side, all alveolar margins are preserved, and it is that side that forms the basis for the following description.

The incisors and canines are clustered, without significant diastemata, in the thickened and downturned anterior end of the snout. The incisors are aligned transversely anterior to the canines. I^1 and I^2 are small and have transversely compressed roots. I^1 is smaller than I^2, and both teeth are implanted essentially vertically in the palate. The I^3's are much larger, being approximately four times the diameter of I^2 at the alveolar rim. Unlike the medial incisors, the I^3's are procumbent and deeply rooted in the premaxilla between the canine and the incisive foramen. The left I^3 measures 18.2 mm anteroposteriorly and 12.4 mm transversely at the alveolar rim. A diastema of 4 mm separates the alveolus for the left I^3 from that of the upper canine. The canine alveolus is oval and measures 20 mm anteroposteriorly and 17 mm transversely at the alveolar rim. The bulge in the lateral side of the rostrum indicates that the root for the canine is extremely long and extends nearly as far into the rostrum as the lateral edge of the nasal bone. The root is procumbent.

The cheek-tooth row curves laterally from the canine posteriorly to M^1, then M^2 is positioned more medially. P^1 has a single root that is round in cross-section, procumbent, and closely appressed to the posterior side of the canine alveolus. The alveolus indicates that the root was tapered, approximately 7 mm in diameter at the alveolar margin, and extended for approximately 15 mm into the maxilla.

P^2 is a robust tooth, with two roots and a large smooth crown. The tooth is oriented obliquely to the axis of the cheek-tooth row, the anterior root medial to the axis. The posterior root is on the axis of the tooth row and is approximately twice the diameter of the anterior root. The tooth tilts medially into the oral cavity. The crown of this tooth has a flat apical wear facet on the principal cusp. A smooth cingulum borders the lingual side of the crown from the anterior to the posterior border of the tooth. The posterior part of the crown is formed into a talon lying between the principal cusp and the posterior end of the cingulum.

P^3 had roots aligned in the axis of the cheek-tooth row. Judged by the size of the alveoli, the two roots of this tooth were more nearly equal in size than those of P^2, the posterior one being only slightly larger in diameter than the anterior one. The maxilla projects ventrally, forming a crest of bone between the two roots of this tooth.

P^4 was a large tooth, nearly as large as M^1, and had three roots. Of these, the medial (protocone) root is the largest, being more than twice the depth and diameter of either of the lateral (paracone and metacone) roots. Between P^3 and P^4, the lateral margin of the maxilla begins a strong lateral bend, so that P^4 is oriented obliquely to the cheek-tooth row. A diastema of approximately 3 mm separates the anterior (paracone) root of P^4 from the posterior root of P^3.

M^1 is a massive tooth. It appears to have been approximately 30% larger than P^4 in surface area. It is greatly expanded transversely and is triangular in occlusal view. It has five mammiform cusps of nearly equal sizes. The lateral two cusps are the paracone and metacone; the most medial cusp forms the apex of the triangle and is the protocone; intermediate cusps are the para- and metaconules. The surface of each M^1 shows extensive wear that breaks through the enamel to expose the inner dentinal core. There is a labial cingulum between the para- and metacones, but other cingula are lacking.

The M^2 alveoli indicate that this tooth was approximately half the size of the M^1. M^2 is positioned lingually opposite the talon of M^1. Like both P^4 and M^1, M^2 had three roots. Of these, the anterolateral (paracone) root was broadly joined with the medial (protocone) root to form a transversely oriented bilobate root. The posterior root is the metacone root and is rotated so that it is actually the most medial root of the tooth.

Kolponomos newportensis, new species

Figures 1-12

Kolponomos clallamensis Stirton, 1960. Barnes et al., 1985:43, figs. 9a, b.

Diagnosis.—A species of *Kolponomos* differing from *K. clallamensis* in the following derived cranial features: broad muzzle flaring laterally above canines and incisors; mastoid process twisted clockwise, extending forward beneath external auditory meatus as far as postglenoid process; intercondylar notch lacking so that the articular surfaces of the occipital condyles are continuous ventrally. In addition, *K. newportensis* is distinguished from *K. clallamensis* by the following primitive features: infraorbital foramen smaller and lacking marked excavation of maxilla anterior to it; prominent masseteric process of maxilla lacking and masseteric process on jugal reduced; jugal forming anterior rim of orbit; paroccipital process smaller and less downwardly pointing; paroccipital process lacking hyoid fossa.

Holotype.—USNM 215070, cranium lacking parts of dorsal surface with only right and left P^2 *in situ*; mandible lacking tips of coronoid processes and lacking incisors and right P_1; isolated associated right I^3 and C, right P^1, left P^1, left P^3, right P^4, left M^1, and right and left M^2. Recovered from the same concretion were the axis, third cervical vertebra, a broken proximal lumbar vertebra, a sternebra, a proximal part of an anterior rib, a thyrohyal lacking the proximal end, a complete ?ceratohyal, a metapodial lacking the distal end and half of the proximal end, a median phalanx, and unidentifiable bone fragments. The original half of the concretion containing the occipital part of the skull and most postcranial elements was collected by Douglas R. Emlong, October 1969 (Emlong field no. 603). On 26 January 1976 Emlong found the remainder of the concretion, containing the balance of the skull, mandible, and isolated teeth (Emlong field no. E76-B), recognizing it as associated and pertaining to *Kolponomos*.

Type locality.—A concretion found on the beach at low tide line, approximately 300 yards (274 m) south of the mouth of Big Creek and 100 yards (91 m) seaward of the sea cliff just north of Newport, Lincoln County, Oregon.

Formation and age.—Lower part of the Nye Mudstone, representing the early Pillarian Molluscan Stage (Addicott 1976a; Moore and Addicott 1987), correlative with the Late Arikareean Land Mammal Age, early Miocene.

Etymology.—Named for the town near the type locality to record the occurrence of the type species in a manner similar to that for the genoholotype.

Skull.—The skull of USNM 215070 lacks most of the dorsal surface and is toothless except for both P^2's, which are crushed into their alveoli and forward into those for P^1. The concretion enclosing the specimen was subspherical and aproximately 27 cm in diameter. Prior to its consolidation, all upper teeth except left and right P^2 had fallen out. In the course of gross preparation these were found in a tight cluster beneath the palate and between the horizontal rami of the mandible. Also prior to consolidation, the mandible had slipped out of articulation and moved forward and upward forcibly, coming to rest in a symmetrical undershot false occlusal position, undoubtedly causing the anterior displacement of left and right P^2 and severely crushing and comminuting the thin alveolar walls of left and right M^2 and M^1 and, to a lesser extent, the alveolar margins of the upper premolars. The apices of the coronoid processes were removed by abrasion of the smooth surface of the concretion as was much of the dorsal surface of the skull. The tightly appressed mandible was painstakingly separated from the skull and the tightly clustered isolated teeth were extracted by Gladwyn B. Sullivan in 1976 in the course of gross preparation of the specimen. This specimen represents an old individual as judged by its heavily worn teeth and advanced cranial fusion. Despite the latter, it is possible to make out many sutures, particularly in the orbital region.

A striking major feature of the skull, in common with all remains of the genus, is the flexure of the facial part of the skull relative to the basicranial plane (Fig. 2). Measured as the angle between the palate and basisphenoid, the flexure is approximately 155° in USNM 215070. The widely flaring zygomatic arches, the forward-oriented orbits, and the great hypertrophy of the mastoid processes are also distinctive features of the remarkable skulls of *Kolponomos*.

In USNM 215070 the muzzle is nearly as broad at the carnassial as the palate. The large anteroposteriorly elongated incisive foramina lie in the trough of the strongly arched palate with distinct grooves extending anteriorly from them nearly to the incisor alveoli. The interforamen septum forms a low S-curve anteriorly. Posteriorly the vaulted palate has strong anteroposteriorly oriented depressions along either side of the flattened medial part of the palate, becoming progressively deeper posteriorly and leading into the anterior palatine foramina at the maxillary–palatine suture adjacent to the anterior root of M^2. Behind that a series of pits extends the posterior palatine groove to a foramen that penetrates the thin rim of the palatine portion of the palate.

The pterygoid hamuli are arcuate in palatal view and terminate in dorsoventrally flattened processes. Sutures with bones surrounding the pterygoid are too coossified for the precise outline of this element to be determined. The anterior or pterygoid process of the alisphenoid is defined by its suture with the palatine; with the palatine it forms a strong strut bracing the back of the palate against the braincase. Ventral to this strut a depression for the origin of the pterygoid muscle extends downward toward the hamular process. The posterior end of the large alisphenoid canal penetrates the base of the strut. This opening is closely followed by the foramen ovale, which lies in a common pit with the opening of the canal on the left side of USNM 215070, but on the right a groove joins these orifices as in most arctoids. The dorsal and posterior sutures of the alisphenoid with adjacent bones are closed.

The basisphenoid and basioccipital bones are strongly coossified and the sutures between them are eliminated. They form a trapezoidal figure with its base lying across the rectus capitis insertions just anterior to the posterior lacerate foramina. Thus the basioccipital is broadest across the rectus insertions where the winglike lateral processes of this bone overlap the medial edge of the petrosal and presumably floor the large tract for the inferior petrosal sinus. The knoblike processes for the rectus are situated bilaterally at the posterolateral corners of ovoid shallow depressions for muscle insertion that presumably extend forward onto the basisphenoid and medially to a low crest at the midline. The exoccipital is solidly fused with surrounding elements, except for its irregular contact with the posterior end of the bulla (caudal entotympanic). This bone contains the hypoglossal foramen, which is situated posteromedial to the posterior lacerate foramen as well as the posterior rim of the latter opening. Presumably the exoccipital also forms the medial wall and spine of the paroccipital process. The occipital condyles protrude slightly posterior to the nuchal crest. There is no intercondylar notch as the condyles are conjoined ventrally, uniting their articular surfaces. A shelflike extension of the floor of the foramen magnum extends posteromedially beyond these articular surfaces. Inside the foramen magnum the paired posterior openings of the hypoglossal foramina can be seen on its floor. An additional pair of foramina lying on the lateral wall of the foramen magnum at the level of the dorsal part of the condyles presumably accommodated venous drainage for sinuses within the occiput.

The auditory region is very small and nestled deeply within the ventrally projecting elements surrounding it, particularly the greatly hypertrophied mastoid process. The bulla is uninflated and extensively coossified with surrounding elements; nevertheless, most of its outline as well as its composition can be determined from bilaterally symmetrical suture traces and rugose coossification tracts. These observations indicate that the ectotympanic lacks an ossified meatal tube; its anterior limb spreads over the posteromedial surface of the postglenoid, forming the posterior wall of the slitlike postglenoid foramen. Anteromedially the ectotympanic overlaps the entotympanic and coossifies laterally with the alisphenoid behind the foramen ovale. A styloid process of the ectotympanic lies beneath the opening for the eustachian tube. The posterior limb of the ectotympanic is fused to the base of the mastoid process. Behind this union, the stylomastoid foramen emerges from the mastoid. The facial canal is thus separated from the large pit for the tympanohyal that opens above a prominent hyoid process of the entotympanic at the posterolateral corner of the bulla. There is no large hyoid fossa excavated into the anterior wall of the paroccipital process as in *K. clallamensis*.

The entotympanic is irregularly exposed along the medial edge of the bulla because of variable overlap of the ectotympanic; posteriorly the caudal element is sutured to a process from the exoccipital and posterolaterally to a process from the mastoid. There is a large posterior opening of the carotid canal well anterior to the posterior lacerate foramen. This opening is formed medially by the basioccipital wing and laterally by the entotympanic, but anteriorly the arterial tube is nearly completely surrounded by the entotympanic. The anterior carotid foramen lies medial to the styloid process of the ectotympanic and opens into a groove in the basisphenoid anterior to the median lacerate foramen. From this groove the artery must loop posteriorly to enter the median lacerate foramen and/or the presumed channel in the basioccipital that accommodates the inferior petrosal sinus.

The large mastoid process takes the form of an anteroposteriorly flattened column bending outward and downward from its base and curving forward at its tip to pass nearly under the postglenoid process (Fig. 7C). Its components are totally coossified, but the nuchal crest extends along the lateral surface of the process, thus marking the position of the mastoid–squamosal suture and indicating that the process is composed about equally of the two elements. The process terminates in a raised ovoid area that lies within the suture. This element may represent the secondary ossification center (epiphysis) frequently observed at the tip of the mastoid process in adult ursids. A ridge arises from the posteroproximal surface of the mastoid process and passes upward and posteriorly to join the paroccipital process. The paroccipital process curves posteroventrally and terminates in a sharp point.

The supraoccipital bones are solidly coossified with surrounding elements. They are concave and highly rugose beneath the nuchal crest; a thin ridge is present sagittally. At their lateral extremities a shallow pit is present dorsal to the base of the paroccipital processes. The lateral processes of the nuchal crest extend behind the inion and beyond the occipital condyles; consequently, the crest has a broad inflection at the midline. The parietal and squamosal bones are coossified, but their junction is probably marked by the bilaterally symmetrical collapse of the braincase wall under lithostatic load. Breakage dorsally has removed most of the sagittal crest of the parietal, but the remaining evidence indicates the presence of at least a low crest. The squamosal apparently makes a significant contribution to the anterior part of the mastoid process. Its glenoid fossa forms a cylindrical articulation nearly at right angles to the basicranial axis. Prominent recurved postglenoid processes are present, deepest medially, and the anterolateral part of the articular surface is bordered by a low preglenoid process. Most of the squamosal–jugal suture is visible; the squamosal contribution to the zygomatic arch seems to taper out at the base of the jugal postorbital process.

The anterior ends of the frontals have been removed by erosion, exposing a natural section of the narial cavity. Frontal–parietal sutures are coossified and not traceable, but they may have crossed the midline at about the point where the parasagittal crests appear to diverge anteriorly. The frontal sinuses seem to have extended backward over the braincase to about this point. Beneath these sinuses the braincase is sharply constricted anteriorly, probably indicating the greatly constricted form of the olfactory lobes of the brain as shown by the holotype of *K. clallamensis*.

Sutures in the orbital wall can be partially seen and the relative position of foramina and bones can be determined. In general the arrangement is like that described by Stirton for the holotype of the genotypic species. There is a large common opening for the anterior orifice of the alisphenoid canal, the foramen rotundum, and the anterior lacerate foramen as in pinnipeds. Anterodorsal to this opening the slitlike small optic foramen opens into a short groove. Dorsal to the

TABLE 1. Measurements (in mm) of crania of *Kolponomos clallamensis* and *K. newportensis*, new species.

	Kolponomos newportensis	*Kolponomos clallamensis*	
	USNM 215070	UCMP 50056[a]	LACM 131148[b]
Total (condylobasal) length	253.1	—	258.4
Postpalatal length (palatal notch to basion)	107.3	—	107.0
Basion to anterior edge of zygomatic root	155.2	—	153.7
Length C alveolus to M^2 alveolus	114.2	ca. 108	117.7
Width of rostrum across canines	75.2	—	(71)
Width of skull across alveoli of M^1	ca. 110	ca. 98	119.6
Width of skull at infraorbital foramen	78.3	75.2	74.3
Width of skull across antorbital process	74.9	80.9	(82)
Width of greatest intertemporal constriction	46.2	46.8	45.4
Width of braincase, anterior edge of glenoid fossa	72.3	—	82.3
Zygomatic width	179.5	—	(178)
Auditory width	137.0	—	141.2
Mastoid width	182.0	—	183.7
Paroccipital width	116.5	—	123.0
Greatest width of occipital condyle	61.5	—	74.0
Greatest width, anterior nares	—	37.0	38.5
Greatest height, anterior nares	—	36.3	—
Greatest width of foramen magnum	26.8	—	33.3
Greatest height of foramen magnum	18.3	—	15.0
Transverse diameter of infraorbital foramen	11.1	11.6	13.0
Height of infraorbital foramen	11.3	20.0	21.6

[a] For additional measurements see Stirton (1960:355).

[b] Bilateral measurements of the referred cranium of *K. clallamensis* are made on the left side. Parentheses indicate estimated measurements made by doubling a half width.

TABLE 2. Measurements of cheek teeth and mandible of *Kolponomos*. Where available, measurements of the left side entered first.

	K. newportensis (USNM 215070)	*K. clallamensis* (LACM 131148)
Upper teeth (length × width)		
I^3	12.8 × 10.7	—
C	15.4 × 13.9	—
P^1	7.3 × 11.5	—
P^2	16.2 × —	15.7 × 10.3
	17.2 × 12.5	
P^3	ca. 16 × 12	—
P^4	18.5 × 25.5	—
M^1	22.3 × 28.9	21.9 × 31.4
M^2	16.8 × 16.4	—
	17.8 × 17.1	
Lower teeth (length × width)		
C	17.2 × 13.1	—
	16.5 × 13.5	
P_1	— × ca. 9	—
	7.6 × 9.9	
P_2	13.7 × 10.8	—
	14.0 × 10.5	
P_3	16.1 × 11.2	—
	16.2 × 11.1	
P_4	18.0 × 14.0	—
	18.7 × 13.6	
M_1 length	27.3; 27.5	—
M_1 width trigonid	24.0; 24.5	—
M_1 width talonid	— ; 22.7	—
M_2	21.5 × 22.3	—
	21.3 × —	
Mandible		
Length of horizontal ramus, condyle to tip of rostrum	201.5	—
Length of base of coronoid process	55.5; 55.7	—
Depth of mandible beneath P_2	59.5; 59.8	—
Depth of mandible beneath anterior part of M_1	43.8; 44.2	—
Depth of mandible beneath posterior part of M_2	40.0; 42.2	—
Width of mandible at P_3	18.8; 20.5	—
Width of mandible at M_2	21.8; 24.2	—
Length of symphysis	53.5	—

optic foramen lies the equal-sized ethmoid foramen. The orbitosphenoid bone containing these foramina seems to pass anterodorsally along the orbital wall to a greater extent than in *K. clallamensis*. Ventral to these foramina, the sphenopalatine and posterior palatine foramina are closely associated, the former on the orbitosphenoid–palatine suture and the latter penetrating the adjacent palatine bone. The sphenopalatine foramen is about twice the size of the posterior palatine foramen; neither is as large as its counterpart in *K. clallamensis*. Indistinct sutures suggest that the palatine is attenuated between the frontal and maxilla and fails to reach the anterior end of the orbital fossa. There is a very small lacrimal foramen but no trace of the limits of the corresponding lacrimal bone.

The jugal forms the ventral part of the orbit and appears to extend nearly to the lacrimal foramen (in contrast to *K. clallamensis*). With the maxilla it forms the roof of the short infraorbital canal. There is a strong postorbital process and a low, elongated, rugose masseteric process formed by the jugal.

The dorsal part of the maxilla is eroded away so that only the lateral and palatal parts of this bone are preserved. The oval infraorbital canal penetrates the zygomatic process of the maxilla. This canal is large (see Table 1) and short (11.0 mm left), as is characteristic of *Kolponomos* and pinnipeds. It opens onto the face into a shallow depression (infraorbital fossa) that is more extensively developed in *K. clallamensis*. There appears to have been a shallow fossa for the levator labii marked by a dorsal preorbital fossa as in *K. clallamensis*. The suture with the premaxilla is thoroughly coossified. The rostrum anterior to the canines is laterally expanded and bears low rises over the roots of the canine and I^3.

A natural oblique section through the narial cavity exposes the dorsal part of this region from the level of the canines to just behind the orbits, showing that the ethmoturbinals are placed laterally and are excluded from the narial opening as in other arctoids. The dorsal frontal sinus is also evident and must extend backward close to the frontoparietal suture.

Upper dentition.—Most of the upper cheek teeth of USNM 215070 (Fig. 8), with the exception of the *in situ* P^2's, were found grouped together in the matrix between the rami of the associated mandible. When prepared and fitted into their respective alveoli the following teeth were recovered: right I^3, C, right P^1, left P^1, left P^3, right P^4, left M^1, and right and left M^2. All except I^3 and C are highly worn and so furnish little information about their crowns' morphology.

The alveoli for I^{1-2} indicate that these teeth were much smaller than I^3. I^3 is procumbent and has a long cylindrical root and a relatively short crown with a recurved tip. There is no cingulum or carina. A facet for the lower canine is present, worn through the enamel at the posterolateral base of the crown. The tip has been fractured and a transverse groove has been cut across the anterior face of the crown, both probably representing damage during use of this tooth as a lever. The upper canine is broken across the root so that only about half the total length of the tooth remains. It is also procumbent; its crown is an attenuated cone, slightly recurved at the tip, and has no cingulum or carina. A wear facet for the lower canine extends from the tip to within 2 mm of the base of the crown. The tip is also worn apically, and a short transverse groove cuts the anterior face near the tip.

The P^1 is closely appressed to the canine. Its crown is oriented transverse to the axis of the tooth row. The crown has an ovoid outline and a posterior cingulum. Heavy wear has truncated the apex to a medially sloping wear surface cut to the crown's base. Its single root is anteroposteriorly flattened and bends posteriorly to accommodate the roots of C and P^2. The P^2 has two roots; its crown is an elongated oval in occlusal outline with cingular shelves anterior and posterior to the stout principal cusp. Wear has formed a medially truncated surface across the principal cusp that has cut nearly to the crown's base. P^3 is only slightly larger than P^2 and two-rooted, the more anterior root passing inside the posterior root of P^2 so that the tooth has an orientation oblique to the tooth row. The crown is ovoid in occlusal outline; wear has removed the principal cusp and anterior cingulum, but the posterior cingular shelf remains. This cingulum bears a low cuspule laterally and is bounded medially by a well-developed facet of interdental wear.

P^4 bears three roots, the lateral pair about the size of those of the anterior premolars, although the most posterior is slightly smaller than the anterior. A large medial root is nearly symmetrically placed with the lateral roots, but the whole tooth has an oblique orientation to align with the anterior surface of M^1, thus removing the embrasure pit found in most carnivores where carnassial shear is important. At the advanced stage of wear shown by the P^4 only an encircling band of thin enamel remains. The enamel is broken on the posterior side by abrasion between P^4 and the adjacent M^1. A remnant of the metastyle remains on the posterolateral part of the crown marked by a notch that may represent the base of the carnassial notch. Dentine-filled pulp cavities on the gently concave worn crown indicate the presence of a principal external cusp or coalesced cusps forming an anteroposteriorly elongated structure and large internal cusp ("protocone") supported by the strong internal

Figure 8. Upper cheek teeth of holotype of *Kolponomos newportensis* n. sp., USNM 215070. Right side with left P^2, P^3, and M^{1-2} reversed to restore the complete cheek-tooth series.

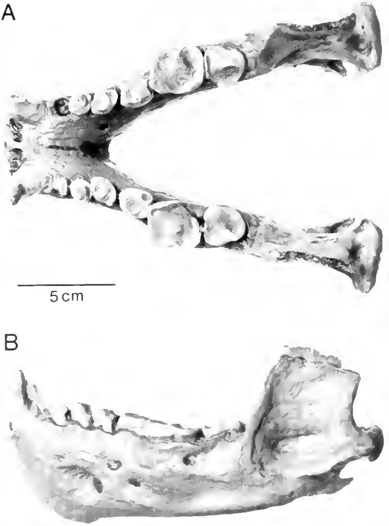

Figure 9. Mandible of *Kolponomos newportensis* n. sp., holotype, USNM 215070. A, occlusal view; B, left side. At same scale as figures of crania.

root. Anterolateral to the latter a filled pulp cavity indicates the presence of another smaller cusp linked to the "protocone," probably indicating that the anterior cingulum bore a cusp analogous to the paraconule of tribosphenic molars. Thus the upper carnassial of USNM 215070 has been molarized, its sectorial nature changed to function with the molars as part of the masticatory battery.

The first upper molar has three roots. The labial roots supporting the paracone and metacone are anteroposteriorly compressed structures; the lingual root supporting the protocone is a short faceted cone. Filled pulp cavities indicate a pattern of cusps similar to the M^1 of *K. clallamensis*. A short section of the labial cingulum bridges the indentation between the paracone and metacone and, as in *K. clallamensis*, indicates that the paracone was larger than the metacone. Thin enamel rims the concave wear surface of this tooth, broken only at the junction with P^4. The M^2 is triangular in form and least worn on the left side. It is positioned lingually opposite the M^1 talon, in contrast to a labial position opposite the trigon as in most carnivorans. It bears two short stout roots; the anterior is anteroposteriorly flattened, the posterior triangular. The worn crown shows four inflated cusps that have coalesced, separated only by thin grooves similar to the condition in the less worn M^1 of *K. clallamensis*. These are interpreted as follows: the most labial is the paracone with the closely allied metacone immediately posterolingual to it; the large protocone occupies the anterolingual border, the labial projection of its wear facet representing the paraconule; the cusp at the posterolingual corner of the tooth is the metaconule. The enamel covering of these cusps is remarkably thin, as revealed by apical wear. An interdental wear facet with M^1 occurs on the anterior face of the tooth.

Mandible.—The nearly complete mandible of 215070 lacks only the tips of both coronoid processes (Figs. 9, 10). The rami are thoroughly ankylosed at the symphysis; the junction is raised externally, creating a symphyseal boss ventrally. The horizontal ramus is deepest at this boss and shallowest posteriorly. Anteroventrally paired foramina lie on either side of the symphyseal suture about at mid-depth. Laterally there are three mental foramina; the largest is the most ventral, lying beneath P_3 at the posterior end of a shallow depression. A second foramen lies anterodorsal to the first and beneath P_2 on the right side or posteriorly beneath the anterior root of P_4 on the left side. The third and most posterior foramen lies at mid-depth of the horizontal ramus beneath the posterior root of P_4. The rami are markedly rugose beneath the molars; the right side shows bone resorption around the protoconid root of M_1, and on the left side there is a pit in the lateral surface adjacent to the hypoconid root of the same tooth. The masseteric fossa has a deep anteroposteriorly elongated pit in its deepest recess. The masseteric crest does

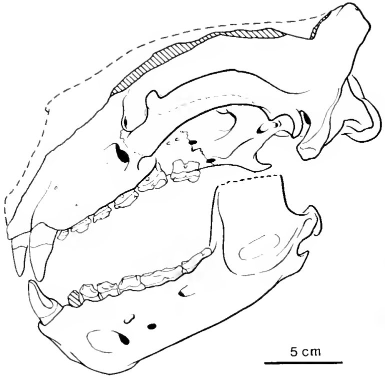

Figure 10. Outline drawing of the holotype of *Kolponomos newportensis* n. sp., USNM 215070, viewed from the left. Upper dentition restored from isolated teeth found with the type.

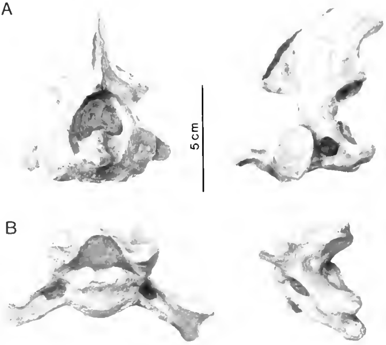

Figure 11. Cervical vertebrae of holotype of *Kolponomos newportensis* n. sp., USNM 215070. A, axis, anterior and left lateral views, lateral view reversed from right side; B, third cervical, anterior and left lateral views.

not extend to the anterior end of the fossa but arises just above the base of the angular process and passes to the articular condyle. In harmony with the form of the glenoid fossa, the articular condyle is cylindrical, pointed laterally, and deepest medially; a pit for insertion of the external pterygoid muscle occurs at the anteromedial base of the condyle. The angular process is relatively small and markedly inflected medially. Its dorsal surface has a pit and ridge, and the medial surface is rugose, all for insertion of parts of the internal pterygoid muscle. There is a large mandibular foramen that lies below the level of the tooth row and the condyle and just above the level of the dorsal surface of the angular process, about midway along the base of the ascending ramus.

Lower dentition.—The central incisors seem to have been lost in life in USNM 215070 but it is not certain that I_1 was in fact present. The position of this tooth is occupied by spongy bone. The alveolus for the right I_2 is filled with spongy bone but the alveolus for the left I_2 is discernable. The roots of both I_3's are present. The canine has a long root and short crown. It is fully preserved only on the left side; the right canine appears to have had its apex broken away in life; the broken surface is polished and a secondary wear facet was established on the medial side of the broken tip. Occlusion with the upper canine has worn the tip and posterolateral side of each lower canine.

The premolar row diverges slightly posteriorly along an axis that lies wholly inside the axis of the molar row. The left P_1 is badly broken; the right P_1 was recovered from the surrounding matrix. Like its counterpart in the maxilla, the P_1 is anteroposteriorly compressed to fit between the base of the canine and the overhanging anterior margin of P_2. Its crown is heavily worn apically on a posteriorly slanting surface. There is a posterior cingulum pitted by breakage. The P_2 and P_3 are similar in form; the P_3 is larger. The apically worn crowns show a robust principal cusp and anterior and posterior cingular cusps connected by a lingual cingulum. There is no labial cingulum. The P_4 departs from this form in that a strong posterolingual cusp is also present; the anterior cingular cusp and posterolabial cingular shelf combine to give this tooth a molariform appearance.

The M_1 is offset laterally so that only the anterolingual face of its paraconid overhangs the posterolabial cingulum of P_4; its crown is only a little longer than wide and worn nearly flat. On the left side the entoconid region is worn away, but on the right the crown is complete with its encircling thin enamel. A remnant of the enamel in the right talonid basin is preserved at this advanced stage of wear. Filled pulp cavities indicate the full tribosphenic complement of cusps; the protoconid, metaconid, and hypoconid were subequal in size, the paraconid and entoconid smaller. There are indentations internally at the carnassial notch and externally between the talonid and trigonid. There is no trace of a cingulum.

M_2 is wider than long, triangular in occlusal outline, and widest across the trigonid. Wear has removed the anterolingual corner of the right M_2 but not the left, which has lost marginal enamel along the anterior part of the tooth. Filled pulp cavities indicate the presence of three trigonid cusps and the hypoconid, which is represented by encircling enamel on the right and has not worn into the pulp cavity on the left. The pulp cavities seem best interpreted in comparison with the trigonid of M_1: a large protoconid on the anterolabial corner, a small paraconid directly lingual to it, and a large metaconid on the median lingual margin. Pulp cavities of the latter two cusps are connected. There is no M_3.

Postcranial skeleton.—An axis and third cervical vertebra are available and all structures are preserved on one side or the other of these bones. The axis (Fig. 11) has a short centrum and high neural spine as in pinnipeds and lutrine mustelids. The general form of the bone most resembles that seen in phocids or *Enhydra*, although the neural spine is larger overall than in the latter. The odontoid process points anterodorsally as in terrestrial carnivores and in contrast to most pinnipeds, and there is a shallow groove on its dorsal surface for the transverse ligament of the atlas, a feature usually missing in pinnipeds. A broad ridge continues the odontoid process into the spinal canal. The atlantoaxial articulations are joined beneath the odontoid process as in ursids, not separated by a notch as in pinnipeds. The centrum (less the odontoid process) is wider than long. Its

Figure 12. Metapodial and phalanx of holotype of *Kolponomos newportensis* n. sp., USNM 215070. A, metapodial, dorsal and ventral (right) views; B, phalanx, dorsal and ventral (right) views.

posterior articulation is dorsoventrally flattened. A marked ventral keel leads from the joined atlantoaxial articulation to the posterior articular epiphysis where there is a thickening of the keel into a low process. *Enhydra* and phocids show a similar structure. The robust transverse process sweeps in an arc backward beyond the centrum, as in pinnipeds. The vertebrarterial canal pierces the base of the transverse process. It is of large caliber as in pinnipeds and lutrine mustelids. The neural arch has a narrow base corresponding to the short centrum. The postzygapophyses project as flanges laterally; their articulations slant upward posteriorly and laterally. The high bladelike neural spine hooks posteriorly beyond the neural arch of the third cervical when in articulation. It is strongly inclined anteriorly, ending in a process for the rectus capitis that lies above the base of the odontoid. The neural spine is thin, wider only at the rectus capitis origin. Its form most approximates that of phocids rather than that of otariids or ursids, in which the spine is more robust and has a marked posterior process. The postzygapophyses lack dorsal processes for insertion of the axial muscles, but the base of the arch beneath the overhanging neural spine is excavated for the more medial elements of this muscle system.

The centrum of the third cervical vertebra is about as long as wide, and flattened dorsoventrally (Fig. 11) and keeled with a posterior enlargement, as in pinnipeds. The prominent transverse processes sweep posterolaterally and terminate in twin processes. They seem to lack an anterior spine as in phocids and in contrast to other carnivores. Large vertebrarterial canals pierce the bases of the transverse processes. The neural arch is low, and the neural canal is correspondingly flattened dorsoventrally, as in pinnipeds. Pre- and postzygapophyses are stout; the latter have low processes for the axial musculature on their dorsal surfaces. This vertebra lacks a neural spine as in phocids, *Enhydra*, and ursids.

Elements of the foot of *K. newportensis* are represented only by a much eroded metapodial and a nearly complete median phalanx (Fig. 12). The proportions of the metapodial suggest that it may be a third metatarsal, but without the proximal end this identification is uncertain. The shaft of this bone is markedly flattened dorsoventrally, as in pinnipeds. Enough remains of the distal end to indicate that the articulation was hemispherical and had a well-developed ventral keel, as in terrestrial carnivores. The median phalanx is also markedly flattened but not elongated as in pinnipeds or *Enhydra*. Its distal end is trochleated, and the proximal articulation indicates that the distal end of the proximal phalanx was also trochleated. The proximal end has strong lateral processes for flexor tendons and a dorsomedial process for extensors, implying powerful movement of the digits.

DISCUSSION

Relationships Between the Species of *Kolponomos*

Although we have only one nearly complete cranium of each species, the characters cited in the diagnoses are similar to those that distinguish other nominal species of arctoid carnivores. Moreover, the two specimens of *K. clallamensis* are similar in important particulars that separate them from the specimen here described as *K. newportensis*, lessening the possibility that the differences between the specimens from Washington and Oregon are due to sexual dimorphism or individual variation. Nor is there evidence that the individuals differ in ways usually associated with sexual dimorphism in arctoid carnivores (gross size, size of canines, and development of muscular processes of the skull).

In some ways the cranium of *Kolponomos newportensis* seems the more primitive of the two, having some characters more like those seen in other arctoids. It has a less highly arched palate, a shorter paroccipital process, a smaller hyoid fossa, and a smaller infraorbital foramen. Also, the jugal rims the anteroventral part of the orbit. Some of its other diagnostic characters, however, such as the broad snout, lack of an intercondylar notch, and the more extremely developed mastoid process, are derived relative to *K. clallamensis* and other arctoids. *K. clallamensis* appears to have had a more specialized feeding mode, a more modified rostrum, and greater innervation to the fleshy lips.

Relationships of *Kolponomos* Among the Arctoid Carnivora

In 1960 Stirton compared *Kolponomos clallamensis* extensively with *Allocyon loganensis* Merriam, 1930, from the mid-Arikareean (Oligocene) John Day Formation at Logan Butte, Crook County, Oregon, and concluded that *A. loganensis* was "the carnivore most closely related to *Kolponomos*." Among the 29 features that he delineated, the following similarities seem most informative cladistically: presence of a nasolabialis fossa dorsoanterior to the orbit, short infraorbital canal and large infraorbital foramen with infraorbital fossa, and lack of a postorbital process. With the additional material of *Kolponomos* now available the following can be added: the basioccipital is wide posteriorly, the mastoid process is hypertrophied, and there is a depression anterior to the median lacerate foramen for the first loop of the internal carotid. The latter feature is correlated in *Allocyon* with a deeply excavated lateral margin of the basioccipital for reception of the carotid artery and inferior petrosal sinus, typical of ursids and amphicyonids.

Allocyon (Figs. 13, 14) and *Kolponomos* are similar in the following dental features that appear to represent synapomorphies:

P^4 is triangular in outline with a protocone nearly the size of (*Allodesmus*) or larger than (*Kolponomos*) the paracone; M^2 has a posteriorly expanded "heel" (the metaconule and posterior cingulum), and the M_1 talonid is as wide and long as the trigonid.

All of these features seem to support the close phyletic relationship between *Allocyon* and *Kolponomos*. In many features *Allocyon* is more primitive than *Kolponomos*, especially those that can be interpreted as adaptations to molluscivory in the latter. Since the relationships of *Allocyon* have not been made explicit heretofore, we explore the evidence here as a means of placing *Allocyon* and thus *Kolponomos* within the Carnivora.

The synapomorphies listed above uniting *Allocyon* and *Kolponomos* also support their relationship with basal members of the arctoid clade, especially the amphicyonids and ursids. Particularly important is the presence of the "ursid loop" in which the internal carotid artery is nested in the inferior petrosal sinus (Hunt 1977). This system has a clear bony signature in the deep marginal invagination of the basioccipital. Although this feature cannot be completely seen in *Kolponomos*, it can in *Allocyon*, and it is entirely comparable to the structure in amphicyonids and ursids. A position closer to ursids is supported dentally by loss of M^3, enlargement of the protocone of P^4, and development of a "heel" in M^2 by enlargement of the metaconule and associated posterior cingulum.

Within the Ursidae significant autapomorphies unite the subfamilies Hemicyoninae and Ursinae and exclude *Allocyon* and *Kolponomos*, whose relationships lie near or within the most basal ursoid group, usually referred to as the Amphicynodontinae (Simpson 1945). *Amphicynodon* and *Pachycynodon* are the most completely known taxa (Cirot and de Bonis 1992; Cirot 1992) included in this group. The latter, and larger, form resembles *Allocyon* particularly in its posteriorly extended palate (Fig. 14), but it resembles both *Allocyon* and *Kolponomos* in having a short infraorbital canal, fossa nasolabialis, enlarged infraorbital foramen, and a similarly reduced postorbital process.

Our conclusions about the relationships of *Allocyon* and *Kolponomos* with the primitive ursoids are similar to those postulated for the most primitive pinnipedimorph, *Enaliarctos*, by Flynn et al. (1988), Berta (1991), and Hunt and Barnes (1994, this volume). In cranial morphology *Kolponomos* and *Allocyon* resemble the pinnipedimorphs in having a fossa for the origin of the nasolabialis muscle, a short infraorbital canal, a large infraorbital foramen opening into a fossa, a small optic foramen, and in lacking a postorbital process. Furthermore, in *Kolponomos* the lacrimal is small, fusing early to adjacent bones, and in *K. clallamensis* the maxilla forms the anterodorsal orbital rim. In *Kolponomos* the foramen rotundum has a common opening with the anterior lacerate foramen, the postglenoid foramen is vestigial, the posterior carotid foramen is clearly anterior to the posterior lacerate foramen, and M_3 is absent. Some of these features and others noted in the vertebral column may represent trends parallel to those seen in pinnipeds, especially with respect to aquatic adaptation (e.g., emphasis on the internal jugular drainage of the cranium and thus loss of the postglenoid exit), but the sum total suggests that *Allocyon* and *Kolponomos* represent early offshoots of the same stock that yielded enaliarctine pinnipedimorphs and that both have their roots in the earliest differentiation within the Superfamily Ursoidea.

A more explicit hypothesis of the relationships of *Kolponomos* to other ursoids and pinnipedimorphs can be made by using the

TABLE 3. Distribution of cranial and dental features discussed in the text (0, primitive state; 1, derived state).

	Taxon[a]							
Derived state	AMP	MUS	URS	AMC	PAC	ALL	KOL	ENA
1. Basioccipital excavated laterally	1	0	1	1	1	1	1	1
2. Shallow suprameatal fossa	0	1	1	1	?	0	0	0
3. M^3 absent	0	1	1	1	1	1	1	1
4. Basioccipital wide posteriorly	0	0	1	1	1	1	1	1
5. P^4 large protocone	0	0	1	1	1	1	1	1
6. M^2 with "heel"	0	0	1	1	1	1	1	1
7. M^{1-2} loss parastyle	0	0	1	1	1	1	1	0
8. M^{1-2} loss paraconule	0	0	1	1	1	?	0	0
9. M^1 lingual metaconule	0	0	1	0	1	?	0	0
10. M_2 reduced paraconid	0	0	1	1	1	?	0	?
11. M_2 size metaconid = protoconid	0	0	1	1	1	?	1	?
12. Infraorbital canal short	0	0	0	1	1	1	1	1
13. Infraorbital foramen large	0	0	0	1	1	1	1	1
14. P_4 short metastyle	0	0	0	1	1	1	1	1
15. Palate posteriorly extended	0	0	0	0	1	1	0	1
16. M_1 talonid as wide as trigonid	0	0	0	0	1	1	1	0
17. M_1 metaconid large	0	0	0	0	1	1	1	0
18. Nasolabialis fossa present	0	0	0	0	0	1	1	1
19. Infraorbital fossa present	0	0	0	0	0	1	1	1
20. Mastoid process large	0	0	0	0	0	1	1	0
21. Postorbital process absent	0	0	0	0	0	1	1	1
22. Alisphenoid "strut" present	0	0	0	0	0	0	1	1
23. Postglenoid foramen vestigial	0	0	0	0	0	0	1	1
24. M^2 lingual to M^1	0	0	0	0	0	0	1	1
25. Anterior lacerate foramen and foramen rotundum in common fossa	0	0	0	0	0	0	1	1
26. M_3 absent	0	1	0	0	0	0	1	1

[a] AMP, Amphicyonidae; MUS, Mustelida; URS, Ursinae and Hemicyoninae; AMC, *Amphicynodon*; PAC, *Pachycynodon*; ALL, *Allocyon*; KOL, *Kolponomos*; ENA, *Enaliarctos*.

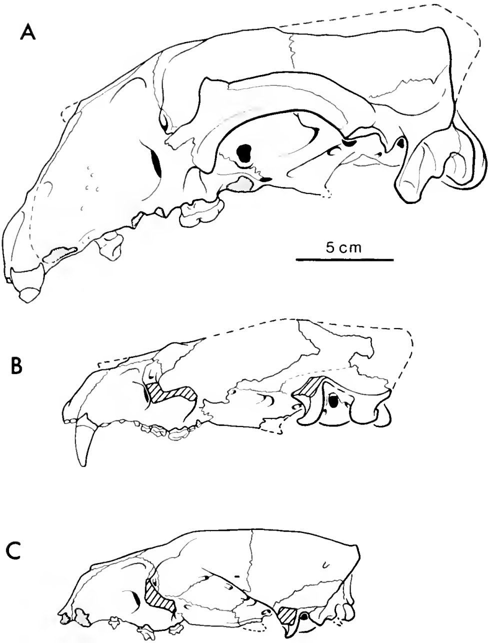

Figure 13. Comparative outline drawings of left side of crania. A, *Kolponomos clallamensis* Stirton, 1960, referred, LACM 131148; B, *Allocyon loganensis* Merriam, 1930, holotype, UCMP 24106, from Merriam (1930: fig. 1); C, *Pachycynodon boriei* (Filhol, 1877), holotype, from Filhol (1877: fig. 59).

sister taxon, the Mustelida (Procyonidae + Mustelidae), and a basal arctoid group, the Amphicyonidae, as outgroups. For this purpose we scored 26 of the binary characters discussed above among eight taxa (Table 3). The taxa are the Amphicyonidae (represented by *Daphoenodon*), Mustelida (represented by the archaic forms *Mustelictis*, *Amphictis*, and *Plesictis*; Schmidt-Kittler 1981), Ursidae (including the hemicyonine *Cephalogale* and the ursine *Ursus*), *Amphicynodon* (mostly *A. typicus*, BM(NH) M7491), *Pachycynodon boriei* (Filhol 1877:pl. 58–60, as *Cynodictis gryei*; Cirot 1992), *Allocyon* (Merriam 1930, UCMP 24106), *Kolponomos* (both species), and *Enaliarctos* (mostly *E. mealsi*, but also data from other species described by Berta 1991). The branch-and-bound algorithm of PAUP (2.4.1) found a single most parsimonious tree (Fig. 15) with a branch length of 36, a consistency index of 0.72, and a retention index of 0.73. Further explanation of the characters used as synapomorphies are as follows:

1. *Basioccipital deeply excavated laterally.*—As Hunt (1977) has shown in living ursids, the large inferior petrosal sinus containing the intracranial loop of the internal carotid artery lies in a deep excavation in the lateral margin of the basioccipital that extends to the posterior lacerate foramen. A morphologically identical structure occurs in the amphicyonids (including the daphoenines), implying a similar vascular pathway and a synapomorphy for the Arctoidea. Amphicynodontids and pinnipedimorphs (*Enaliarctos*; Hunt and Barnes 1994, this volume) retain this feature. Derived pinnipeds and members of the Mustelida lack it.

2. *Shallow suprameatal fossa present.*—All arctoids above the Amphicyonidae show a suprameatal fossa that may be later transformed into a deep pit in the squamosal dorsal to the external auditory meatus or may exist as shallow structures floored by the auditory tube and obliterated in ontogeny by fusion with the meatus (Schmidt-Kittler 1981). A small shallow fossa excavated dorso-

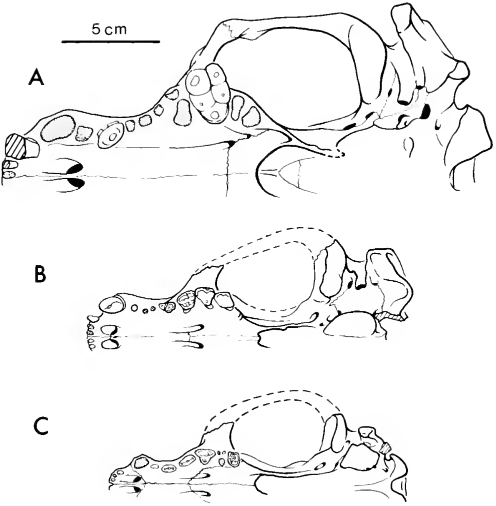

Figure 14. Comparative outline drawings of ventral side of crania. A, *Kolponomos clallamensis* Stirton, 1960, referred, LACM 131148; B, *Allocyon loganensis* Merriam, 1930, holotype, UCMP 24106, from Merriam (1930: fig. 3); C, *Pachycynodon boriei* (Filhol, 1877), holotype, from Filhol (1877: fig. 60).

posteriorly into the squamosal contribution to the mastoid process seems to be the most primitive state of this feature. In ursids and amphicynodontids this structure is shallow primitively and is lost in derived taxa rather than being obliterated by growth of the tubular external auditory meatus.

3. *M^3 absent.*—A feature uniting all arctoids above the Amphicyonidae.

4. *Basioccipital wide posteriorly.*—The greater width of the basioccipital across the posterior lacerate foramen versus its width at the basisphenoid suture is a derived feature of ursids and higher arctoids. This feature was cited by Wyss (1987) as a pinniped synapomorphy, later modified by Berta (1991: table 7, no. 44) to indicate the short and wide basioccipital that describes the condition of pinnipeds above the Otariidae.

5. *Fourth upper premolar with large protocone.*—All ursoids have an upper carnassial with a broad protocone that is usually shelflike because of incorporation of the lingual cingulum. Further enlargement of this cusp in *Kolponomos* relative to the labial cusps is an autapomorphy that serves to "molarize" the carnassial.

6. *Second upper molar with "heel."*—All ursoids have an M^2 that differs from the tribosphenic form of that of other arctoids by the posterior shelf or "heel" formed by a well-developed posterior cingulum, often incorporating the metaconule. This appears to be the case in *Kolponomos* and probably *Allocyon*. Although the M^2 of *Enaliarctos* is very reduced it seems to include a shelflike heel behind the trigon (as in *E. emlongi*; Berta 1991) and so is coded as derived in this feature.

7. *Reduction and loss of parastyle on M^{1-2}.*—Early parastyle reduction and loss is a feature of ursines and hemicyonines. Amphicynodontids lost this cusp later in phylogeny as similarly hypocarnivorous forms (e.g., *Pachycynodon*) arose.

8. *Reduction and loss of paraconule on M^{1-2}.*—Full loss of the paraconule took place at different times in the ursine, hemicyonine, and amphicynodontid lineages, but reduction in the size of this cusp characterizes the early members of all groups. Curiously, *Kolponomos* retains this cusp, inflated like all the molar cusps, to form the broad grinding surface as in another molluscivore, *Enhydra*.

9. *Lingual position of M^1 metaconule.*—The ursid metaconule is strongly connected to the longitudinally elongated protocone in M^1 (and M^2). It has lost its primitive connection with the metacone and occupies a more lingual position on the crown (Cirot and de Bonis 1992). *Amphicynodon* retains a primitively labial position of the M^1 metaconule but this cusp is large and well connected to the protocone by a crista. *Kolponomos* also retains a primitive tribosphenic form of M^1 but all cusps are inflated and lack connecting cristae.

10. *Reduction of paraconid of M_2.*—Modification of M_2 in ursoids involves enlargement of the talonid relative to the trigonid. Reduction and loss of the paraconid accompanies attainment of subequal size of the metaconid and protoconid and their assumption of a more transverse relationship. Again, *Kolponomos* appears to retain a paraconid in its large M_2 trigonid.

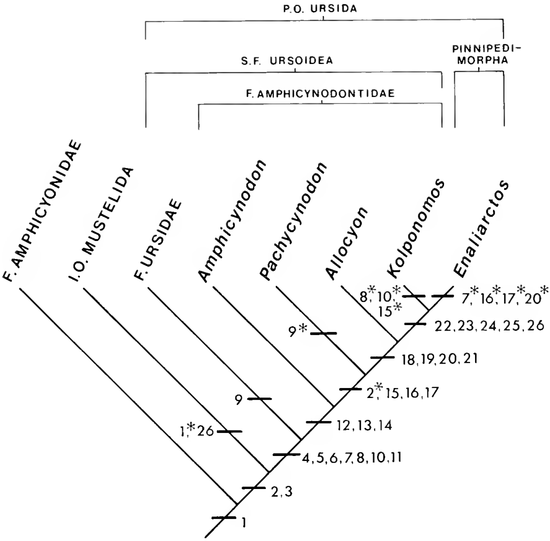

Figure 15. Phyletic relationships of taxa discussed in the text. For character numbers see text and Table 3. Asterisks indicate reversal to primitive state.

11. *Size of metaconid equal to protoconid on* M_2.—The reduction of the trigonid relative to the talonid in the M_2 of ursids and amphicynodontids involves enlargement of the metaconid to the same size as the protoconid.

12. *Infraorbital canal short.*—The distance from the anterior edge of the orbit to the opening of the canal is unusually abbreviated in the amphicynodontid ursoids and pinnipedimorphs.

13. *Infraorbital foramen large.*—Amphicynodontid ursoids and pinnipedimorphs also have a very large anterior opening of the short infraorbital canal.

14. *Metastyle of* P^4 *short.*—In a trend toward hypocarnivory the amphicynodontids shorten the carnassial blade by reduction of the metastyle.

15. *Palate posteriorly extended.*—The palate is prolonged in the midline by posterior extension of the palatine bones so that the internal nares lie at a considerable distance behind the tooth row. This condition is derived in the Ursoidea but has an independent distribution that implies some homoplasy (i.e., it is present in the Ursinae and some amphicynodontids but not in *Kolponomos* or pinnipedimorphs generally).

16. M_1 *talonid as wide as or wider than trigonid.*—Corresponding to modification of the M^1 talon (character 9), amphicynodontids enlarge the talonid of the lower carnassial to accommodate the longitudinal protocone and associated metaconule of M^1.

17. M_1 *metaconid large.*—Modification of the M_1 trigonid more for crushing in derived amphicynodontids involved enlargement of the metaconid relative to surrounding cusps. In volume it comes to match the paraconid and is nearly as high in the unworn crown as the protoconid.

18. *Nasolabialis fossa present.*—A prominent fossa just dorsoanterior to the orbital rim, presumably for the nasolabialis muscle, is a derived condition in *Allocyon*, *Kolponomos*, and primitive pinnipedimorphs. From the perspective of pinniped evolution Berta (1991) coded the loss of this feature in pinnipeds as derived, i.e., a reversal to the primitive arctoid state.

19. *Infraorbital fossa present.*—This broad depression lies just anterior to the opening of the infraorbital canal onto the face. It is not correlated with the large foramen of amphicynodontids but characterizes *Allocyon*, *Kolponomos*, and pinnipedimorphs.

20. *Mastoid process hypertrophied.*—This is a synapomorphy for *Allocyon* and *Kolponomos*, although the latter has greatly elongated the process ventrally. The massive backward-pointing paroccipital process in *Allocyon* is an autapomorphy for that genus.

21. *Postorbital process lacking.*—In contrast to other arctoids, in *Allocyon* and *Kolponomos* the postorbital processes of the frontals are lacking. Low supraorbital ridges at the anterior ends of the parasagittal crests represent the position of the processes in these genera and in primitive pinnipedimorphs (Berta 1991).

22. *Alisphenoid "strut" present.*—A reinforced region extends from the palatine process of the alisphenoid dorsoanteriorly to a correspondingly reinforced pterygoid process of the palatine. These elements combine to form a strut bracing the posterior part of the palate against the braincase. Such a structure is present in *Kolponomos* and pinnipedimorphs.

23. *Postglenoid foramen vestigial.*—Reduction of this opening is correlated with greater emphasis on the internal jugular system as the main venous drainage of the braincase. Although the posterior lacerate foramen in *Kolponomos* is not conspicuously enlarged, the postglenoid foramen is very reduced as in pinnipedimorphs.

24. *M^2 lingual to M^1.*—A peculiar feature of the dentition of pinnipedimorphs (and *Potamotherium*) that retain M^2 is the lingual position of this tooth adjacent to the talon of M^1 rather than labial as in most carnivores (M. Wolsan, pers. comm.). *Kolponomos* shows this feature.

25. *Foramen rotundum and anterior lacerate foramen lie in a common fossa.*—Berta (1991) discussed the distribution of this pinnipedimorph synapomorphy. It also clearly occurs in *Kolponomos*, but other amphicynodontids have the primitive state in which these foramina are separated by a bony lamina visible in lateral view of the skull.

26. *M_3 absent.*—As in pinnipedimorphs this tooth is absent in *Kolponomos*.

Figure 15 summarizes the distribution of these synapomorphies, indicating the paraphyly of the Amphicynodontidae when the Pinnipedimorpha (sensu Berta 1991) are placed within this group as the sister taxon of *Kolponomos*. Some of the characters thought to be synapomorphies of the Pinnipedimorpha by Berta (1991) actually have a wider distribution (e.g., characters 13, 21, 23, 25, and 26) within the Ursoidea or have ursoid precursor states (character 4). Synapomorphies specifically linking the Pinnipedimorpha with *Allocyon* and *Kolponomos* (characters 18, 19, and 21–26) indicate that these terrestrial and amphibious arctoids, although dentally specialized for hypocarnivory, approximate the stem group for the pinnipedimorphs.

A classification consonant with the phyletic relationship postulated for the carnivorans discussed above is indicated in Figure 15. The Pinnipedimorpha were not ranked by Berta (1991) and are so indicated on Figure 15 as an unranked taxon within the parvorder Ursida of Tedford (1976). Since the traditional "suborder" Pinnipedia is subsumed in the Pinnipedimorpha it too must remain unranked in the present attempt to construct a taxonomy that expresses the phylogenetic conclusions of this paper.

Speculations About the Mode of Life of *Kolponomos*

The few postcranial bones presently known indicate that *Kolponomos* was not fully aquatic, at least in the sense that the pinnipeds are. Its foot bones clearly indicate retention of significant ability for terrestrial locomotion and an amphibious existence. It was probably littoral in distribution. All known specimens are from near-shore, shallow-water marine deposits that contain abundant fossil mollusks, including large mussels and giant pectinids. The broad, sea-otterlike crushing cheek teeth would have been ideally suited to a diet of hard-shelled marine invertebrates. The teeth are well worn, indicating that the diet included very hard-shelled animals, possibly mussels, limpets, abalone, pectinids, and echinoids. Coupled with accidentally ingested abrasive sediment, these would account for the heavily worn condition of the cheek teeth. The orbits are directed anteriorly rather than laterally as in living bears, suggesting that *Kolponomos* probably could view objects directly in front of its head. This would be of benefit to an animal selectively eating rock-dwelling benthic or attached (sessile) marine invertebrates. The infraorbital foramen is large, quite so in *K. clallamensis*, and the mental foramina on the lateral side of the dentary of *K. newportensis* are also large. These probably indicate enhanced tactile sensitivity of the lips and muzzle. *Kolponomos* might also have had a large upper lip approaching that in living walruses, and this would be concomitant with the depth of the premaxilla between the incisors and the narial opening. Walruses have very sensitive lips and tactile vibrissae that apparently aid in distinguishing prey items when visibility is poor (Fay 1982). *Kolponomos* might also have had highly developed tactile vibrissae. The palate is flexed downward relative to the basicranial plane; the occipital condyles face ventrally and are positioned posteroventrally relative to the basicranium, suggesting that the head was carried downward in relation to the vertebral column. The upper canine and incisor teeth are large and clustered in thickened bone at the extreme anterior end of the downturned snout. The nasal opening is retracted posteriorly, an adaptation that would keep the nostrils away from the substrate. Large paroccipital and mastoid processes indicate powerful neck muscles that could have provided strong downward movements of the skull. All these adaptations suggest that *Kolponomos* fed on epifaunal marine invertebrates living on rocky substrates. *Kolponomos* probably obtained its food by levering tightly clinging animals off the substrate and twisting and prying with its head. The robust median phalanx also suggests that the digits were capable of powerful movement and these too may have been used to procure food. This method of feeding is somewhat different from that of living sea otters. Sea otters actively swim in shallow to moderate depths and obtain bottom-dwelling animals, largely by pulling and prying them off rocks with their forelimbs. Sea otters have relatively long digits and strong forelimb musculature. They have large, flat, crushing cheek teeth, but they do not have enlarged mastoid and paroccipital processes. This correlates with the fact that they do not pull their food off rocks by using their heads.

Kolponomos also is unlike the living walrus, which belongs to a pinniped group that later in the Tertiary became very diverse, successful, and widespread along the coasts of the northern hemisphere. Modern walruses occupy shorelines, at least part of the time, when they haul out at specific locations along the shore. When feeding, however, they are offshore, diving pinnipeds. They typically dive only to shallow or moderate depths, where they exploit food resources for the most part different from those of other pinnipeds, mostly benthic shelled and nonshelled invertebrates. They do not crush mollusk shells by chewing (Fay 1982) but rather use the tongue in a pistonlike method to suck the soft parts out of gaping bivalve shells. They also use the tongue as a piston to direct a jet of water from the mouth onto the substrate in a method of hydraulic mining of infaunal prey. Walruses do not chew up shells of their prey and they do not swallow shells or broken shells, so, although the general category of food of walruses is the same as that proposed for *Kolponomos*, the locating of the food and manner of gathering and eating it is apparently different.

The specialized dusignathine otariid *Gomphotaria pugnax* may be a relatively close functional counterpart to *Kolponomos*. This large pinniped is known from upper Miocene rocks of the California coast. Like *Kolponomos*, *Gomphotaria* had elongated upper as well as lower canines, even more fully developed as tusks. Also like *Kolponomos*, *Gomphotaria* had large cheek teeth, which although not expanded transversely were broken and worn during life from feeding on resistant prey. Barnes and Raschke (1991) proposed that *Gomphotaria* was a shallow-water or littoral pinniped that pried its food off rocks, the food presumably being shelled mollusks as we have postulated for *Kolponomos*, and that rather than sucking its food into the mouth it crushed the animals with the cheek teeth.

Kolponomos appears to be an ursid variation on the sea otter adaptation. On the west coast of North America, middle and upper Miocene horizons bearing fossil marine vertebrates have been extensively prospected, much more extensively than have the lower Miocene deposits. Nothing related to *Kolponomos* has as yet been found in these younger deposits. *Kolponomos* might very well be the end of its lineage.

ACKNOWLEDGMENTS

We thank Albin Zukofsky, II, for his donation of the important skull of *Kolponomos clallamensis* from Clallam Bay. We thank Robert L. (Fritz) Clark for preparing and casting this new skull. The photographs of the specimen were made by LACM staff photographer Donald Meyer. We thank Donald E. Savage and J. Howard Hutchison for making the holotype of *Kolponomos clallamensis* available for our work. We thank Jim Goedert for making observations relating to the collecting sites of the holotype and referred specimens of *Kolponomos clallamensis*, for making notes on the stratigraphy, and for analyzing the associated mollusks to make inferences about the paleoecology. The holotype of *Kolponomos newportensis* was collected by the late Douglas Emlong in two fragments of one concretion, found on separate occasions more than six years apart. Emlong recognized that the second, major part pertained to the first, minor one, even though the latter had no intelligible bone showing and had not been seen by him for several years. Assembly of the broken concretion containing the type of *K. newportensis* and gross preparation, including separation of the jammed mandible and skull and loose teeth, was done by Gladwyn B. (Tut) Sullivan. Final preparation of the type specimens of *K. clallamensis* and *K. newportensis* was skillfully done by Edward Pedersen of the American Museum of Natural History. Photographs of these specimens and line drawings were carefully prepared by Chester Tarka and Lorraine Meeker of the American Museum. Xiaoming Wang helped with the PAUP analysis of phylogeny.

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Pinniped Phylogeny

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ABSTRACT.—In our view, presentations inferring pinniped diphyly provide inadequate evidence of "otarioid" monophyly and inadequate evidence that phocids are related to some nonpinniped group. The integrated assessment of higher-level pinniped relationships presented here, based on cranial, postcranial, and soft-anatomical characters from most living and adequately known fossil pinnipeds, supports pinniped monophyly. We scored more than 150 character transformations on a generic-level character matrix and used a computer parsimony algorithm (PAUP) to construct a maximally parsimonious phylogenetic hypothesis for the group. Its major outlines are as follows: (*Enaliarctos* (*Pteronarctos* (Otariidae (Odobenidae (*Pinnarctidion*, *Desmatophoca*, *Allodesmus* (Phocidae))))). Internally, the data are highly consistent. Convergence is much less pervasive than generally assumed, with reversals being the dominant pattern of homoplasy.

INTRODUCTION

Few mammalian examples more forcefully illustrate the impact of phylogenetic systematic methods on notions of a particular group's evolutionary history than does the case of the pinnipeds. Recent cladistic studies have addressed questions of relationships within the otariids (fur seals and sea lions) (Berta and Deméré 1986) and phocids (true seals) (Muizon 1982a; Wyss 1988b), odobenid (walrus) affinities (Wyss 1987), and the placement of certain archaic fossil taxa (Wyss 1987; Berta et al. 1989; Berta 1991). The net result of these efforts is a concept of pinniped relationships drastically different from what was generally accepted until relatively recently. We outline here the novel aspects of these recent proposals and present their methodological basis. In addition to providing new information on the distribution of morphological characters, we combine and revise the data sets of these previous studies in an attempt synthesize what we regard to be the currently best supported hypothesis of pinniped relationships. We present the evidence for this hypothesis in the form of a taxon–character matrix in hopes that it may serve as a starting point for future phylogenetic analyses of pinnipeds. If this matrix generates debate about character coding, or discussion over the in- or exclusion of certain characters in the analysis, or if it inspires the examination and description of additional characters that either support or refute the relationships we favor, in short, if it evolves, it will have served its purpose.

HISTORICAL CONSIDERATIONS

All recent workers agree that pinnipeds are members of a carnivoran subclade, the Arctoidea, that includes among terrestrial lineages mustelids, ursids, and procyonids (Tedford 1976). Controversy about relationships among the major groups of pinnipeds centers on the relationship of phocids to the rest of the Arctoidea. This disagreement reduces to two fundamental questions of monophyly. Before we consider these (to eliminate possible ambiguity) we must define our usage of "monophyly." We use the term (sensu Hennig 1966) to denote a group of taxa derived from a common ancestor and including all of the descendants of that common ancestor. Evidence for monophyly of a particular group consists of the shared possession of evolutionary novelties (synapomorphies) by its members. The two central questions concerning the phylogenetics of "fin-footed" arctoids are (1) is the group as a whole descended from an exclusive common ancestor? (i.e., are pinnipeds monophyletic?) and (2) do pinnipeds excluding phocids have a common ancestor not also shared by phocids? (i.e., are the Otarioidea, defined as the Otariidae and Odobenidae plus certain extinct forms, monophyletic?) (Fig. 1).

The question of single versus multiple origin(s) dates from Mivart's (1885) suggestion that the group's origin was likely compound, with sea lions and walruses derived from ursids and true seals derived from mustelids, otters in particular (Fig. 1B). Although this view was dismissed by several workers over the next half century (e.g., Weber 1904; Gregory 1910), it was not discounted altogether by others (e.g., Kellogg 1922; Howell 1929; Simpson 1945). Thereafter, the notion of multiple pinniped origins regained wide support in the morphological and paleontological literature (McLaren 1960; Tedford 1976; Muizon 1982a,b), a shift influenced particularly by the detailed descriptions of the fossil taxa *Potamotherium* (Savage 1957) and *Enaliarctos* (Mitchell and Tedford 1973). More recently, one of us argued, on the basis of anatomical criteria, in favor of a return to the single-origin interpretation (Wyss 1987) (Fig. 1A), a conclusion consistent with but independent of certain biomolecular and cytologic results (Fay et al. 1967; Arnason 1986; de Jong 1982, 1986). Several subsequent studies (Flynn et al. 1988; Berta et al. 1989; Wyss 1988, 1989) have yielded additional evidence supporting this conclusion, but it continues to engender debate (Wozencraft 1989; Repenning 1990; Bonner 1990).

The second question concerns the phylogenetic validity of the Otarioidea. Since their recognition as distinct groups of mammals, otariids and odobenids have nearly universally been regarded as being more closely related to each other than either is to some third taxon. The observation that the walrus is in many respects more nearly intermediate between otariids and phocids than had been previously appreciated (Fay et al. 1967) signaled an important break from this view. The argument that odobenids are related more closely related to phocids than to otariids took this suggestion one logical step further (Wyss 1987). This proposed phocid–odobenid linkage opened the broader question of where this pair should be placed relative to the other arctoids. Either a special link between mustelids and phocids (plus now odobenids) could continue to be recognized (rendering the Otarioidea polyphyletic), or the association of phocids and odobenids could be recognized within the context of a monophyletic Pinnipedia (rendering the Otarioidea paraphyletic). Thus the questions of otarioid and pinniped monophyly are to some degree interwoven, yet if care is taken both may be evaluated with considerable independence.

To two phylogenetic questions, are pinnipeds monophyletic and are otarioids monophyletic, there are four alternative pairs of responses. All except one of these have recent historical precedent: affirmative, affirmative (no recent proponents); affirmative, negative (Fig. 1A) (Wyss 1987; Berta et al. 1989; Flynn et al. 1988; Wyss and Flynn 1993); negative, negative (Mitchell and Tedford

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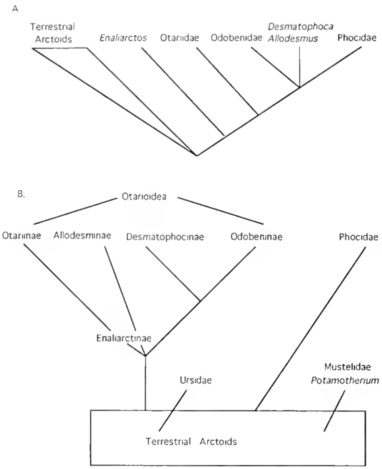

Figure 1. Two competing hypotheses regarding phylogenetic relationships among pinnipeds. A. Current view of pinniped monophyly proposes common ancestry for all pinnipeds from a terrestrial arctoid and supports a sister-group relationship between walruses, seals, and their extinct relatives (Wyss 1987; Berta et al. 1989; Flynn et al. 1988). B. Alternative view of otarioid monophyly proposes independent origins of otarioid and phocid lineages from different terrestrial artcoid groups and supports a sister-group relationship between walruses, sea lions, and their supposed fossil relatives (Barnes 1989, and others).

1973: 205, 278); negative, affirmative (Fig. 1B) (Barnes 1989; Wozencraft 1989; Repenning et al. 1979). We begin with the otarioid question because in some senses it is less complex and easier to address in isolation. We emphasize again that to test the hypothesis of otarioid monophyly apart from the question of pinniped monophyly we must restrict our attention to those derived features characteristic of otarioids not also occuring in phocids.

OTARIOID MONOPHYLY

Were pinnipeds demonstrably polyphyletic both the otarioids and phocids could be diagnosed with characters each shares but acquired independently. But because we view otarioid monophyly as a hypothesis in legitimate need of testing we regard claimed otarioid synapomorphies occurring also in phocids as questionable, at least for the initial part of the analysis.

Barnes (1989: fig. 9) presented the most recent, most detailed, and, so far as we are aware, only nominally cladistic diagnosis of the Otarioidea (= his Otariidae). He listed on a branching diagram 20 characters diagnostic of the Otarioidea.

Following the procedure of Wible (1991), we evaluated these 20 features, grouping them as follows: (1) characters for which the reported derived state occurs in relevant outgroups (i.e., nonpinniped Arctoidea) and are therefore primitive and phylogenetically uninformative, (2) characters for which the derived state occurs also in phocids and thus are of uncertain value, (3) characters dubiously described, and (4) characters for which descriptions and distribution are correct but for which we offer comment. Characters are labeled with letters corresponding to the order in which they were listed by Barnes (1989: fig. 9) at node 1, the basal node of his branching diagram.

Barnes' otarioid "synapomorphies" occurring also in relevant outgroups.—The derived state of the following characters occurs elsewhere among the Arctoidea and thus represents a level of generality broader than supposed by Barnes (1989).

(a) Neck lengthened. Wyss (1987: 11) discussed previously problems associated with this character. Even if it did characterize otarioids primitively (among odobenids, it doesn't characterize at least *Odobenus*, the only odobenid for which this character can currently be scored), it is not a derived feature among the Carnivora (Bisaillon et al. 1976).

(e) Foramen ovale and posterior opening of alisphenoid canal joined in an elongated recess. The arrangement in ursids is identical (Davis 1964) and almost certainly represents the ancestral condition of the Arctoidea.

(h) Embayment formed in lateral edge of basioccipital for loop of median branch of internal carotid artery. This character is well known in ursids (Hunt 1974) and amphicyonids (Hunt 1977) and is unquestionably derived at a level broader than the Otarioidea. Although this embayment is absent in all living pinnipeds, in certain phocids (e.g., *Monachus*) sharp crests on the dorsal surface of the basioccipital may represent an osseous vestige of it.

(j) Basal whorl of cochlea directed posteriorly. As discussed by Wyss (1987), this condition characterizes all therian mammals except phocids, which are uniquely specialized in having a more transversely oriented basal whorl.

(l) Auditory ossicles not enlarged. This feature is obviously primitive; the derived condition (ossicles enlarged) originated three times among otarioids according to Barnes' scheme and again (presumably independently) in phocids (see below under Assessing the Pattern of Homoplasy).

(m) Entotympanic restricted to medial part of bulla around carotid canal. This condition corresponds to the type "A" bulla of Hunt (1974), which characterizes ursids, some amphicyonids, some mustelids, and perhaps arctoids ancestrally. It is not uniquely diagnostic of otarioids and is therefore not relevant to the question of otarioid monophyly.

(n) Internal acoustic meatus round. A round internal auditory meatus is widespread among terrestrial carnivorans and is unquestionably primitive at the level suggested here. The partially or completely divided condition seen in certain "otarioids" and phocids is derived (see discussion of character 24 in analysis below). The meatus is not round in odobenids, *Pinnarctidion*, *Desmatophoca*, or *Allodesmus*.

(p) Bony tentorium in braincase closely appressed to dorsal surface of eminence containing semicircular canals and floccular fossa. As discussed by Wyss (1987: 24), this is the typical carnivoran condition and is undoubtedly primitive. Because the bony tentorium varies widely among the Carnivora (Nojima 1990: table 2) and is difficult to identify, we excluded it from our analysis.

Barnes' otarioid "synapomorphies" that occur also in phocids.—The derived state of the following characters occurs also in phocids, a group not included in Barnes' (1989) analysis.

(b) Proximal limb elements shortened. Phocids have previously been recognized as possessing short proximal limb bones (Weber 1904; Howell 1929), and this character has been identified at a more general level, the Pinnipedimorpha, comprising all pinnipeds plus *Enaliarctos* (Berta et al. 1989).

(c) Maxilla forms part of wall of orbit. Wyss (1987) reported that the derived state in which the maxilla makes a significant contribution to the medial orbital wall and forms the anterior orbital rim also occurs in phocids.

(d) Foramen rotundum and anterior opening of alisphenoid canal combined into one large orbital fissure. Barnes' diagram fails to indicate that *Pinnarctidion* and *Desmatophoca* are exceptions. Phocids also share this derived condition (see discussion of character 19, Appendix 1).

(f) Sphenopalatine foramen enlarged. This derived state also occurs in phocids (see character 12, Appendix 1).

(g) Petrosal isolated from surrounding cranial bones. Repenning (1972) discussed this feature as occurring in phocids also. We have not analyzed it because of the difficulty of quantifying it. We observe only subtle differences in this feature among pinnipeds and terrestrial carnivorans.

(o) Posterior lacerate foramen enlarged, not expanded transversely. The posterior lacerate foramen is enlarged in all phocids as well. In some, however, it is also expanded transversely, but this is apparently a secondary transformation. The condition likely primitive for phocids (e.g., that seen in *Monachus*) is indistinguishable from the supposed "otarioid" condition.

(q) Postglenoid foramen reduced. Phocids are also characterized by having reduced or lost the postglenoid foramen (see character 40, Appendix 1).

(r) Entepicondylar foramen lost from humerus. An entepicondylar foramen is variably present among phocids. From a previous phylogenetic study of the group (Wyss 1988) and our present analysis, presence of this foramen in phocines and most early fossil "monachines" is probably secondary for the group.

(s) Olecranon process of ulna enlarged. As illustrated by Howell (1929: fig. 10), phocids possess a condition of the olecranon process similar to that seen in otariids and odobenids.

Barnes' description dubious.—(k) Head lost from incus. The loss of a head on the incus presupposes that a head was once present, which to us seems highly unlikely. By comparison with the outgroups identified here, the head on the incus is a phocid autapomorphy, absent in all other carnivorans.

Barnes' (1989) descriptions require modification.—(i) Mastoid process large and cubic. The size and shape of the mastoid process in nonphocid pinnipeds is not significantly changed over the condition in ursids. Wyss (1987) critiqued the use of this feature at greater length.

(t) Aquatic propulsion by fore- and hindlimbs, principally the forelimbs. Living pinnipeds swim in two different ways. Otariids generate propulsion principally by use of the forelimbs, whereas phocids and odobenids use principally the hindlimbs (English 1976; Gordon 1981, 1983). It has been argued that the ancestor of pinnipeds (or even the ancestor of "otarioids," if this group should prove monophyletic) likely generated propulsion by using all four limbs, as *Enaliarctos* probably did (Berta et al. 1989). This argument applies equally to the ancestor of phocids even if they are not related to other pinnipeds. That some distant ancestor of phocids was a four-limb swimmer is indicated by the phocids' forelimbs' being highly modified (used in steering) despite their propelling themselves by the hindlimbs. If phocids had evolved hindlimb swimming directly from a terrestrial ancestor, the forelimbs should not be as highly transformed as they are.

In summary, Barnes' analysis does little to bolster the case for otarioid monophyly; indeed, it fails to reveal a single persuasive synapomorphy for the group. We recognize that a proposed otarioid synapomorphy is not automatically invalidated by its appearance in phocids. Plausibly, the Phocidae and "Otarioidea" could be diagnosed with some of the same (convergently acquired) characters, provided that additional characters demonstrated a phylogenetic separation between the two groups.

Historically, the assumed linkage between phocids and mustelids provided this separation, but, as discussed below, recent reviews of characters previously cited in support of this pairing call it into question. The weakness of the evidence supporting the relationship of one pinniped subgroup (phocids) to a terrestrial arctoid lineage (mustelids) to the exclusion of other pinnipeds (a requisite for the acceptance of convergence between otarioids and phocids) leads us to dismiss at least initially apomorphies occurring in both "otarioids" and phocids as necessarily indicating "otarioid" monophyly. Certain "otarioid" synapomorphies might represent convergences; however, we fail to see the logic of accepting this claim in the absence of phylogenetic evidence substantiating a linkage of phocids to some terrestrial lineage of arctoids.

Citing Repenning and Tedford (1977), Wozencraft (1989: 516) argued that there are "many" synapomorphies supporting a walrus–otariid clade, yet he did not list a single shared derived feature in support of this contention. Of the 11 features listed as diagnostic of otarioids in the earlier study, all are primitive or of otherwise unclear phylogenetic significance (Wyss 1987). Thus neither Barnes' nor Wozencraft's analyses identify synapomorphies corroborating otarioid monophyly.

PINNIPED MONOPHYLY

Before addressing the question of pinniped monophyly, we first examine the recent arguments in favor of pinniped diphyly. Acceptance of pinniped diphyly requires that two criteria be satisfied: evidence of otarioid monophyly and evidence that phocids are related to some nonpinniped terrestrial group. We concluded in the previous section that otarioid monophyly was not well founded. With respect to the second question, Wyss (1987) reviewed the characters used by Tedford (1976) and Muizon (1982a) to unite phocids and mustelids, concluding that no strong case could be made for a mustelid–phocid pairing. Wozencraft (1989) argued in favor of a mustelid–phocid link but did not discuss the synapomorphies supporting nodes on his maximally parsimonious trees.

To consider all possible pinniped–terrestrial arctoid pairings we include as outgroups the Ursidae, Mustelidae, Procyonidae, and extinct Amphicyonidae. The monophyly of these groups is generally accepted (Flynn et al. 1988). Principal references for these taxa are as follows: Amphicyonidae, Hunt (1974), Hough (1948); Ursidae, Davis (1964), Beaumont (1965); Mustelidae, Savage (1957), Schmidt-Kittler (1981); Procyonidae, Baskin (1982), Wozencraft and Decker (1991).

METHODS AND MATERIALS

Our assessment of relationships among pinnipeds relies upon outgroup comparison. Flynn et al. (1988) reviewed the relationship of pinnipeds to other arctoids, proposing two principal hypotheses: pinnipeds as the sister group of ursids and pinnipeds as part of a polytomy with other arctoid families. Berta (1991) used the Ursidae and the Amphicyonidae as the first and second outgroups to pinnipedimorphs on the basis of their retaining the excavated bassioccipital and presumed loop of the internal carotid artery, a synapomorphy (see Hunt and Barnes 1994, this volume). It is worth mentioning that no extant pinnipeds have the internal carotid loop, and the excavated basioccipital, most extreme in *Enaliarctos*, is presumably lost. Fortunately, strong postcranial evidence that *Enaliarctos* is related to pinnipeds supports the presumed loss of this feature at the level of the Pinnipedia. Proponents of both di- and monophyly must accept this loss. Thus this feature can in no way be judged to favor a monophyletic Otarioidea. Four synapomorphies link ursids and pinnipedimorphs: (1) shelflike anteromedially placed P^4 protocone, (2) narrow M^1 with longitudinally elongated protocone (Flynn et al. 1988), (3) knoblike acromion process of scapula, and (4) robust olecranon process on ulna (Berta 1991). Wyss and Flynn (1993) used similar evidence to support a sister-group relationship between the Ursoidea (defined as the common ancestor of ursids and amphicyonids plus all of its descendants) and the Pinnipedia.

In addition to living representatives of the three pinniped families, we include, as terminal taxa, their extinct relatives and indicate their degree of completeness (Table 1). With two exceptions the monophyly of these taxa is generally accepted. On the basis of comparative anatomical evidence Wyss (1988) questioned the monophyly of "*Monachus*" (indicated by quotes). Berta (1991) recognized *Enaliarctos* as a metataxon [term formulated by Gauthier (1986); see also Gauthier et al. (1988) and Donoghue (1985)] since there is no unambiguous evidence supporting either its monophyly or paraphyly. Initially we included all fossil taxa and in later runs of the data selectively removed them to determine their effect on the tree.

PAUP ANALYSIS

We scored 143 skeletal character transformations on a taxon–character matrix (Table 2). Of these characters, 73 were craniodental (64 binary and 11 multistate), 52 were postcranial (48 binary and 4 multistate), and 15 were soft anatomical. Some 160 character transformations were possible.

We subjected the data to Swofford's (1991) computer algorithm PAUP, version 3.0s, using the heuristic search option. In all runs multistate characters were entered as unordered. In the initial PAUP run eight characters, 8, 13, 37, 47, 63, 74, 82, and 138, were excluded since they could not be unambiguously polarized. Our initial PAUP analysis considering all fossil taxa resulted in over 100 most parsimonious trees. Principal differences among the 100 trees were in the position of poorly known odobenids including *Alachtherium*, *Dusignathus*, *Pliopedia*, and *Pontolis*. Later analyses excluded these taxa, including only those at least 53% complete. We obtained the same result, 100+ most parsimonious trees. Each cladogram had a branch length (BL) of 239, a consistency index (CI) of 0.640, and a rescaled consistency (RC) index of 0.554. The RC excludes autapomorphies from the analysis as well as totally homoplastic characters (see Wiley, et al. 1991). A strict-consensus tree is presented in Fig. 2.

TABLE 1. Completeness of fossil taxa studied as a percentage of the number of characters scored (Appendix 1).

	Percentage Complete	
Taxon	Cranial	Postcranial
Enaliarctos	93	78
Pteronarctos	94	0
Thalassoleon	93	71
Imagotaria	91	60
Aivukus	77	33
Desmatophoca	90	0
Allodesmus	86	93
Pinnarctidion	53	0
Piscophoca	77	58
Acrophoca	60	73
Homiphoca	90	45
Gomphotaria	63	45
Alachtherium	16	0
Pontolis	23	0
Pliopedia	0	24
Prorosmarus	4	0
Dusignathus	26	0

DISCUSSION

Pinniped monophyly is supported by diverse anatomical data. We discuss below the major groupings shown in Fig. 2. The various characters are numbered as in Appendix 1. Diagnostic characters for the nodes and terminal taxa in Fig. 2 are listed in Appendix 2.

Pinnnipedimorpha

Berta et al. (1989) proposed the name Pinnipedimorpha as a term for the monophyletic group including *Enaliarctos* and the Pinnipediformes. Postcranial (Berta and Ray 1990) and cranial features (Berta 1991) have been used to diagnose the group (Table 2, Figs. 3–5). We recognize 18 unequivocal characters and 6 equivocal characters diagnosing the Pinnipedimorpha. Among unequivocal synapomorphies are 10 craniodental features: (11) infraorbital foramen large (Fig. 3), (15) anterior palatine foramina anterior of maxillary–palatine suture, (25) round window large with round window fossula developed, (27) basal whorl of scala tympani enlarged, (40) postglenoid foramen vestigial or absent, (43) jugular foramen enlarged, (48) processus gracilis and anterior lamina of malleus reduced, (66) M^{1-2} reduced in size relative to premolars, (67) M^{1-2} cingulum reduced or absent, and (72) M_1 metaconid reduced or absent.

Unequivocal postcranial synapomorphies of pinnipedimorphs include structural details of the flippers such as (87) greater and lesser humeral tuberosities enlarged (Fig. 4), (88) deltopectoral crest strongly developed (Fig. 4), (90) humerus short and robust, (92) olecranon fossa shallow, (98) digit I on the manus emphasized (Fig. 4), (105) digits I and V on the pes emphasized (Fig. 5), (110) ilium short, and (118) and femoral condyles strongly inclined medially.

An additional 16 equivocal synapomorphies might be diagnostic of this clade but are subject to equally parsimonious alternative distributions. Seven of these characters, not preserved in *Enaliarctos*, we assigned to the less inclusive level of the Pinnipedia: (31) cochlear aqueduct large, (49) middle ear cavity and external auditory meatus with distensible cavernous tissue, (54) deciduous teeth fewer, (60) number of lower incisors reduced, (101) metacarpal 1 longer than metacarpal II, (103) foreflipper claws short, and (104) manus, digit V, intermediate phalanx strongly reduced.

The oldest known pinnipedimorph, *Enaliarctos*, described on the basis of crania and isolated teeth (Mitchell and Tedford 1977; Barnes 1979), is now known from a nearly complete skeleton collected from the late Oligocene or early Miocene Pyramid Hill Sandstone Member of the Jewett Sand in central California (Berta et al. 1989; Berta and Ray 1990). Other crania and associated lower jaws and postcranial elements referred to this taxon are described from deposits of similar age in coastal Oregon (Berta 1991).

Pinnipediformes

The name Pinnipediformes encompasses the ancestor of *Pteronarctos* and all its other descendants, the Pinnipedia. This group can be diagnosed on the basis of 14 characters, two of which are unequivocal: (14) embrasure pit on palate between P^4 and M^1 shallow to absent and (24) mastoid process close to paroccipital process, the two connected by a high continuous ridge (state 1 of multistate character).

TABLE 2. Distribution among pinniped taxa and relevant outgroups of characters scored. Numbers in heading correspond to numbers of characters in Appendix 1. 0, Ancestral state; 1, 2, and 3, derived states; ?, character missing or not preserved.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Amphicyonidae	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0
2	Mustelidae	0	0	0	0	0	1	0	1	0	0	0	0	0/1	0	0	0	0	0	?	0/1	0	0	0	0
3	Procyonidae	0	0	0	0	0	1	0	1	0	0	0	0	0/1	0/1	0	0	0	0	?	0	0	0	0	0
4	Ursidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Enaliarctos	0	0	0	0	0	1	0	0	?	?	1	0	0	0	1	0	1	0	1	0	0	0	0	0
6	Pteronarctos	0	0	1	0/1	0	1	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	0	0	1
7	Arctocephalus	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	3	0	1	0	0	0	0	1
8	Callorhinus	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	3	0	1	0	0	0	0	1
9	Otariinae	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	3	0	1	0	0	0	0	1
10	Thalassoleon	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	3	0	1	0	0	0	0	1
11	Aivukus	0	0	1	0	0	1	1	?	1	1	1	0	0	1	?	1	2	0	1	0	0	0	0	1
12	Alachitherium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Dusignathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
14	Gomphotaria	?	?	0	?	?	?	1	1	1	1	1	1	0	1	1	1	0	0	?	0	0	0	0	?
15	Imagotaria	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	2	0	1	0	0	0	0	1
16	Odobenus	1	0	2	0	0	1	1	1	1	1	1	1	0	1	1	1	2	0	1	0	0	0	0	1
17	Pliopedia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Pontolis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	1
19	Allodesmus	1	1	0	0	1	2	1	1	1	1	1	0/1	1	1	1	0	1	0	1	0	0	1	0	2
20	Desmatophoca	1	1	0	0	1	2	1	1	1	1	1	0	1	1	1	0	1	0	1	0	0	1	0	2
21	Pinnarctidion	?	?	?	?	?	2	0	1	?	1	1	?	1	1	?	0	1	0	0	0	0	1	0	2
22	Acrophoca	?	?	?	?	1	1	?	1	?	?	?	?	1	1	?	0	2	0	?	1	?	?	1	2
23	Cystophora	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	?	2	1	1	1	1	1	1	2
24	Erignathus	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	1	1	1	1	2
25	Homiphoca	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	2	0	?	1	0	?	1	2
26	Lobodontini	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	1	0	1	1	2
27	Mirounga	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	1	0	1	1	2
28	"Monachus"	1	0/1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	2	0	1	1	0	1	1	2
29	Phocini	1	0/1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	2	1	1	1	1	1	1	2
30	Piscophoca	1	?	0	0	1	1	1	1	1	1	1	?	1	1	1	0	2	0	?	1	?	?	1	2

		25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
1	Amphicyonidae	?	?	?	?	0	0	?	?	0	0	0	0	?	0	0	0	0	0	0	?	?	?	?	0
2	Mustelidae	0	?	?	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Procyonidae	0	?	?	0	0	?	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0
4	Ursidae	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	1	0
5	Enaliarctos	1	0	1	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
6	Pteronarctos	1	0	1	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
7	Arctocephalus	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
8	Callorhinus	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
9	Otariinae	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
10	Thalassoleon	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	?	?	?
11	Aivukus	1	?	?	0	0	1	?	?	0	1	0	0	1	0	0	1	0	1	1	0	0	?	?	?
12	Alachitherium	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Dusignathus	?	1	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Gomphotaria	?	?	?	0	?	1	?	?	0	?	?	0	0	0	0	1	?	?	?	0	?	?	?	?
15	Imagotaria	1	1	1	0	0	1	?	?	0	1	0	0	1	0	0	1	0	1	1	0	0	1	?	1
16	Odobenus	1	1	1	0	0	1	1	1	0	1	0	0	1	0	0	1	0	1	1	0	0	1	1	1
17	Pliopedia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Pontolis	?	1	?	0	?	1	?	?	0	1	0	0	1	0	?	1	0	1	1	0	0	?	?	?
19	Allodesmus	1	1	1	0	?	1	?	?	0	1	1	0	1	?	2	1	0	1	1	0	1	1	1	?
20	Desmatophoca	1	2	1	0	0	1	?	?	0	1	1	0	1	?	1	1	0	1	1	0	1	?	1	?
21	Pinnarctidion	?	2	?	0	?	1	?	?	0	1	1	0	1	?	1	1	0	1	1	0	1	?	?	?
22	Acrophoca	?	2	?	?	1	?	?	?	?	1	1	1	2	?	2	1	1	1	1	0	0	?	?	?
23	Cystophora	1	?	1	1	1	1	1	1	1	1	1	0	2	1	2	?	1	1	2	1	0	1	1	1
24	Erignathus	1	2	1	1	1	1	1	1	1	1	1	0	2	0	2	1	1	1	1	1	0	1	1	1
25	Homiphoca	1	2	1	1	1	1	1	?	1	1	1	1	2	?	2	1	1	1	1	0	0	1	1	1
26	Lobodontini	1	2	1	1	?	1	1	1	1	1	1	1	2	0	2	?	1	1	1	0	0	1	1	1
27	Mirounga	1	2	1	1	1	1	1	1	1	1	1	0	2	0	2	1	1	1	1	0	0	1	1	1
28	"Monachus"	1	2	1	1	0/1	1	1	1	1	1	1	0	2	0	2	1	1	1	1	0	0	1	1	1
29	Phocini	1	2	1	1	1	?	1	1	1	1	1	0	2	1	2	0/1	1	1	2	1	0	1	1	1
30	Piscophoca	?	?	?	?	1	?	?	?	?	1	1	1	2	?	2	1	1	1	1	0	0	1	1	1

TABLE 2 (continued).

		49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
1	Amphicyonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Mustelidae	0	0	0	0	0	0	0	0	1	0	?	0	0	0	1	0	0	0	0	0/1	0	0	0	0
3	Procyonidae	0	0	0	0	0	0	0	0	?	0	?	0	0	0	1	0	0	0	0	0	0	0	0	0
4	Ursidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Enaliarctos	?	1	0	0	0	?	0	0	0	0	0	?	0	0	0	0	1	1	1	0	0	1	0	1
6	Pteronarctos	?	0/1	0	0	0	?	0	0	0	0	0	?	0	0	0	1	1	1	1	0	1	0	0	1
7	Arctocephalus	1	0	0	0	0	1	0	0	0	0	1	1	0	1	1	3	2	1	1	0	0	0	1	1
8	Callorhinus	1	0	0	0	0	1	0	0	0	0	1	1	0	1	1	3	2	1	1	0	1	0	1	1
9	Otariinae	1	0	0	0	0	1	0	0	0	1	1	1	0	1	1	3	2	1	1	0	0/1	0	1	1
10	Thalassoleon	?	0	0	0	0	?	0	0	0	0	1	1	0	0	1	2	1	1	1	0	0	0	1	1
11	Aivukus	?	0	?	?	?	?	1	0	?	1	1	1	1	1	1	3	?	1	1	1	0	0	1	1
12	Alachitherium	?	?	1	0	?	?	?	?	?	?	?	1	1	1	?	?	?	?	?	?	0	0	1	1
13	Dusignathus	?	?	1	0	0	?	?	?	?	?	?	1	0	1	1	3	2	?	1	1	0	0	1	1
14	Gomphotaria	?	0	1	0	0	?	1	0	?	?	?	1	1	1	?	3	1	?	?	1	0	?	?	?
15	Imagotaria	?	0	?	0	0	?	0	0	?	1	1	1	0	0	1	2	1	1	1	0	0	0	1	1
16	Odobenus	1	0	1	0	0	1	1	0	?	?	?	1	1	1	1	3	2	1	1	1	0	0	1	1
17	Pliopedia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Pontolis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Allodesmus	?	0	1	1	1	?	0	0	?	0	?	1	0	1	1	3	2	1	1	0	0	0	1	1
20	Desmatophoca	?	0	1	1	1	?	0	0	?	0	1	?	0	1	1	2	1/2	1	1	0	0	1	1	1
21	Pinnarctidion	?	0	?	?	?	?	?	0	?	0	?	?	?	0	0	0	1	?	?	1	?	?	?	?
22	Acrophoca	?	0	1	1	1	?	?	?	?	?	?	?	0	0	1	2	2	1	?	1	0	0	1	1
23	Cystophora	2	0	?	1	0	1	1	0	1	?	1	1	0	0	1	3	2	1	1	1	0	0	1	1
24	Erignathus	2	0	?	1	0	1	0	1	1	?	1	1	0	0	1	3	2	1	1	1	0	0	1	1
25	Homiphoca	?	0	1	1	?	?	1	1	1	?	?	1	0	0	1	2	2	1	1	1	0	0	1	1
26	Lobodontini	2	0	1	1	0	1	1	1	1	1	1	1	0	0	1	3	2	1	1	1	0	0	1	1
27	Mirounga	2	0	1	1	0	1	1	1	1	1	1	1	0	0	1	3	2	1	1	1	0	0	1	1
28	"Monachus"	1/2	0	1	1	0	1	1	1	1	1	1	1	0	0	1	3	2	1	1	1	0	0	1	1
29	Phocini	2	0	?	1	0	1	0	0	1	0	1	1	0	0	1	3	2	1	1	1	0	0	1	1
30	Piscophoca	?	0	1	1	1	?	1	1	?	1	?	1	0	0	1	2	1	1	1	1	0	0	?	?

		73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
1	Amphicyonidae	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Mustelidae	0	1	0	?	?	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0/1
3	Procyonidae	0	1	0	?	?	0	?	?	0/1	0	?	?	0	0	0	0	0	0	0	0	?	0	0	0
4	Ursidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0
5	Enaliarctos	0	1	0	?	?	0	0	1	0	0	0	0	1	?	1	1	0	1	1	1	0	0	0	1
6	Pteronarctos	0	1	0	?	?	0	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
7	Arctocephalus	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1
8	Callorhinus	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1
9	Otariinae	1	1	0	0	?	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1
10	Thalassoleon	1	1	0	?	?	?	?	?	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1
11	Aivukus	1	1	0	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	2
12	Alachitherium	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Dusignathus	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Gomphotaria	1	1	0	?	?	?	?	?	?	0	0	0	1	?	?	1	1	1	1	1	?	1	1	?
15	Imagotaria	1	1	0	?	?	0	?	?	?	0	0	0	1	0	1	1	1	1	1	1	1	1	1	2
16	Odobenus	1	1	0	1	1	1	1	1	0/1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	2
17	Pliopedia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	2
18	Pontolis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Allodesmus	0	1	1	0	0	0	0	1	1	0	0	0	1	?	1	1	1	1	1	1	0	1	1	1
20	Desmatophoca	0/1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21	Pinnarctidion	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Acrophoca	1	1	1	1	1	1	1	1	?	0	?	?	1	0	1	1	1	1	1	1	0	1	1	2
23	Cystophora	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	2	0	1	0	1	0	1	1	1
24	Erignathus	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	2	0	1	0	1	1	1	1	1
25	Homiphoca	1	1	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	0	1	?	1	1	2
26	Lobodontini	1	1	1	1	1	1	1	1	1	1	0	2	1	0	1	1	1	1	1	1	0	1	1	1
27	Mirounga	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	0	1	1	2
28	"Monachus"	1	1	1	1	1	?	1	1	1	0	0	1	1	0	1	1	1	1	1	1	0	1	1	2
29	Phocini	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	2	0	1	0	1	1	1	1	1
30	Piscophoca	1	1	1	1	1	1	1	?	?	1	?	1	1	0	1	1	1	1	1	1	0	1	1	2

TABLE 2 (continued).

		97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
1	Amphicyonidae	?	0	0	0	?	?	?	?	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	?
2	Mustelidae	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?
3	Procyonidae	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	?	0	0	?	?	?	0
4	Ursidae	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Enaliarctos	0	1	0	0	?	?	?	?	1	0	?	0	0	1	0	0	0	0	0	0	0	1	0	1
6	Pteronarctos	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	Arctocephalus	0	1	0	1	1	1	1	1	?	0	0	1	1	1	0	0	0 / 1	0	1	0	1	1	1	1
8	Callorhinus	0	1	0	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	0	1	1	1	1
9	Otariinae	0	1	0	1	1	1	1	1	1	0	0	1	1	1	0	0	0	0	1	0	1	1	1	1
10	Thalassoleon	0	1	0	1	1	?	?	?	?	0	0	1	1	1	0	0	1	0	1	0	1	1	1	?
11	Aivukus	?	1	2	1	?	?	?	?	?	?	?	1	?	?	?	0	?	?	1	?	?	?	?	?
12	Alachitherium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Dusignathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Gomphotaria	?	?	?	1	?	?	?	?	?	?	?	1	?	?	?	0	0	?	1	?	1	1	?	1
15	Imagotaria	1	1	1	1	?	?	?	?	?	?	?	1	?	?	?	0	?	?	1	0	1	1	1	0
16	Odobenus	0	1	2	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1
17	Pliopedia	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Pontolis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Allodesmus	0	1	0	1	1	1	1	?	1	0	?	1	1	1	0	0	1	0	1	1	1	1	1	1
20	Desmatophoca	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21	Pinnarctidion	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Acrophoca	?	1	0	1	?	?	?	?	1	1	?	1	1	1	0	1	0	1	1	1	1	1	1	?
23	Cystophora	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	1	1	1	1	1	1	0
24	Erignathus	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1	1	0
25	Homiphoca	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0 / 1	0	1	1	1	1	0	?
26	Lobodontini	0	1	0	1	1	0 / 1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0
27	Mirounga	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0
28	"Monachus"	0	1	0	1	1	0	1	0 / 1	1	1	1	1	1	1	0	1	0 / 1	1	1	1	1	1	1	0
29	Phocini	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0
30	Piscophoca	?	1	0	1	?	?	?	?	1	?	?	1	1	1	0	1	0	1	?	?	?	?	0	?

		121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143
1	Amphicyonidae	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2	Mustelidae	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	?	?	0	0	?	0	0	0
3	Procyonidae	?	0	0	0	0	0	?	0	0	0	?	?	?	?	0	?	?	?	0	?	0	0	0
4	Ursidae	0	0	0	0	0	0	0	0	0	0	?	?	0	?	0	?	0	?	0	?	0	0	0
5	Enaliarctos	0	0	?	?	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
6	Pteronarctos	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	Arctocephalus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
8	Callorhinus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
9	Otariinae	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
10	Thalassoleon	0	0 / 1	0	?	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
11	Aivukus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	Alachitherium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Dusignathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Gomphotaria	?	0	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15	Imagotaria	0	?	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Odobenus	0	0	0	1	1	1	1	1	1	2	0	1	0	?	0	1	0	1	1	1	1	0	0
17	Pliopedia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Pontolis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Allodesmus	0	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20	Desmatophoca	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21	Pinnarctidion	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Acrophoca	0	1	0	1	0	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Cystophora	1	1	0	1	0	2	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0
24	Erignathus	1	1	0	1	0	2	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	0
25	Homiphoca	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	Lobodontini	?	1	0	1	0	2	1	1	1	1	1	1	0 / 1	0	0	1	1	1	1	1	1	1	0
27	Mirounga	0	1	0	1	0	2	1	1	0 / 1	2	0	1	1	1	0	1	1	1	1	1	1	1	0
28	"Monachus"	0	0 / 1	0	1	0	2	1	1	1	2	0	1	0 / 1	1	0	1	0	1	1	1	1	0 / 1	0
29	Phocini	1	1	0	1	0	2	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0
30	Piscophoca	?	?	?	1	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

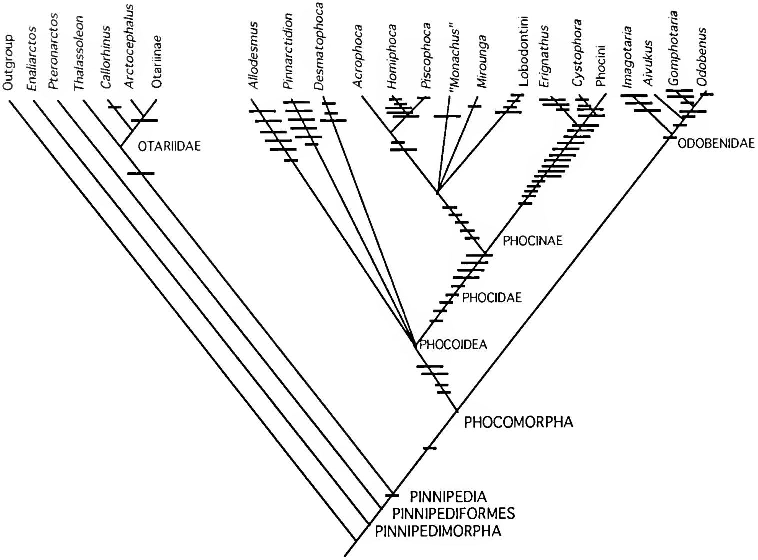

Figure 2. Strict-consensus cladogram of 100 equally parsimonious trees identified by PAUP analysis. Character distributions are listed in Table 2. Short bars, convergences; long bars, reversals.

An additional 12 characters are identified as equivocal synapomorphies at this node. Because 6 of these are unknown in *Pteronarctos* we considered them diagnostic of the Pinnipedia, the least inclusive level at which their distribution can be confirmed (see below).

Pteronarctos, the oldest known member of the Pinnipediformes, has been described on the basis of crania and lower jaws (Barnes 1989; Berta, in press) from the Miocene Astoria Formation of coastal Oregon. This taxon provides the first definitive evidence of development of the pinnipeds' unique orbital wall, to which the maxilla contributes significantly (9), and a lacrimal that fuses early in ontogeny and does not contact the jugal (10). Both of these features may be present in *Enaliarctos*, but available material is not sufficiently well preserved to determine this.

Pinnipedia

Illiger (1811) proposed the name Pinnipedia to unite the otariids, odobenids, and phocids. Of the nine characters diagnosing this group only three craniodental ones are unequivocal synapomorphies: (30) pit for tensor tympani absent, (59) I^3 lingual cingulum absent, and (71) M$_{1-2}$ trigonid suppressed. Potential synapomorphies with other equally parsimonious explanations are (7) fossa nasolabialis absent, (8) fossa muscularis absent, (16) antorbital processes large and well developed, (63) P^4 protocone shelf absent, (64) P^4 double or single rooted, and (73) M$_2$ absent.

These characters' being relatively few should not be interpreted as weakness of the case for pinniped monophyly. If only living forms were considered all pinnipedimorph and pinnipediformes synapomorphies described above would represent pinniped synapomorphies. For example, the following synapomorphies, equivocal at the level of the Pinnipedimorpha or Pinnipediformes, are unambiguous at the level of the Pinnipedia: (81) lumbar vetebrae five, (94) olecranon process laterally flattened with expanded distal half, (95) radius with marked anteroposterior flattening and expanded distal half, (109) pubic symphysis unfused, (115) fovea for teres femoris ligament strongly reduced or absent, and (117) greater femoral trochanter large and flattened. These are in addition to the two confirmed pinnipediform synapomorphies and the 18 pinnipedimorph synapomorphies listed in Appendix 1.

Otariidae

Relationships among the fur seals and sea lions based on cladistic analysis (Berta and Deméré 1986) are being reanalyzed by Berta using two different, more appropriate outgroups, *Pteronarctos* and the Phocomorpha. Our analysis here supports the latter study in

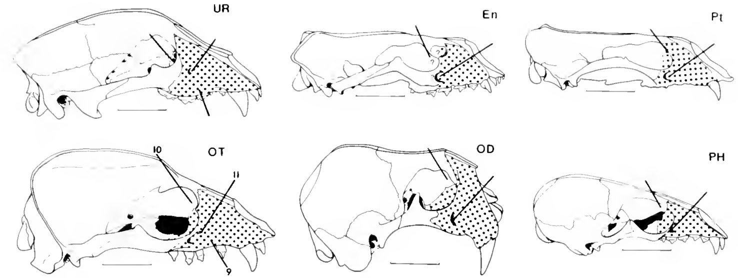

Figure 3. Lateral views of the skulls of representative pinnipeds and a generalized terrestrial arctoid. Extent of maxilla indicated by stippling. En, *Enaliarctos emlongi*; OD, Odobenidae (*Odobenus rosmarus*); OT, Otariidae (*Zalophus californianus*); PH, Phocidae (*"Monachus" schauinslandi"*); Pt, *Pteronarctos goedertae*; UR, Ursidae (*Ursus americanus*). Pinnipedimorph synapomorphies: 10, lacrimal greatly reduced; 11, infraorbital foramen large.

progress in recognizing a sister-group relationship between the southern fur seals, *Arctocephalus* and the sea lions, the Otariinae. The northern fur seal, *Callorhinus*, and the extinct taxon *Thalassoleon* are positioned as sequential sister taxa to this clade. Two unequivocal osteological characters diagnose the otariid clade: (17) supraorbital processes large and shelflike, particularly among adult males (state 3 of multistate character), and (86) secondary spine on scapula present. Two additional unequivocal synapomorphies based on soft-anatomical characters diagnose the extant Otariidae: (135) pelage units uniformly spaced and (143) trachea with bifurcation of bronchi posterior. An additional character possibly diagnostic of this group is (4) frontals extending anteriorly between the nasals, but this feature is also incipiently developed in some species of *Pteronarctos* (Barnes 1989; Berta, in press).

Basal members of this clade (e.g., *Pithanotaria* and *Thalassoleon*) are known from the late Miocene in California and Baja California (Repenning and Tedford 1977).

Phocomorpha

We propose the name Phocomorpha for the monophyletic group that includes the most recent common ancestor of the odobenids and phocoids plus all its descendants (see Fig. 2). A sister-group alliance between the odobenids and phocids was originally proposed by Wyss (1987) and endorsed by Flynn et al. (1988) and Berta et al. (1989). Our analysis provides additional characters supporting this hypothesis. We identified nine unequivocal synapomorphies: (26) canals for facial and vestibulocochlear nerves incipiently or completely separated (state 1 of multistate character), (32) canal for cochlear aqueduct merged or nearly merged with round window, (34) petrosal visible in posterior lacerate foramen, (42) basioccipital short, broad, and widened posteriorly, (46) auditory ossicles enlarged, (51) angular process on mandible reduced and elevated above the base of ascending ramus, (124) calcaneal tuber short, (126) caudally directed process of astragalus at least incipiently present (state 1 of multistate character), and (127) baculum enlarged. An additional seven soft-anatomical and behavioral synapomorphies diagnose extant members of this clade: (128) testes abdominal, (129) copulation aquatic, (132) primary hair nonmedullated, (136) subcutaneous fat thick, (139) external pinnae absent, (140) opening of sweat duct proximal, and (141) venous system with inflated hepatic sinus, well-developed caval sphincter, large intervertebral sphincter, duplicate vena cava, and gluteal route for hindlimbs.

In addition, nine equivocal synapomorphies were identified at this level. Six of these potential osteological synapomorphies require reversals within some phocoids or independent evolution in odobenids and phocids: (76) cervical vertebrae with small transverse processes and neural spines, (77) cervical vertebrae smaller than thoracic or lumbar vertebrae with spinal canal nearly as large as centrum, (79) neural spines on thoracic vertebrae low, (107) hindflipper claws reduced, (114) ischial spine large, and (116) lesser femoral trochanter reduced or absent.

Odobenidae

Relationships among walruses are the subject of current study (see Deméré 1994, this volume). Although our data do not resolve relationships at the generic level, we identified six characters as supporting monophyly of the group. Two of these are unequivocal synapomorphies of the postcranial skeleton: (99) pit or rugosity on metacarpal I and (125) medial process on calcaneal tuber. An additional three equivocal synapomorphies may diagnose this clade but are subject to other equally parsimonious interpretations. These are (17) supraorbital processes completely absent (state 2 of multistate character), (58) I^3 terete and caniniform, and (93) diameter of humeral trochlea larger than that of distal capitulum.

Odobenids are first recognized from the middle Miocene of California. Not included in our study and undoubtedly representing a significant position in odobenid evolution is *Neotherium mirum*, new material of which is being studied by L. G. Barnes.

Phocoidea

As defined by Wyss and Flynn (1993), the Phocoidea are a clade including the common ancestor of phocids and desmatophocids plus all of its descendants. Seven unequivocal synapomorphies diagnose this clade: (5) posterior termination of nasals posterior to frontal–maxillary contact, (22) pterygoid process with flat, concave lateral margin, (24) mastoid process distant from paroccipital process (state 2 of multistate character), (26) internal auditory meatus absent and canals for vestibulocochlear nerve completely separated (state 2 of multistate character), (35) auditory bulla underlaps basioccipital, (52) bony flange below ascending ramus, and (142) peri-

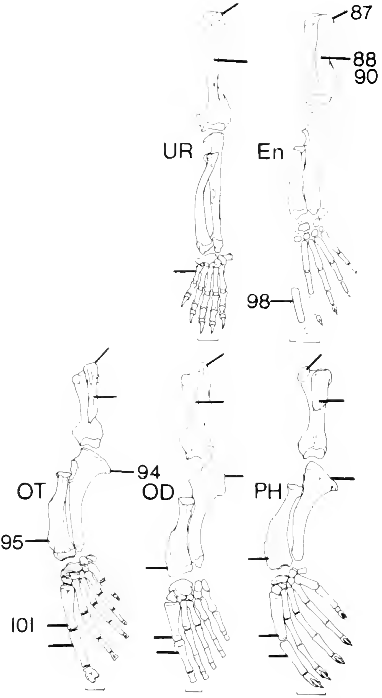

Figure 4 Left forelimb of representative pinnipeds and a generalized terrestrial arctoid in dorsal view. En, *Enaliarctos emlongi*; OD, Odobenidae (*Odobenus rosmarus*); OT, Otariidae (*Zalophus californianus*); PH, Phocidae ("*Monachus*" *schauinslandi*); UR, Ursidae (*Ursus americanus*). Pinnipedimorph synapomorphies: 87, greater and lesser humeral tuberosities enlarged; 88, deltopectoral crest strongly developed; 90, humerus short and robust; 94, olecranon process laterally flattened and posteriorly expanded; 95, distal half of radius expanded; 101, digit I of manus enlarged (see Appendix 1).

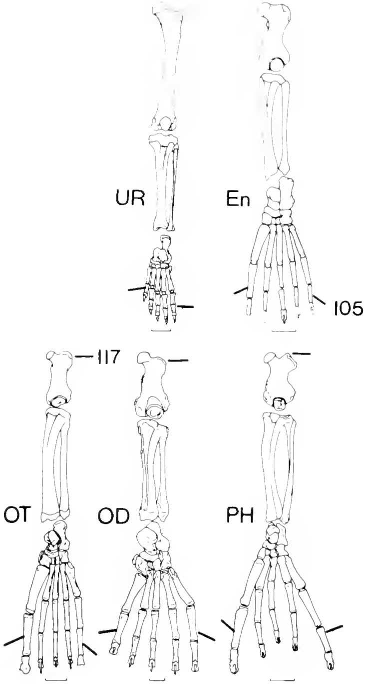

Figure 5. Left hindlimb of representative pinnipeds and generalized terrestrial arctoids in dorsal view. En, *Enaliarctos emlongi*; OD, Odobenidae (*Odobenus rosmarus*); OT, Otariidae (*Zalophus californianus*); PH, Phocidae ("*Monachus*" *schauinslandi*"); UR, Ursidae (*Ursus americanus*). Pinnipedimorph synapomorphy: 105, digits I and V of pes elongated (see Appendix 1).

cardial plexus well developed. Two of 13 equivocal synapomorphies most likely represent reversals near the base of the clade: (3) nasal processes prominent and (16) antorbital process of frontal large and well developed.

Phocidae

Relationships among extant phocids have recently been analyzed cladistically (Muizon 1982a; Wyss 1988b). We identify as a monophyletic clade the archaic seals *Piscophoca*, *Homiphoca*, and *Acrophoca* and hypothesize a sister-group relationship between *Piscophoca* and *Homiphoca*. Elephant and monk seals (*Mirounga* and "*Monachus*") and extant lobodontines are more closely related to the archaic seal clade than they are to phocine seals. The Phocinae (consisting of *Erignathus*, *Cystophora*, and the Phocini) are recognized as a monophyletic group in agreement with Burns and Fay (1970), Muizon (1982a), and Wyss (1988b). The Phocidae are diagnosed by 26 derived characters, eight of which are unequivocal synapomorphies for the group: (20) alisphenoid canal absent, (23) mastoid heavily pachyostotic, (28) basilar cochlear whorl directed transversely, (29) dorsal region of petrosal expanded, (33) opening of cochlear fenestra outside tympanic cavity, forming a cochlear foramen, (41) pit for tympanohyal anterior to stylomastoid foramen, (112) insertion for ilial psoas muscle on ilium, and (126) process of astragalus directed caudally (state 2 of multistate character). Eleven other characters are potential synapomorphies.

This phylogeny implies many character reversals at the base of the phocine seal clade, a pattern discussed further below.

Our apparent endorsement of "monachine" monophyly is based on our not treating "*Monachus*" *schauinslandi* as a separate taxon. Outside the subfamily Phocinae, we don't attribute much significance to the intraphocid relationships depicted in Figure 2. For example, our results reveal a puzzling arrangement in which reported fossil lobodontines (*Homiphoca*, *Acrophoca*, and *Piscophoca*) are not nested among extant lobodontines. Of the three synapomorphies linking fossil lobodontines, none is unequivocal. One character, (53) mandibular condyle elevated above tooth row, requires a reversal among modern lobodontines. For another character, (64) P^4 double rooted, fossil lobodontines represent an intermediate transformation, P^4 becoming single rooted among modern lobodontines and other phocids. A third character, (36) mastoid lip covering or partially covering external cochlear foramen, either reverses in "*Monachus*" and *Mirounga* or originated independently among fossil and modern lobodontines. Thus, this arrangement separating fossil from extant lobodontines is poorly supported.

Although phocids have a temporal range extending back into the middle Miocene, much of the material is fragmentary. Later archaic phocids are represented by abundant well-preserved material of *Acrophoca* and *Piscophoca* from the early Pliocene of Peru (Muizon 1981) and of *Homiphoca* from late Miocene or early Pliocene of South Africa (Hendey and Repenning 1972; Muizon and Hendey 1980).

EXPERIMENTAL MANIPULATIONS OF DATA

We performed several experimental manipulations of the data set. In one run we forced otarioid monophyly. The strict-consensus tree that resulted from 100 trees was 34 steps longer than our preferred tree. In another run to address the question of diphyly we forced the monophyly of musteloids and phocids. The strict-consensus tree that resulted from 100 trees was 77 steps longer than our preferred tree. Finally, in an attempt to determine the role of fossils in pinniped phylogeny, we excluded all fossil taxa. The resulting tree showed no major change in topology.

ASSESSING THE PATTERN OF HOMOPLASY

There has been a widespread recent tendency among carnivoran systematists to assume pervasive convergence of pinnipeds (Wyss 1989), sometimes when such assumptions are unnecessary. Wozencraft (1989:504) saw the controversy of pinniped monophyly vs. diphyly as centering "on the treatment of parallel and convergent characters," suggesting that monophyly is favored only if aquatic adaptations are not excluded. In our view this line of reasoning is flawed in two respects: (1) it assumes convergence at the outset, something for which one needs a phylogeny to uncover, and (2) it assumes that because a particular structure has some "adaptational" or functional significance it probably originated independently and is therefore irrelevant phylogenetically. The implausibility of the latter view is patent: taken to its logical extreme one would have difficulty in defending the monophyly of even noncontroversial groups of pinnipeds. The posterior process on the phocid calcaneum, for example, has important functional implications in keeping the hindlimb posteriorly extended, yet it has never been rejected as supporting a common origin for the group. We regard the distinctively reduced fifth intermediate phalanx on the pinniped manus (among numerous other features) as equally deserving of serious phylogenetic consideration.

Barnes (1989: fig. 9) assumed convergence even when such an assumptions was unnecessary. For example, he viewed enlarged ear ossicles as originating independently in the Desmatophocinae, walruses (though he showed these taxa as sister groups), and in a clade including the Allodesminae and *Pinnarctidion*, though no characters bar a linkage between this clade and his desmatophocine–walrus clade. Thus three originations of this character are proposed where one would have sufficed. Additionally, the assumption of convergence implies that the ossicles enlarged independently in the phocids, too. Thus assuming convergence may violate parsimony. There is nothing to prevent one from suggesting that any character has originated independently in every terminal taxon.

We mapped patterns of homoplasy on our strict-consensus tree (Fig. 2). Reversals exceed convergences 48 to 41. Our analysis establishes that the majority of reversals, excluding those confined to terminal taxa, occurred among the phocine seals, a pattern previously noted by Wyss (1988b) and referred to by Howell (1929) as "retrogressive" evolution. Reversals are more than twice as common here as at any other place on the tree. Nearly all of these reversals occurred at the base of the phocine clade rather than among terminal taxa. These reversals are confined largely to details of flipper structure (see Wyss 1994, this volume, for further discussion) and include (85) supraspinous fossa slightly larger than infraspinous fossa, (89) supinator ridge of humerus well developed, (91) entepicondylar foramen present, (100) metacarpal heads keeled with trochleated phalangeal articulations, (101) metacarpal I equal in length to others, (103) foreflipper claws long, (104) intermediate phalanx of digit V unreduced, (107) hindflipper claws unreduced, and (108) pes with short, rounded metatarsal shafts with rounded heads, associated with trochleated phalangeal articulations.

MOLECULAR DATA

Studies of DNA hybridization, amino acid sequences, and chromosomes support pinniped monophyly [see Wyss (1987) for a more detailed review], although there is disagreement as to which group of terrestrial arctoids pinnipeds are most closely related, or, in the case of chromosomal work, to which pinnipeds the walrus is most closely related. Arnason and Widegren (1986) demonstrated that pinnipeds share four highly repetitive DNA components unique to pinnipeds or shared with mustelids (with the exception of *Mephitis*). De Jong (1982) found that in the eye-lens protein alpha lens crystallin there are two amino acid replacements uniquely shared by phocids and otariids (the walrus was not sampled). In addition these workers discovered a similarity between the mustelid *Mustela* and the procyonid *Bassariscus* in two amino acid replacements that differ from replacements seen in the other carnivores sampled (de Jong 1986). Significantly, phocids do not share these similarities, thus failing to support a phocid–mustelid alliance. More recently, sequencing by Keith et al. (1991) of the milk protein beta lactoglobin supports a close relationship between phocids and otariids. Their results indicate that these groups are closer to canids than to ursids. Neither the walrus nor mustelids have yet been sampled (Keith, pers. comm.).

The karyological similarity among pinnipeds supports pinniped monophyly. Fay et al. (1967) supported *Odobenus* as a karyological intermediate between phocids and otariids. Arnason (1974), however, disputed this conclusion, arguing for a stronger similarity between otariids and phocids.

We hope future molecular and karyological data will be analyzed cladistically.

CONCLUSIONS

In summary, we believe that the cases for otarioid monophyly and pinniped diphyly have not been established. We urge that those continuing to defend these hypotheses analyze the data explicitly and include character distributions among appropriate outgroups and all members or potential members of the ingroups. Pinniped monophyly is supported overwhelmingly by diverse anatomical data and is strongly suggested by biochemical data as well.

The historical expectation of convergence among pinnipeds has clouded the interpretation of their relationships. In the context of a well-corroborated phylogenetic hypothesis it seems that the pattern of homoplasy argues for character reversals occurring as commonly as convergences.

ACKNOWLEDGMENTS

We thank C. A. Repenning and Richard Tedford for critical readings of the manuscript. Line drawings were skillfully prepared by Corrine Petti (Fig. 3) and Mary Parrish (Figs. 4 and 5). Berta gratefully acknowledges support by the National Science Foundation (BSR 9006535).

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APPENDIX 1

Craniodental, postcranial, and soft-anatomical characters examined among recent and fossil pinnipeds. The discussion of a character's hypothesized sequence of transformation is an *a posteriori* assessment based on the distribution of that feature on our strict-consensus tree.

Skull

1. Premaxilla–nasal contact. 0 = extensive, 1 = reduced. In *Odobenus*, *Allodesmus*, and the Phocidae (Wyss 1987:7, 15, fig. 5) the contact between the premaxilla and nasal is short and narrow. Wozencraft (1989) incorrectly identified phocids and lutrines as sharing a reduced premaxilla–nasal contact. Among lutrines, the premaxilla–nasal contact is reduced only in the sea otter, *Enhydra*. Wyss noted that the premaxillae of *Odobenus* differ from those of phocids in being broadly sutured with the nasals inside the nasal cavity; in phocids no such internal contact occurs. An undescribed fossil odobenid of the genus *Imagotaria* (LACM 118675) shows the primitive condition of a broad contact between the premaxilla and nasals. This derived feature we judge diagnostic of *Allodesmus* + *Desmatophoca* + phocids (Phocoidea) and as an autapomorphy of *Odobenus* or a reversal in *Imagotaria*.

2. Premaxilla. 0 = ascending process visible laterally along entire length, 1 = ascending process dips into nasal aperture. According to Muizon (1982a:186, 187, fig. 4), in "monachines" the premaxilla–maxilla suture is, in its medial part, located inside the nasal aperture." This condition applies strictly to neither "*M.*" *monachus* nor *Homiphoca* and according to our most parsimonious tree is likely primitive for phocids. Although most phocines show the primitive condition of this character, variation exists with *Histricophoca* and *Pagophilus* posessing the derived "monachine" condition (Muizon 1982a). *Allodesmus* and *Desmatophoca* show a similar derived condition (see Barnes 1972, fig. 4; 1987, fig. 1). The derived state is a synapomorphy for phocoids with several reversals.

3. Nasal processes of premaxilla. 0 = not prominent, 1 = prominent, protrude dorsal and anterior to alveolar margin, 2 = well elevated anterior and dorsal to alveolar margin. As Howell (1929) first noted, there is a well-defined process formed by the premaxillary tips in *Zalophus* that is absent in *Phoca*. In *Odobenus*, the nasal processes are elevated well above the alveolar incisor margin, owing to the great modifications of the snout. As noted by Repenning and Tedford (1977:18), this condition distinguishes *Odobenus* from other odobenids.

Prominent nasal processes do not occur in ursids, *Enaliarctos*, *Allodesmus*, *Desmatophoca*, or phocids. An intermediate condition in which the nasal process are prominent and protrude (but are not elevated) dorsal and anterior to the incisor alveolar margin distinguishes *Pteronarctos*, otariids, odobenids, and phocids primitively (i.e., *Imagotaria*, *Aivukus*, and *Homiphoca*). Hence the presence of prominent nasal processes is most parsimoniously interpreted as having originated at the level of Pinnipediformes and having been lost among phocoids. Its presence in *Homiphoca* is regarded as an independent derivation.

4. Frontals. 0 = do not extend anteriorly between nasals, 1 = extend anteriorly between nasals. Otariids display a characteristic W-shaped nasofrontal contact, in which the frontals extend anteriorly between the nasals (King 1983:151, fig. 6.4). In other pinnipeds and most terrestrial carnivorans the frontals and nasals do not show this relationship. Wozencraft (1989:521) incorrectly maintained that odobenids and otariids share the derived condition, a W or divergent shape. Both juveniles and adults of *Odobenus*, as well as *Imagotaria*, maintain a horizontal line of contact between the nasals and the frontals.

The derived condition is an autapomorphy for all taxa more closely related to living otariids than to other pinnipeds. However, it should be noted that in at least one nonotariid, *Pteronarctos goedertae* (see Barnes 1989: figs. 1, 2), the frontals extend slightly between the nasals, which might be interpreted as incipient development of the derived condition; accordingly, we scored the condition scored in this taxon as variable.

5. Posterior termination of nasals. 0 = at or near frontal–maxillary contact, 1 = posterior to frontal–maxillary contact. The nasals' narrowing greatly posteriorly and terminating far posterior of the frontal–maxillary contact is a synapomorphy uniting *Desmatophoca*, *Allodesmus*, and phocids (Berta 1991). In terrestrial carnivorans, *Enaliarctos*, *Pteronarctos*, otariids, and odobenids the nasals terminate at or near the broad frontal–maxillary contact.

6. Palatine process of maxilla. 0 = terminates at last molar, 1 = extends behind last molar, 2 = developed as a shelf (pterygoid process of maxilla, Barnes 1987). Barnes (1979:23) noted that in *Pinnarctidion bishopi* a "wide, thin, squared posterolaterally projecting shelf of the palate is beneath each orbit." Barnes (1987) described this structure, better developed in *Desmatophoca brachycephala*, as an expansive pterygoid process of the maxilla that forms a thin infraorbital shelf with a prominent posterolateral corner. He observed that this structure is more prominent in *D. brachycephala* than in *Allodesmus packardi* and *D. oregonensis*.

Pinnipedimorphs are distinguished ancestrally from terrestrial carnivorans by having an intermediate condition (1) in which the palatine process of the maxilla extends posterior to the last molar. Berta (1991) recognized the presence of a palatine shelf in *Pinnarctidion*, *Desmatophoca*, *Allodesmus* as a second derived condition (2).

7. Nasolabialis fossa. 0 = present, 1 = absent. The nasolabialis fossa, described in *Enaliarctos* by Mitchell and Tedford (1973:220, 234) as a "rather deep fossa for the quadratus labii superioris muscle," is "located on the rostrum, just anterior to the antorbital rim." Among terrestrial carnivorans the nasolabialis fossa is present in the archaic ursids *Allocyon* and *Cephalogale*. It is present in *Enaliarctos*, *Pteronarctos*, and *Pinnarctidion* and absent in all other pinnipedimorphs (Berta 1991), a distribution suggesting that absence of the nasolabialis fossa is a pinniped synapomorphy. We consider its presence in *Pinnarctidion* a reversal to the primitive condition.

8. Fossa muscularis. 0 = present, 1 = absent. In ursids, "immediately behind the lacrimal fossa is a shallow pit, the fossa muscularis, in which the inferior oblique muscle of the eye arises; the thin dry floor of this pit is usually broken through on dry skulls, and then resembles a foramen. . . . In *Ursus* it is relatively enormous, as large as the lacrimal fossa" (Davis 1964:49). The fossil ursid *Cephalogale* has behind its lacrimal fossa a slight depression delimited by a ventrally floored ridge, possibly the precursor of the deep, posteriorly positioned fossa muscularis seen in *Enaliarctos* and *Pteronarctos*.

Because this character could not be unambiguously polarized from our outgroups we excluded it from the initial run of characters.

9. Maxilla. 0 = does not contribute significantly to medial orbital wall, 1 = contributes significantly to orbital wall and forms anterior orbital rim. In terrestrial carnivorans the maxilla is usually limited in its posterior extent by contact of the jugal or palatine with the lacrimal (Wyss 1987). Sutures in the orbital region of available specimens of *Enaliarctos* are fused, hence the arrangement of bones in this region cannot be determined. An undescribed species of *Pteronarctos* (USNM 335432) shows sutures in this region; although a lacrimal is clearly present it contacts neither the palatine nor the jugal.

Therefore, we identify the derived condition as a synapomorphy of *Pteronarctos* plus the pinnipeds (= Pinnipediformes). Additional specimens of *Enaliarctos* may demonstrate this to be a pinnipedimorph synapomorphy. Barnes (1989) used this feature as an "otarioid" synapomorphy.

10. Lacrimal. 0 = distinct, contacts jugal, 1 = fuses early in ontogeny to maxilla and frontal, greatly reduced or absent; does not contact jugal. Associated with the pinniped configuration of the maxilla is the great reduction or absence of the lacrimal. King (1971) demonstrated the presence of a lacrimal in all extant otariids, showing that in them, unlike terrestrial carnivorans, the lacrimal tends to fuse relatively early in ontogeny to the maxilla and frontal, obscuring it. In no otariid, however, does it contact the jugal or palatine. As observed by Wyss (1987), a lacrimal is difficult to identify in phocids and odobenids. Wozencraft (1989:522) argued that the lacrimal, including in otariids and odobenids an orbital flange, is present in these groups. As noted above, however, this condition is fundamentally different from that in terrestrial carnivorans. In his discussion of a related character, Wozencraft incorrectly argued that lack of contact between the jugal and lacrimal also characterizes ursids and mustelids. On the contrary, terrestrial carnivorans can be distinguished from pinnipeds by their lacrimal's contacting the jugal or being separated from it by at most a thin sliver of the maxilla. The distinctiveness of the orbital mosaic in "otarioids" was highlighted even by a proponent of otarioid monophyly (Barnes 1989); it occurs, however, in phocids also.

Presence of a lacrimal in *Enaliarctos* cannot be determined. In *Pteronarctos repenningi* (USNM 335432) the lacrimal is distinct but fails to contact the palatine or the jugal. The derived condition is a synapomorphy linking *Pteronarctos* and pinnipeds (Berta 1991).

11. Infraorbital foramen. 0 = small, 1 = large. A large infraorbital foramen is a pinnipedimorph synapomorphy (Berta 1991). Infraorbital foramina are small in most terrestrial carnivorans except amphicynodont ursids (see Tedford et al., 1994, this volume).

12. Orbital vacuities. 0 = absent, 1 = present. Wyss (1987:16, fig. 5) noted in pinnipeds an unossified space (orbital vacuity) in the ventral orbital wall near the juncture of the frontal, maxilla, and palatine. Such orbital vacuities characterize pinnipedimorphs exclusive of *Enaliarctos*, *Pteronarctos*, *Imagotaria*, *Aivukus*, and *Desmatophoca* (Berta 1991).

Wozencraft (1989:522) distinguished differences among pinnipeds in the formation of orbital vacuities. According to him, an enlarged sphenopalatine foramen eclipses the orbitosphenoid (creating an orbital vacuity) in otariids and odobenids but not phocids. Phocids do, however, possess an orbital vacuity that variably includes the sphenopalatine foramen.

The distribution of this character suggests that orbital vacuities evolved independently in the three major pinniped groups, among otariids, in *Odobenus*, and among some phocoids (*Allodesmus* + phocids).

13. Palate. 0 = parallel-sided, 1 = posteriorly widening. In phocids, *Allodesmus*, and to a lesser degree *Pinnarctidion*, unlike otariids and odobenids, the palate widens posteriorly, a derived condition (Wyss 1987). In contrast, Wozencraft (1989:521) identified a posteriorly broad palate as the primitive condition among carnivorans. While we recognize that the palate diverges widely in most terrestrial carnivorans, it does not in ursids or amphicyonids. *Enaliarctos* and otariids retain what we interpret to be the ancestral condition for the Pinnipedimorpha. This condition is a synapomorphy uniting phocoids. Because of the variability among outgroups we polarized this character on a second run of characters.

14. Embrasure pit between P^4 and M^1. 0 = deep, 1 = shallow or absent. *Enaliarctos* is distinguished from *Pinnarctidion*, *Pteronarctos* (Barnes 1979, 1989) and all other pinnipedimorphs by its deep embrasure pit for the crown of M_1 between P^4 and M^1. Barnes further noted that reduction of this pit indicates a corresponding reduction in the size of the lower carnassial. Terrestrial carnivorans typically possess a deep embrasure pit on the palate. We here regard this character as a *Pteronarctos* + pinniped synapomorphy.

15. Anterior palatine foramina. 0 = on or slightly posterior to maxillary–palatine suture, 1 = anterior of maxillary–palatine suture. The major palatine foramen (= anterior palatine foramen or anterior opening of the palatine canal; see Novacek 1986) is situated anterior of the maxillary–palatine suture in otariids, phocids, and odobenids but lies on the suture in other arctoids (Davis 1964; Burns and Fay 1970). Wozencraft (1989) incorrectly argued that the primitive condition is characteristic of all three extant pinniped families.

Although Barnes (1979) distinguished *Enaliarctos mitchelli* from *E. mealsi* by its paired posterior palatine foramina (= anterior palatine foramina), additional material of the latter shows the derived condition to characterize all pinnipedimorphs (Berta 1991).

16. Antorbital process of the frontal. 0 = absent or small, 1 = large and well developed. Barnes (1979) noted that the antorbital process (often referred to as the lacrimal process) of *Pinnarctidion* is not as broadly based as in *Enaliarctos* and that it protrudes farther from the side of the skull. We maintain that well-developed antorbital processes do not occur in *Enaliarctos* or *Pinnarctidion*. As coded here the derived condition occurs in otariids and odobenids. We interpret it as a convergence of those two families or as having been present in the Pinnipedia primitively then reversed in the Phocoidea. Although the antorbital process is lacking in "*Monachus*" it occurs among some phocids (*Erignathus*, *Mirounga*, Lobodontini), we infer as a secondary derivation.

17. Supraorbital process. 0 = distinct and blunt, 1 = reduced to a supraorbital ridge, 2 = completely absent, 3 = large and shelflike. The primitive condition seen in terrestrial carnivorans is a frontal with a small, rounded supraorbital process. State 1 in which the supraorbital process is reduced is seen in *Enaliarctos*, *Pteronarctos*, *Allodesmus*, *Desmatophoca*, and *Pinnarctidion*. Phocids and odobenids except *Gomphotaria* have lost the process completely (2). The large shelflike supraorbital processes (3) of otariids we consider an autapomorphy of the group.

Barnes (1989:18) argued that absence of supraorbital processes is primitive for otarioids. He noted that *Pteronarctos* can be distinguished from *Enaliarctos* on the basis of its larger supraorbital processes. Additional specimens of these taxa (Emlong collection), however, show that this distinction does not hold. *Enaliarctos* and *Pteronarctos* both possess small tuberosities or ridges in this region. Therefore we interpret the reduction of supraorbital ridges in *Enaliarctos*, *Pteronarctos*, and archaic phocoids as independently derived. Alternatively, the condition in *Enaliarctos* and *Pteronarctos* may be primitive for pinnipedimorphs.

18. Least interorbital width. 0 = occurs in posteriormost portion of interorbital septum, 1 = occurs in the anterior half of the

interorbital septum. Burns and Fay (1970) noted that in *Cystophora* and the Phocini, the interorbital distance is least in the anterior half of the interorbital septum. In other pinnipedimorphs and in other carnivorans the interorbital region is narrowest in the posteriormost section.

19. Foramen rotundum. 0 = separate from anterior lacerate foramen, 1 = merged with anterior lacerate foramen [see also discussion of Barnes' character (d) under Otarioid Monophyly].

Pinnarctidion can be distinguished from *Enaliarctos* and other pinnipeds by its having the foramen rotundum separate from the anterior lacerate foramen. Canids and ursids also share the condition of a separate foramen rotundum (Barnes 1979, 1987).

Our phylogeny implies that *Pinnarctidion* is an exception among pinnipedimorphs in displaying the primitive condition. We suggest that the derived condition is a pinnipedimorph synapomorphy, reversed in *Pinnarctidion*.

20. Alisphenoid canal. 0 = present, 1 = absent. Since the alisphenoid canal is widespread among terrestrial carnivorans, including all ursoids, its presence in pinnipeds is undeniably primitive. Thus presence of an alisphenoid canal in the "Otarioidea" does not support the unity of this group, as argued by Barnes (1989). Absence of the alisphenoid canal among phocids has long been regarded as a synapomorphy of that group or as a synapomorphy of mustelids + phocids.

21. Mastoid visible in dorsal view of skull. 0 = no, 1 = yes. A lateral swelling of the mastoid is visible in a dorsal view of the skull in phocine but not "monachine" phocids (King 1966; Burns and Fay 1970). This is regarded as the derived condition because it does not occur in terrestrial carnivorans or other pinnipedimorphs.

22. Pterygoid process. 0 = rounded with convex lateral margin, 1 = flat with concave lateral margin. According to Barnes (1989) *Pinnarctidion*, *Allodesmus*, and *Desmatophoca* are distinguished from other "otarioid" pinnipeds by their flat pterygoid strut with a concave lateral margin. We found that phocids also possess the derived condition.

23. Mastoid. 0 = composed of cancellous bone, 1 = heavily pachyostic. A pachyostotic mastoid is unique to phocids (Burns and Fay 1970).

24. Mastoid process. 0 = close to paroccipital process, the two connected by a low discontinuous ridge, 1 = close to paroccipital process, the two connected by a high continuous ridge, 2 = distant from paroccipital process. In ursids and other arctoids the mastoid process fails to form a complete ventral ridge that extends back to the paroccipital process as it does it otariids and odobenids. A high, continuous ridge joins these processes in *Pteronarctos*, otariids, and odobenids and is thus likely primitive for pinnipedimorphs. In *Pinnarctidion* the two processes are separated and not broadly continuous, although they are connected by a crest (Barnes 1979).

The plesiomorphic condition occurs in terrestrial carnivorans, including ursids (Mitchell and Tedford 1973:248) and *Enaliarctos*. State 1 occurs in *Pteronarctos*, otariids, and odobenids. State 2 occurs in phocids, *Pinnarctidion*, *Allodesmus*, and *Desmatophoca*.

25. Round window. 0 = unenlarged, 1 = large, with round window fossula. In pinnipeds the round window is large and the fossula apparently serves to shield the secondary tympanic membrane from the distensible cavernous tissue of the middle ear (Repenning 1972). This fossula is absent in other carnivorans except perhaps *Potamotherium* and the lutrines, in which a very shallow fossula may incipiently (and variably) be present (Tedford 1976; pers. obs.). In these latter forms the round window is not greatly enlarged. Among pinnipeds the round window is most expanded in phocids but it is also very large in odobenids. The derived condition is a pinnipedimorph synapomorphy.

26. Internal auditory meatus. 0 = present and canals for vestibulochochlear and facial nerves closely adjacent, 1 = present and canals for vestibulocochlear and facial nerves incipiently separated, 2 = absent and canals for vestibulocochlear and facial nerves completely separated. Derived state 1 occurs in *Odobenus* and *Imagotaria* (Repenning and Tedford 1977); state 2, in phocids, *Allodesmus*, *Desmatophoca*, and *Pinnarctidion*.

27. Basal whorl of scala tympani. 0 = unenlarged, 1 = very enlarged. The basal whorl of the cochlea is greatly enlarged in width and diameter in all pinnipeds (Repenning 1972). This expansion appears to be most marked in odobenids and phocids. Pending comparative measurements, it may actually prove to be a phocoid + odobenid synapomorphy.

28. Basal cochlear whorl. 0 = posterolateral to long axis of skull, 1 = transversely directed. In phocids, the basal whorl of the cochlea runs transverse to the long axis of the skull, rather than posterolaterally as in other carnivores including otariids and odobenids (Repenning 1972). The derived condition is thus a phocid synapomorphy.

29. Dorsal region of petrosal. 0 = unexpanded, 1 = expanded. Repenning and Ray (1977) observed that "*Monachus*" *schauinslandi* can be distinguished from all other phocids by its having a relatively unexpanded dorsal petrosal region (see also discussion in Wyss 1988: fig. 2).

30. Pit for tensor tympani. 0 = present, 1 = absent. In terrestrial carnivorans the tensor tympani originates from a small pit in the petrosal anterior to the oval window. In pinnipeds this pit is lost and the muscle originates with the bony eustachian tube (Repenning 1972). Among pinnipedimorphs, this pit is present in *Enaliarctos* (Mitchell and Tedford 1973) and *Pteronarctos* (Berta 1991). Hence, the derived condition is a pinniped synapomorphy.

31. Cochlear aqueduct. 0 = small, 1 = large. As noted by Fleischer (1973) the pinnipeds' cochlear aqueduct is greatly enlarged. Pending a quantified survey among the carnivores of cochlear aqueduct dimensions, we tentatively regard this character as a pinniped synapomorphy.

32. Canal for cochlear aqueduct. 0 = separate from round window, 1 = merged or nearly merged with round window. In pinnipeds the cochlear aqueduct is only narrowly separated from the round window, and in phocids at least the canal for the aqueduct strictly speaking does not exist (Fleischer 1973). In terrestrial carnivorans the cochlear aqueduct is a very narrow canal that passes about half the width of the promontorium through the petrosal itself. In phocids and *Odobenus* the connection of the cochlear aqueduct to the cochlea is via the round window, although *Odobenus* may still have a narrow, bony separation between the round window and the cochlear aqueduct. Otariids retain a condition more primitive than in other pinnipeds in that their cochlear aqueduct still pierces the petrosal. Accordingly, the derived condition is an odobenid + phocid synapomorphy.

33. External cochlear foramen. 0 = absent, 1 = present. Phocids display a unique external cochlear foramen (Burns and Fay 1970), an opening at the bulla–mastoid junction just posterior to the auricular foramen and stylomastoid foramen.

34. Petrosal. 0 = not visible in posterior lacerate foramen, 1 = visible in posterior lacerate foramen. Burns and Fay (1970) and King (1966) have discussed the visibility in phocids of the petrosal in ventral view through the posterior lacerate foramen. The petrosal is also visible in *Odobenus* and its fossil allies (Repenning and Tedford 1977), *Pinnarctidion*, *Desmatophoca*, and *Allodesmus* (Wyss 1988b; Berta 1991). In the primitive condition seen in terrestrial carnivorans, *Enaliarctos*, *Pteronarctos*, and otariids the petrosal is not visible in ventral view from the posterior lacerate foramen.

35. Auditory bulla. 0 = abuts basioccipital, 1 = underlaps basioccipital. In ventral view, the bulla abuts the basioccipital in ursids, *Enaliarctos*, *Pteronarctos*, otariids, and odobenids. In the derived condition seen in *Pinnarctidion*, *Desmatophoca*, *Allodesmus*, and phocids, the bulla underlaps the basioccipital (Berta 1991).

36. Mastoid lip. 0 = not extensive, 1 = covers or partially covers external cochlear foramen. As noted by numerous workers (Repenning and Ray 1977; Muizon and Hendey 1980; Muizon 1982a) extant lobodontine phocids uniquely show a mastoid lip overlapping the posterior bullar wall and covering the external cochlear foramen. The derived condition is also seen in fossil lobodontines, *Homiphoca* (Muizon and Hendey 1980), *Acrophoca*, and *Piscophoca* (Muizon 1981). The primitive condition in which the mastoid lip does not cover the external cochlear foramen is seen in *Mirounga*, "*Monachus*," and phocines (Wyss 1988).

37. Caudal entotympanic. 0 = uninflated, 1 = inflated, 2 = greatly inflated. *Odobenus*, *Allodesmus*, and *Pinnarctidion* show an intermediate condition, a bulla slightly inflated, whereas in phocids the bulla is greatly inflated (Wyss 1987:24). Wozencraft (1989:523) identified inflation of the caudal entotympanic as a feature shared by canids, procyonids, some mustelids, and phocids. We agree that some mustelids and procyonids possess an inflated entotympanic (although not necessarily primitively), but in ursids the caudal entotympanic is not inflated. From this distribution we interpret the inflation of the entotympanic in some mustelids and procyonids as an independent acquisition.

We excluded this character from the initial run of characters because of the variability among mustelid and procyonid outgroups.

38. Posterior opening of carotid canal. 0 = visible in ventral view, posteromedial process present, 1 = not visible in ventral view, posteromedial process absent. In the phocines excluding *Erignathus* the posterior opening of the internal carotid canal is not visible in ventral view owing to prominent bullar inflation (Burns and Fay 1970). In other pinnipeds a bony shelf projects from the dorsal and or medial margin of the aperture toward the posterior lacerate foramen. Hence we recognize the derived condition as a synapomorphy of the Phocini plus *Cystophora*.

39. Squamosal–jugal articulation. 0 = splintlike, 1 = mortised, 2 = exaggeratedly mortised. Barnes (1979:23) described in *Enaliarctos* and otariids a splintlike arrangement of squamosal and jugal in which the jugal tapers to a sharp point and the squamosal does not touch the postorbital process of the jugal. In *Pinnarctidion bishopi* the squamosal does not taper but ends in a blunt, vertically expanded tip. It not only touches the postorbital process of the jugal but fits into a shallow notch on its posterior side. Barnes further observed that the mortised articulation in which both the postorbital process of the jugal and the zygomatic process of the squamosal are expanded dorsoventrally is more greatly developed in *Allodesmus* than in phocids.

Condition 1 unites *Pinnarctidion* and *Desmatophoca*; condition 2 unites *Allodesmus* and the phocids (Berta 1991). Barnes (1989:18) argued that a mortised squamosal–jugal articulation occurs in the Odobenidae also, an observation with which we disagree [e.g., *Imagotaria* (Repenning and Tedford 1977: fig. 4)].

40. Postglenoid foramen. 0 = large, 1 = vestigial or absent. The primitive condition occurs in *Cephalogale*, *Allocyon*, and amphicyonids. In *Enaliarctos* the postglenoid foramen is small (Mitchell and Tedford 1973:249). It is absent in "*Monachus*" but relatively large in *Phoca*, suggesting it may be secondarily derived among some phocids. We have coded the Phocini as polymorphic for this character since this foramen was present in most but not all specimens of *Histricophoca* examined by Burns and Fay (1970). Berta (1991) identified the derived condition as a pinnipedimorph synapomorphy.

41. Pit for tympanohyal [= vagina processus styloidei of Mitchell and Tedford (1973:227, fig. 9) and Mitchell (1968)]. 0 = closely associated with stylomastoid foramen, 1 = anterior to stylomastoid foramen. In ursids (including *Cephalogale*) the pit for the tympanohyal lies with the stylomastoid foramen in a common fossa (Mitchell and Tedford 1973:246), contradicting Wozencraft's (1989) statement that ursids are characterized by the derived condition. In all pinnipedimorphs except phocids the tympanohyal pit lies very close and posteromedial to the stylomastoid foramen. By contrast, in phocids the tympanohyal lies ventral and anterior to the stylomastoid foramen.

42. Basioccipital. 0 = long and narrow, 1 = short, broad, and widened posteriorly. The derived condition unites odobenids, phocids, *Allodesmus*, and *Desmatophoca* (Wyss 1987; Berta 1991).

43. Jugular (= posterior lacerate) foramen. 0 = unenlarged, 1 = enlarged, 2 = further enlarged medial to basioccipital. Enlargement of the jugular foramen is a pinnipedimorph synapomorphy (Wyss 1987; Berta 1991). We disagree with Wozencraft's (1989:523) claim that a large posterior lacerate foramen also characterizes canids and ursids.

A secondary modification of this feature in which the posterior lacerate foramen extends medial to the tympanic bulla unites the phocines (see Wyss 1988b:16).

Barnes' (1989) use of an expanded posterior lacerate foramen as an "otarioid" synapomorphy substantiates our recognition of the derived condition as distinct from that seen in terrestrial carnivorans and validates its use in phylogenetic analysis. If this feature is reliable enough to diagnose "otarioids," it is equally valid in diagnosing pinnipedimorphs.

44. Basioccipital–basisphenoid region. 0 = strongly concave, 1 = flat to convex. Burns and Fay (1970) noted that in all phocines the basioccipital–basisphenoid region is flat to convex. In ursids, *Enaliarctos*, "monachines," otariids, odobenids, *Allodesmus*, and *Desmatophoca* this region is strongly concave (Davis 1964; Barnes 1972; Repenning and Tedford 1977; Barnes 1987; Wyss 1988b). Hence, the derived condition is a phocine synapomorphy.

45. Paroccipital process. 0 = small, 1 = enlarged posterolaterally. Related to conformation of the mastoid process (character 24) is the morphology of the paroccipital process. In ursids, *Enaliarctos*, *Pteronarctos*, otariids, odobenids, and phocids the paroccipital processes are small. In *Desmatophoca*, *Allodesmus*, and *Pinnarctidion* (Berta 1991) these processes are enlarged posterolaterally.

46. Auditory ossicles. 0 = unenlarged, 1 = enlarged. Enlarged ossicles unite odobenids, *Allodesmus*, phocids, *Desmatophoca*, and *Pinnarctidion*. Related to this character is the size of the epitympanic recess containing the ossicles. Many mustelids, however, have large epitympanic recesses (sinuses) without enlarged ossicles.

47. Muscular process of malleus. 0 = present, 1 = very reduced or absent. Among terrestrial carnivorans only ursids have lost the muscular process (site for insertion of tensor tympani) (Doran 1878). This process is absent in all pinnipeds also. Wozencraft (1989) incorrectly argued that absence of the muscular process is primitive.

Flynn et al. (1989:94) followed Segall (1943), who reported that ursids possess at most a very reduced muscular process. Because Segall united ursids and procyonids on the basis of the reduced muscular process Flynn et al. did not treat this feature as an ursid–pinnipedimorph synapomorphy. Wozencraft (1989:524) distinguished ursids, melines, mephitines, and lutrines from canids, procyonids, and mustelines by their small rather than large muscular processes. Wyss has rechecked Segall's carnivoran ossicle collection at the Field Museum of Natural History (Chicago) and reaffirmed that the muscular process is indeed invariably absent in bears and present in procyonids.

The derived condition, extreme reduction or loss of the muscular process on the malleus, we recognize as an ursid–pinnipedimorph synapomorphy. Because of the variation in the outgroups, this character was polarized on subsequent runs of the data.

48. Processus gracilis and anterior lamina of malleus. 0 = unreduced, 1 = reduced. As observed by Doran (1878), in terrestrial carnivorans as in most mammals there is a slender process and a broad lamina extending between the head region and the manubrial base. In phocids, otariids and *Odobenus* the processus gracilis and associated lamina are greatly reduced or absent. Wozencraft (1989) reversed the polarity of this character.

Berta (1991) used the derived condition to unite all pinnipeds excluding *Enaliarctos*. Without further quantification the condition in *Enaliarctos* cannot be judged significantly different from that of other pinnipedimorphs.

49. Middle ear cavity and external auditory meatus. 0 = cavernous tissue absent, 1 = cavernous tissue developed, 2 = unique pattern of tissue development. The middle ear cavity of pinnipeds is filled by a distensible tissue thought to inflate with blood in response to increasing external pressure during diving (Repenning 1972). Phocids (exclusive of at least "*Monachus*" *schauinslandi* show a unique (at least among pinnipeds) pattern of distribution of the cavernous tissue, thickest near the floor and roof of the middle ear cavity, thinning near the eustachian tube, across the tympanic membrane, and in the epitympanic recess (Wyss 1988b).

50. Pseudosylvian sulcus. 0 = weakly present or absent, 1 = strongly developed. In *Enaliarctos mealsi* the "sylvian fossa (or more correctly pseudosylvian sulcus) is enlarged to a broad and deep crease down the side of the brain, effectively separating the cerebrum into front and back halves. Sunken within the fossa is the gyrus arcuatus primus" (Mitchell and Tedford 1973:237). According to Barnes (1979) the "Enaliarctinae" can be distinguished from other pinnipeds by their prominent pseudosylvian sulcus. He distinguished *Pteronarctos* from *Enaliarctos* by its shallower pseudosylvian sulcus (Barnes 1989). Our comparisons with additional specimens of *Pteronarctos* show that *P. goedertae* (USNM 335432) has strongly developed pseudosylvian sulci.

The pseudosylvian sulcus does not appear in amphicyonids or, from the skull and endocranial cast, strongly in *Cephalogale*. The derived condition occurs in *Enaliarctos* and variably in *Pteronarctos* (Berta 1991).

Mandible

51. Angular (= pterygoid) process. 0 = unreduced and located near base of ascending ramus, 1 = reduced and elevated above base of ascending ramus. A well-developed angular process positioned near the base of the ascending ramus characterizes terrestrial carnivorans, *Enaliarctos*, and otariids. The derived condition occurs in "monachine" phocids, odobenids, *Allodesmus*, and *Desmatophoca* (Emlong specimens).

52. Flange below ascending ramus. 0 = absent, 1 = present. A thinning and ventral extension of the posterior end of the mandibular ramus to form a bony flange below the angular process unites *Allodesmus*, *Desmatophoca*, and phocids (Berta 1991). Terrestrial carnivorans and other pinnipedimorphs do not develop this flange.

53. Mandibular condyle. 0 = at or slightly above level of tooth row, 1 = well elevated above tooth row. The mandibular condyle in *Allodesmus*, *Desmatophoca*, *Piscophoca*, and *Acrophoca* is elevated above the tooth row. In most terrestrial carnivorans and all other pinnipedimorphs the condyle is low.

Dentition

54. Deciduous dentition. 0 = unreduced, 1 = reduced. Numerous authors (e.g., King 1983) have noted that in pinnipeds the size of the deciduous teeth is reduced.

55. Upper incisors. 0 = six, 1 = four. Living and fossil monachines have reduced the upper incisors to four from the typical pinniped and terrrestrial carnivoran number of six (King 1966; Muizon 1982). The apparently reduced I^1 in *Allodesmus* may indicate a trend toward incisor reduction early in phocoid evolution (Wyss 1988b). This tooth is reduced or lost in the odobenines (Barnes 1989).

56. Upper incisor roots. 0 = transversely compressed, 1 = round. As noted by King (1966), the roots of the upper incisors, particularly the first two, generally are extremely compressed transversely among carnivorans (including otariids, *Enaliarctos*, *Pteronarctos*, early odobenids, *Desmatophoco*, *Allodesmus*, *Cystophora*, and the Phocini). "Monachines" and *Erignathus* are characterized by roots rounder in cross-section. We recognize the derived condition as a phocid synapomorphy with a reversal in phocines.

57. I^{1-2}, transverse groove. 0 = present, 1 = absent. In otariids the first two upper incisors have a deep transverse groove (King 1983:165). This "double cusping" is also present in ursids, canids, amphicyonids, *Enaliarctos*, *Pteronarctos*, and early odobenids. The derived condition unites phocids.

58. I^3. 0 = incisiform with oval cross-section, 1 = caniniform with circular cross-section. In fur seals the lateral incisor is incisiform with an oval cross-section, whereas in sea lions it is caniniform with a circular cross-section (Repenning et al. 1971). Berta and Deméré (1986) identified *Enaliarctos* and the fossil otariids *Thalassoleon* and *Pithanotaria* as sharing the primitive condition. The Otariinae (*Zalophus*, *Otaria*, *Eumetopias*, *Neophoca*, and *Phocarctos*) and Odobenidae share the derived condition.

In *Desmatophoca* I^3 is procumbent and oval in cross-section (Barnes 1987). This tooth is absent from reported specimens of *Allodesmus*, although Barnes (1972:14) mentioned its procumbent roots.

59. I^3, lingual cingulum. 0 = present, 1 = absent. A simple lateral incisor lacking a lingual cingulum characterizes most fossil and modern otariids (Berta and Deméré 1986). *Pithanotaria starri* shows the primitive ursid condition, in which the crown of I^3 broadens posteriorly near the base and has a distinct posteromedial lingual cingulum (Repenning and Tedford 1977). The derived condition also occurs in phocids, odobenids, and *Desmatophoca* (Berta 1991). This character is usually but not always associated with "double cusping" of I^{1-2} and is a further extension of it on the lateral incisor.

60. Number of lower incisors. 0 = three, 1 = two or none. Pinnipeds have two lower incisors (King 1983); ursids, amphicyonids, and canids have three. Because the number of lower incisors is unknown for *Enaliarctos* or *Pteronarctos* we tentatively regard this character as a pinniped synapomorphy, recognizing that it might be as general as the Pinnipedimorpha.

61. Upper canines. 0 = same size as lower, 1 = larger than lower. *Dusignathus* and *Imagotaria* can be distinguished from other odobenids by their upper and lower canines of similar sizes (Repenning and Tedford 1977). In contrast, odobenines (*Aivukus*, *Alachtherium*, *Gomphotaria*, *Odobenus*) have elongated upper canines, as a derived condition. *Enaliarctos*, *Pteronarctos*, otariids, and phocoids share the primitive condition.

62. P^3. 0 = double rooted, 1 = single rooted. The third premolar of terrestrial carnivorans and *Enaliarctos* bears two separate roots. Barnes (1989) distinguished *Pteronarctos* from *Enaliarctos* by the former's bilobed posterior root. Primitively in otariids, as judged from *Pithanotaria* and *Thalassoleon* (Repenning and Tedford 1977), P^3 is double rooted. In odobenids, *Allodesmus*, and

Desmatophoca P^3 has a single root with two or three lobes. The double-rooted condition of this tooth among phocids represents an apparent reversal to the primitive condition (Berta 1991), or, if odobenids are monophyletic, it could be a convergence in *Desmatophoca, Allodesmus*, and odobenids.

63. P^4, protocone shelf. 0 = present 1 = absent. The presence of a protocone shelf on the upper carnassial has been used to distinguish *Enaliarctos* and *Pteronarctos* from all other pinnipedimorphs (Barnes 1979, 1989). The shelflike protocone is an ursid–pinnipedimorph synapomorphy (Flynn et al. 1989; Berta et al. 1989). The occurence of a protocone shelf in *Pinnarctidion* we regard as a reversal. Because this character could not be unambiguously polarized it was excluded from the initial run of characters.

64. P^4. 0 = three-rooted, 1 = three-rooted with posterior root bilobed, 2 = double rooted, 3 = single rooted. *Enaliarctos* and apparently *Pinnarctidion* (Barnes 1979:24) possess three separate roots on the upper carnassial, the primitive condition seen in terrestrial carnivorans. Three derived states may be recognized. In *Pteronarctos* the posterior root is bilobed (1). Otariids (e.g., *Thalassoleon, Pithanotaria*), odobenids (e.g., *Imagotaria*), and *Desmatophoca* primitively possess the double-rooted condition of this tooth (2). In other otariids, other odobenids, most phocids, and *Allodesmus* P^4 has only a single root (3).

65. M^1. 0 = three-rooted, 1 = double-rooted, 2 = single-rooted. Although M^1 of *Enaliarctos mealsi* was originally described as having three roots, Barnes (1979) determined, in part from additional material, that it had only two roots. In *Cephalogale, Allocyon*, and amphicyonids M^1 is three-rooted. Primitively in otariids this tooth is double-rooted, as in the fossil otariids *Pithanotaria* and *Thalassoleon* (Repenning and Tedford 1977).

The double-rooted (including bilobed and trilobed) condition of M^1 occurs in *Pteronarctos, Desmatophoca oregonensis* (Barnes 1989), *Pinnarctidion, Enaliarctos* (Barnes 1979), the archaic odobenid *Imagotaria*, and phocids. In *Desmatophoca brachycephala* and *Allodesmus* this tooth is single-rooted (Barnes 1989), as it is in most phocids and some odobenids.

66. M^{1-2}. 0 = unreduced in size relative to premolars, 1 = reduced relative to premolars. According to Mitchell and Tedford (1973) the degree of reduction of the upper molars in *Enaliarctos* is greater than that of any known early arctoid; Berta (1991) identified it as a derived condition. Later pinnipedimorphs also show a reduced M^1 and reduction or loss of M^2 (see character 68).

67. M^{1-2} cingulum. 0 = unreduced, 1 = reduced or absent. Archaic "musteloids," *Cephalogale*, and amphicyonids show the primitive condition, large external cingulae on the upper molars; *Enaliarctos* and other pinnipedimorphs display the derived state in which the external cingulum is reduced or absent (Mitchell and Tedford 1973).

68. M^2. 0 = present, 1 = absent. The occurrence of M^2 varies within each of the major pinniped groups. Among walruses, M^2 is lacking in *Odobenus* and *Aivukus* (Repenning and Tedford 1977). In otariids, M^2 is lacking in *Pithanotaria* (although as noted by Repenning and Tedford this may be an artifact of preservation), *Eumetopias, Neophoca*, and variably in *Zalophus* (King 1983). Among phocoids *Desmatophoca* and *Allodesmus* possess this tooth but phocids do not.

M^2 is present in all ursids and amphicyonids and variably present among archaic "musteloids" such as *Mustelictis, Amphictis, Amphicticeps*, and *Plesictis robustus* but not *P. genettoides*; see Hough (1948).

69. Lower cheek-tooth row. 0 = long, 1 = short. A short row, defined relative to the distance from P_1 to the ascending ramus, occurs in *Callorhinus, Otaria* (Berta and Deméré 1986), and *Pteronarctos* (Berta, in press). The distribution of this feature suggests it originated separately in each taxon.

70. Lower premolars, large anterior cusp. 0 = absent, 1 = present. A large anterior cusp on the lower premolars occurs in *Enaliarctos* and *Desmatophoca* (Berta 1991). The primitive condition, lack of this cusp, characterizes *Cephalogale*, amphicyonids, and "musteloids" (Beaumont 1964; Baskin 1982). We suggest independent acquisition of this feature in *Enaliarctos* and *Desmatophoca*.

71. M_{1-2}, trigonid and talonid. 0 = present, 1 = suppressed. The lower molars of amphicyonids, *Cephalogale, Enaliarctos*, and *Pteronarctos* possess a trigonid. Among all pinnipedimorphs except *Enaliarctos* and *Pteronarctos* the trigonid has been suppressed. In *Cephalogale*, a crestlike entoconid and distinct hypoconid occur, whereas in *Enaliarctos* and *Pternarctos* only the hypoconid is present, an intermediate condition (Mitchell and Tedford 1973; Berta, in press). In all other pinnipedimorphs the talonid has been suppressed.

72. M_1, metaconid. 0 = present, 1 = reduced or absent. In amphicyonids the metaconid is variable, being large (*Daphoenus, Daphoenocyon*) or reduced (*Daphoenictis*) (Hunt 1974). In *Cephalogale* the metaconid is subequal to the paraconid but is progressively reduced through the lineage (Beaumont 1965:6, 33). *Enaliarctos* is characterized by a greatly reduced metaconid (Mitchell and Tedford 1973), and this cusp is suppressed in all pinnipeds except *Enaliarctos* and *Pteronarctos* (Berta, in press).

73. M_2. 0 = present, 1 = absent. All pinnipedimorphs except *Enaliarctos* and *Pteronarctos* lack M_2 (Berta 1991). This tooth is consistently present among terrestrial carnivorans, in one species of *Desmatophoca, D. oregonensis* (Berta, in press), and perhaps in *Pithanotaria* (see Repenning and Tedford 1977:58).

74. M_3. 0 = present, 1 = absent. The third lower molar is absent in all pinnipedimorphs but present in *Amphicynodon, Pachycynodon, Allocyon, Cephalogale*, and amphicyonids. Tedford (1976) united mustelids, procyonids, and phocids (Mustelida) partly on the basis of the loss of M_3. He interpreted the loss of M_3 in "otarioids" as independent. We interpret this tooth to have been lost independently among "musteloids" and pinnipedimorphs.

75. Cheek tooth crowns. 0 = compressed, 1 = bulbous. Bulbous cheek-tooth crowns characterize *Allodesmus, Desmatophoca*, and *Dusignathus* (Barnes 1989) as well as phocids.

Axial Skeleton

76. Cervical vertebrae, transverse processes and neural spines. 0 = large, 1 = small. Howell (1929:20) noted that well-developed transverse processes and neural spines on the cervical vertebrae characterize otariids, whereas the cervical vertebrae are smaller and the transverse processes less stout in phocids. The cervical vertebrae of *Odobenus* more nearly resemble those of phocids in their small size (see comments below). The primitive condition characterizes ursids (Davis 1964:78). The condition in *Enaliarctos* is unknown. The derived condition is thus either a synapomorphy uniting odobenids and phocoids, with *Allodesmus* representing a reversal, or originated independently in odobenids and phocids.

77. Cervical vertebrae. 0 = larger than thoracic and lumbar, with spinal canal less than one-half the diameter of the centrum, 1 = smaller than thoracic and lumbar, with spinal canal nearly as large as centrum. *Odobenus* and phocids share cervical vertebrae that are smaller than the thoracics and lumbars (Fay 1981:10). In otariids the cervical vertebrae are larger than the thoracics, a condition we regard as primitive on the basis of outgroup comparison. The condition in *Enaliarctos* is unknown (Berta and Ray 1990). In *Allodesmus* the cervical vertebrae appear larger than the thoracics (Mitchell 1966:8, pl. 7).

Like the previous character, this one is an odobenid + phocoid synapomorphy, with *Allodesmus* representing a reversal, or a feature independently derived in odobenids and phocids.

78. Atlas, vertebrarterial (= transverse) foramen. 0 = visible in posterior view, 1 = visible in dorsal view. Among phocids two conditions occur (King 1966). In "*Monachus*" *monachus* the foramen is visible only in posterior view, as in most terrestrial carnivorans (except canids), otariids, the fossil odobenid *Imagotaria*, *Allodesmus*, and phocines. In *Mirounga* and lobodontine phocids, the transverse foramen is visible dorsally. In "*Monachus*" *tropicalis* and *Odobenus* the foramen is partially visible in dorsal view (Wyss 1988).

79. Thoracic vertebrae, neural spines. 0 = high, 1 = low. In contrast to phocids and *Odobenus*, which have low neural spines, otariids show high neural spines on the thoracic vertebrae (King 1983:156). Ursids, *Enaliarctos*, and *Allodesmus* possess high neural spines (Davis 1964; Berta and Ray 1990; Mitchell 1966:10, pl. 10).

80. Lumbar vertebrae, transverse processes. 0 = short, 1 = long. Otariid lumbar vertebrae show small transverse processes and closely set zygopophyses, while those of phocids show larger transverse processes and more loosely fitting zygopophyses (King 1983:156). In *Odobenus*, as in the Phocidae, the transverse processes are two or three times as long as wide (Fay 1981:10), whereas in otariids these processes are about as long as wide. In ursids the transverse processes are relatively short (Davis 1964). The transverse processes of the lumbar vertebrae of *Allodesmus* (Mitchell 1968: pl. 11) and *Enaliarctos* (Berta and Ray 1990) are longer than wide. We interpret the derived condition to have arisen independently in *Enaliarctos* and in a group including odobenids, *Allodesmus*, and phocids or as primitive for pinnipedimorphs with a reversal in otariids.

81. Lumbar vertebrae. 0 = six, 1 = five. Five lumbar vertebrae are present in most pinnipeds, although six are more usual in walruses (Fay 1981; King 1983:154). In *Ursus* the number of lumbars is six in 79% of specimens and five in the remaining 21% (Davis 1964:74, table 9). *Enaliarctos* had six lumbar vertebrae (Berta and Ray 1990), whereas *Allodesmus* had five (Mitchell 1966).

As we have coded this character, it diagnoses the pinnipeds with a reversal in walruses.

Pectoral Girdle and Forelimb

82. Scapula, hooklike process of teres major. 0 = absent, 1 = present. This process is common to all phocids except *Mirounga* and "*Monachus*." The shape of the caudal angle in *Mirounga* and "*Monachus*" more nearly resembles that in odobenids, otariids, and *Allodesmus*. Hence we regard the hooklike process as an apomorphy of phocines and lobodontines (Wyss 1988b).

83. Scapula, acromion process. 0 = knoblike, 1 = reduced. The acromion process is reduced in the phocines. A knoblike acromion occurs in ursids, *Allodesmus*, *Odobenus*, otariids, and *Enaliarctos* and is therefore likely primitive for pinnipeds (Wyss 1988b).

84. Scapula, scapular spine. 0 = unreduced, 1 = slightly reduced, 2 = very reduced. Phocids exemplify three distinctive patterns of scapular spine development (Wyss 1988b:17): a strongly developed spine that may extend to the vertebral scapular border, as in phocines, an intermediate condition in which the spine reaches or nearly reaches the scapular margin but is less prominent than in phocines, a condition seen in "*Monachus*" and *Mirounga*, and spine extremely reduced, serving only as a support of the acromion process, as in lobodontines. The scapular spine is large and well developed in ursids (Davis 1964) and amphicyonids, e.g., *Daphoenocyon* (Hough 1948).

85. Supraspinous fossa. 0 = slightly larger than infraspinous fossa, 1 = considerably larger than infraspinous fossa. A large supraspinous fossa is a constant feature in otariids, *Odobenus*, *Allodesmus*, and *Enaliarctos* (Mitchell 1966; Bisaillon and Pierard 1981; Berta and Ray 1990: fig. 3). In relation to the infraspinous fossa, the supraspinous fossa tends to become substantially reduced, particularly among the phocines. As a result the scapula of these taxa could be interpreted as more closely resembling that typical of terrestrial carnivorans than that of any other pinniped (Wyss 1988b). Berta and Ray (1990) identified the derived condition as a pinnipedimorph synapomorphy, as it is considered here. It is one of a very few possible otarioid synapomorphies (accepting a monophyletic Monachinae and convergence between that group and "otarioids"), but is contradicted by overwhelming evidence of pinniped monophyly.

86. Secondary spine of scapula. 0 = absent, 1 = present. A ridge subdividing the supraspinous fossa is present in otariids (King 1983) but not in walruses or phocids (English 1975). The condition of the spine in *Enaliarctos*, *Pteronarctos*, and *Allodesmus* is unknown. Accordingly, we regard the secondary scapular spine as an otariid synapomorphy.

87. Greater and lesser tuberosities of humerus. 0 = unenlarged, 1 = enlarged. In pinnipeds, the greater and lesser tuberosities are very prominent relative to the primitive carnivoran condition, although the greater is considerably more enlarged in otariids and the lesser more enlarged in phocids (Howell 1929). *Enaliarctos* has enlarged humeral tuberosities (Berta and Ray 1990), thus the derived condition is a pinnipedimorph synapomorphy.

88. Deltopectoral crest of humerus. 0 = not strongly developed, 1 = elongated and strongly developed, 2 = short and strongly developed. Pinnipedimorphs are distinguished from terrestrial carnivorans by having strongly developed deltopectoral crests. In "monachine" phocids, otariids, odobenids, and *Allodesmus* the deltoid crest is elongated, extending two-thirds to three-quarters the length of the shaft at which point the crest and shaft merge smoothly. In phocines the deltoid crest extends less than one half the length of the shaft and ends abruptly, in lateral view nearly overhanging the shaft. The insertion of the pectoralis is then more proximally restricted. The shorter, more abruptly ending crest in phocines does not represent the generalized phocid condition but is more likely a secondary derivation (Wyss 1988b), a conclusion supported by our analysis.

89. Supinator ridge of humerus. 0 = well developed, 1 = absent or poorly developed. The supinator ridge, absent in otariids, odobenids, and *Allodesmus* (Repenning and Tedford 1977; Mitchell 1968) is well-developed in terrestrial carnivorans, including ursids, procyonids, some mustelids (Davis 1964), and *Enaliarctos* (Berta and Ray 1990). As noted by King (1966), this ridge is strongly developed in phocines and absent in "monachines."

90. Humerus. 0 = long and slender, 1 = short and robust. Following Wyss (1989), Berta and Ray (1990) identified a short, robust humerus as a pinnipedimorph synapomorphy. In terrestrial carnivorans, the humerus is longer and more slender than that in pinnipeds (English 1975:90).

91. Entepicondylar foramen. 0 = present, 1 = absent. An entepicondylar (= supracondylar) foramen is usually found in phocines but not in "monachines" (some exceptions have been reported among fossil "monachines") or other pinnipeds (King 1983:157). An entepicondylar foramen is absent in *Enaliarctos*. It is present in *Ailuropoda* and *Tremarctos* but otherwise absent in the Ursidae. It is large in *Potamotherium* (Savage 1957) and amphicyonids. Absence of an entepicondylar foramen is the ancestral pinnipedimorph condition (Berta and Ray 1990). Uncertainties

in polarity notwithstanding, absence of this foramen cannot effectively be used to diagnose "otarioids" (Barnes 1989) because this condition also likely pertains ancestrally to phocids.

92. Olecranon fossa. 0 = deep, 1 = shallow. The humerus of all pinnipedimorphs including *Enaliarctos* is characterized by a shallow olecranon fossa. The olecranon fossa of terrestrial carnivorans is deep (Berta and Ray 1990). Hence we regard this feature as a pinnipedimorph synapomorphy.

93. Diameter of humeral trochlea. 0 = same as diameter of distal capitulum, 1 = considerably larger than diameter of distal capitulum. Repenning and Tedford (1977) used this feature to distinguish odobenids from otariids. In odobenids the anteroposterior diameter of the trochlea is considerably larger than that of the distal capitulum. In *Allodesmus* the trochlea is approximately the same diameter as the distal capitulum. In *Erignathus* and the Phocini the trochlea is larger than the distal capitulum. From this distribution, we interpret this character as having arisen independently in the Odobenidae and Phocinae, then having been lost in *Cystophora*.

94. Olecranon process. 0 = knoblike and unexpanded, 1 = laterally flattened and posteriorly expanded. The pinniped condition, in which the olecranon process is laterally flattened and posteriorly expanded, is not seen elsewhere in the Carnivora or in other aquatic mammals (Wyss 1989). As identified by Berta and Ray (1990), the derived condition unites pinnipeds; it does not occur in *Enaliarctos*.

95. Radius. 0 = convexly arched and unexpanded, 1 = markedly flattened anteroposteriorly, with expanded distal half. The derived condition characterizes a group at least as inclusive as the Pinnipedia (Howell 1929; King 1983; Wyss 1988a) and it may be found to characterize the Pinnipediformes once a *Pteronarctos* radius becomes known. It is approached slightly in *Potamotherium* (Savage 1957). In terrestrial carnivorans, the radius is convex and bent in a sigmoid curve in the lateral plane.

96. Pronator teres process. 0 = absent, 1 = present, proximal, 2 = present, distal. Howell (1929) described a well-defined "pronator teres process" on the shaft of the medial side of the radius in pinnipeds. This feature is not strongly marked among terrestrial carnivorans except *Potamotherium* (Savage 1957, fig. 24).

Repenning and Tedford (1977) used the position of the pronator teres process to distinguish otariids, in which the process is more proximal, from odobenids, in which it is more distal. A more distal pronator teres process also characterizes "*Monachus*," *Mirounga*, and the fossil lobodontines *Acrophoca*, *Homophoca*, and *Piscophoca*; in *Allodesmus*, phocines, and extant lobodontines the pronator teres process is positioned proximally.

We consider the pronator teres process a pinnipedimorph synapomorphy. State 1, a proximally positioned process, is common to *Enaliarctos* and otariids. A more distal process, state 2, unites odobenids and phocids primitively, with the condition in *Allodesmus*, lobodontines, and phocines representing reversals.

97. Distally projecting ledge on cuneiform. 0 = absent, 1 = present. King (1966) considered the distally projecting process (palmar process) that arcs over the palmar surface of the fifth metacarpal head as distinctively phocine. This process is absent in otariids, odobenids (except *Imagotaria*), *Allodesmus*, "monachines," and other phocids. Terrestrial carnivorans lack a palmar process (Yalden 1970).

98. Manus. 0 = central digits (II–IV) more strongly developed, 1 = digit I emphasized, digits II–V progressively smaller. In the hand of pinnipedimorphs digit I (metacarpal I and proximal phalanx) is elongated, whereas in other carnivorans the central digits are the most strongly developed (Wyss 1987:18, fig. 6; Wyss 1989). The manus of pinnipedimorphs is ectaxonic (Brown and Yalden 1973), the digits of the pollical side being the longest and those of the ulnar side being smallest (English 1975:110). Terrestrial carnivorans show a more symmetrically arranged mesaxonic manus with digit III the longest, the second and fifth the next longest, and the pollex the shortest (English 1976:3, table 1).

Berta and Ray (1990) considered digit length individually and collectively (i.e., progressive decrease in size of digits I–V) as separate characters.

The derived condition occurs in *Enaliarctos* (Berta and Ray 1990), so we interpret it as a pinnipedimorph synapomorphy.

99. Metacarpal I, pit or rugosity. 0 = absent, 1 = pit present, 2 = rugosity present. According to Barnes (1989) the pit or rugosity on the proximal dorsal surface of metacarpal 1 for attachment of the pollicle extensor muscle distinguishes odobenids from other "otarioid" pinnipeds. He identified the imagotariines *Imagotaria* and *Pliopedia* as bearing a pit, the odobenines *Aivukus* and *Odobenus* as bearing a rugosity. Repenning and Tedford (1977) found the condition in *Dusignathus* similar to that in *Imagotaria*. There is no pit or rugosity in *Allodesmus*, otariids (Mitchell 1968), or phocids (Murie 1871). Therefore we interpret the pit or rugosity on metacarpal I as an odobenid synapomorphy.

100. Metacarpal heads. 0 = keeled with trochleated phalangeal articulations, 1 = smooth, with phalanges flat, articulations hingelike. King (1966) noted that in phocines (as in most terrestrial mammals) a longitudinal ridge divides the distal and palmar surfaces of the metacarpal head. Coinciding with this arrangement, the proximal articulation surfaces of the proximal phalanges are marked by a deep notch on their palmar margins accomodating these metapodial ridges. By contrast, in other phocids the metacarpal heads are smooth and the metacarpophalangeal and interphalangeal articulations are flatter, broader, and hingelike. The "monachine" configuration closely resembles that seen in otariids, odobenids, and *Allodesmus* (Wyss 1988b). As judged from *Enaliarctos* (Berta and Ray 1990), the ancestral pinnipedimorph condition is one in which the metacarpal heads are keeled and the phalangeal articulations are trochleated. The phocine condition thus represents a reversal to the primitive condition.

101. Metacarpal I and II. 0 = approximately equal in size, 1 = metacarpal I longer. Pinnipeds except phocines are characterized by having the first metacarpal greatly elongated and thicker in comparison to metacarpal II (King 1966; Wyss 1988b: fig. 5). Among terrestrial carnivorans these elements are approximately equal in size. Therefore we regard the phocine condition as a reversal to the primitive condition.

102. Digits, cartilaginous extensions. 0 = absent, 1 = present. Cartilaginous rods distal to each digit serve to support an extension of the flipper border; they occur and are long on both the fore- and hindflippers of otariids. Short cartilaginous extensions are present in walruses (Fay 1981) and *Allodesmus* (Mitchell 1966:15). King (1969) reported dimunitive cartilaginous extensions in the phocid *Ommatophoca* and suggested they probably exist in *Hydruga* as well.

As Wyss (1987:23) wrote, "it seems conceivable that the primitive pinniped flipper was approximated by that of the walrus (short cartilaginous extensions present), that in otariids with their emphasis on forelimb propulsion these extensions have become greatly elongate, and that in phocids with their emphasis on hindlimb propulsion the extensions have become secondarily lost. "

The probable development of cartilaginous extensions in *Enaliarctos* (as judged from the flat distal articular surface of the terminal phalanges on both hands and feet) implies they are primitive for pinnipedimorphs.

103. Foreflipper claws. 0 = long, 1 = short. As noted by King

(1966) the fore- and hindflippers of phocines are characterized by well-developed claws; in other phocids the claws tend to be poorly produced. In otariids and *Odobenus* the claws of the manus are reduced, as was probably the case in *Allodesmus*. As long claws on the manus are found among terrestrial carnivorans, we interpret them as primitive.

104. Manus, digit V, intermediate phalanx. 0 = unreduced, 1 = strongly reduced. King (1966) distinguished "monachines" from phocines by the strong reduced fifth intermediate phalanx of their manus. Yet this condition occurs in all other pinnipeds for which the region is known. Wyss (1988b, 1989) and Berta and Ray (1990) listed the derived condition as a synapomorphy of pinnipeds with a reversal in phocines.

105. Pes. 0 = central digits elongated, 1 = digits I and V emphasized. Pinnipedimorphs including *Enaliarctos* have elongated digits I and V (metatarsal I and proximal phalanx) in the pes whereas in other carnivorans the central digits are the most strongly developed in the pes (Wyss 1987:18, fig. 6; Wyss 1988a; Berta and Ray 1990).

106. Metatarsal III. 0 = approximately equal to the others; 1 = much shorter. Among "monachines" and *Cystophora* the third metatarsal is considerably shorter than the others (Wyss 1988b, fig. 7). In other pinnipeds and terrestrial carnivorans the metatarsals are approximately equal. Thus the "monachine" condition is derived, with the lengthening of this element among phocines (exclusive of *Cystophora*) a reversal to the primitive condition, or a convergence in "monachines" and *Cystophora*.

107. Hindflipper claws. 0 = unreduced, 1 = reduced, 2 = markedly reduced. As noted by King (1966) reduced claws on the hindflipper are common among "monachines." Because the hindlimb claws (at least on the central three digits) of other pinnipeds tend to be strongly developed, Wyss (1988b) interpreted this condition as a potential "monachine" synapomorphy. Terrestrial carnivorans show the primitive condition, well-developed claws on both the manus and pes.

108. Pes. 0 = short, rounded metatarsal shafts with rounded heads, associated with trochleated phalangeal articulations, 1 = long, flattened metatarsal shafts with flattened heads, associated with nontrochleated, hingelike phalangeal articulations. Correlated with the morphology of the hand is that of the foot. Pinnipeds (except phocines) are characterized by relatively long, flattened metatarsal shafts with flattened heads associated with smooth, hingelike phalangeal articulations (Wyss 1988, 1989). The ancestral pinnipedimorph condition, seen in *Enaliarctos*, resembles that of terrestrial carnivorans, in which the metatarsal heads are keeled and associated with trochleated phalangeal articulations (Berta and Ray 1990). Therefore we regard phocines as having reverted to the primitive condition.

109. Pubic symphysis. 0 = fused, 1 = unfused. In terrestrial carnivorans the pubic symphysis forms a fully ossified union, whereas in pinnipedimorphs only a ligament binds adjoining bones (Savage 1957). Berta and Ray (1990) identified the derived condition as occurring in all pinnipeds except *Enaliarctos*.

110. Ilium. 0 = relatively long, 1 = short. Compared with that of terrestrial mammals, the pinnipeds' pelvis has a shortened ilium and an elongated ischium and pubis (King 1983; see Tarasoff 1972:340, table 4 for comparisons among *Canis*, *Lutra*, *Pagophilus* and *Zalophus*). Berta and Ray (1990) identified the derived condition as a synapomorphy uniting pinnipedimorphs.

111. Ilium. 0 = anterior termination simple, 1 = strongly everted, laterally excavated anteriorly. Living phocines except *Erignathus* are characterized by a lateral eversion of the ilium accompanied by a deep lateral excavation (King 1966). Terrestrial carnivorans and other pinnipedimorphs possess the primitive condition in which the ilium is not strongly excavated laterally.

112. Insertion for ilial psoas muscle. 0 = on femur, 1 = on ilium. In all phocids the psoas major muscle inserts on the ventral edge of the ilium. In all other pinnipeds and terrestrial carnivorans this muscle inserts on the lesser trochanter of the femur (Muizon 1982: fig. 183). The derived condition is a phocid synapomorphy.

113. Separate foramen in innominate for obturator nerve. 0 = absent, 1 = present. A separate foramen for passage of the obturator nerve, the obturator foramen, occurs in *Thalassoleon mexicanus* and *Allodesmus*, variably in the arctocephaline otariids and *Odobenus* (Repenning and Tedford 1977; Mitchell 1966; Fay 1982). Phocids (exclusive of "*Monachus*" *schauinslandi*, *Piscophoca*, and *Acrophoca*) lack this foramen (Repenning and Ray 1977; Muizon 1981). The absence of the foramen in terrestrial carnivorans and *Enaliarctos* suggests that its absence in phocids (except "*M*". *schauinslandi*, *Piscophoca*, and *Acrophoca*) represents a reversal; a high degree of variability, however, makes this difficult to judge.

114. Ischial spine. 0 = unenlarged, 1 = large. A large dorsally directed ischiatic spine is present in phocids and odobenids. According to King (1983:160, fig. 6.24), muscles attached to this spine help elevate the hindflippers and produce the phocids' characteristic posture.

Ursids have a small ischial spine, the primitive condition (Davis 1964). The ischial spine is small in *Allodesmus* also (Mitchell 1966: pl. 20). Accordingly, this feature is most parsimoniously interpreted either as a synapomorphy uniting odobenids and phocoids [except *Homiphoca* (Muizon and Hendey 1980: fig. 12) and *Allodesmus*] or as independently derived in odobenids and phocids.

115. Fovea for teres femoris ligament (= lig. capitus femoralis). 0 = present and well developed, 1 = strongly reduced or absent. Pinnipeds share the derived condition of the position of the fovea on the head being barely visible and the ligament lacking (King 1983:161). *Enaliarctos* retains the primitive condition, a well-defined pit on the head for the teres femoris ligament (Berta and Ray 1990).

116. Lesser femoral trochanter. 0 = present, 1 = very reduced or absent. According to King (1983:161) "the lesser trochanter is present only as a small knob distal to the head in otariids and is absent in phocids." *Allodesmus* has a rugose raised area representing the lesser trochanter (Mitchell 1966), and *Odobenus* has a similar scar. The lesser trochanter is extremely well developed in the fossil walrus *Imagotaria*, more so than in living otariids, and contrasting even more strongly with the living walrus (Repenning and Tedford 1977:38). Since walruses primitively possess a distinct lesser trochanter, apparently its reduction or loss occurred independently in later walruses and the phocoid clade (*Allodesmus* + phocids), unless it reappeared as an autapomorphy in *Imagotaria*.

117. Greater femoral trochanter. 0 = small and rounded, 1 = large and flattened. The derived condition is a pinniped synapomorphy, as Berta and Ray (1990) identified it in all pinnipedimorphs except *Enaliarctos*. In terrestrial carnivorans and *Enaliarctos* the greater trochanter is separate from the lateral femoral border rather than being broadly continuous with it as in pinnipeds.

118. Medial inclination of condyles. 0 = slight, 1 = strong. The angle of inclination of the femoral condyles is the angle formed across the condyles to a line perpendicular to the shaft (see Tarasoff 1972: table IV for comparisons). A small angle of inclination (approximately 10°) was noted for *Potamotherium* (Savage 1957) and is the common condition for terrestrial carnivorans. With this femoral specialization is associated an increased angle of slope on

the condyles of the tibia. Berta and Ray (1990) used the derived condition to diagnose pinnipedimorphs including *Enaliarctos*.

119. Trochanteric fossa of femur. 0 = unreduced, 1 = reduced or absent. According to King (1983), the trochanteric fossa is small but present in phocines and otariids but absent in "monachines." But, as Muizon (1981) has pointed out, some "monachines" (i.e., *Homiphoca* and *Piscophoca*) have a trochanteric fossa. The primitive condition, a deep trochanteric fossa, is present among ursids (Davis 1964), *Potamotherium* (Savage 1957), and *Enaliarctos* (Berta and Ray 1990). The derived condition unites otariids, odobenids, *Allodesmus*, and phocids (i.e., the Pinnipedia, with reversals characterizing the taxa noted above).

120. Patella. 0 = flat, 1 = conical. According to King (1983:161), the patella of phocids is flatter, that of otariids and walruses, more conical. The flat patella of the fossil walrus *Imagotaria* indicates that the flattened condition may be primitive for walruses. *Allodesmus* possesses a conical patella (Mitchell 1966: pl. 20). Ursids are characterized by a relatively flat patella (Davis 1964). Since the patella of *Enaliarctos* is conical, this condition may be primitive for pinnipeds (Berta and Ray 1990), with the flattened condition representing a reversal, occurring once among early walruses and once among phocids.

121. Post-tibial fossa. 0 = weak, 1 = strong. The post-tibial (= intercondyloid) fossa is more strongly developed in phocines than in "monachines" (King 1966). This fossa is shallow in otariids, *Odobenus*, *Allodesmus*, *Enaliarctos*, and most terrestrial carnivorans. Hence, the derived condition is a phocine synapomorphy.

122. Tibia and fibula. 0 = unfused, 1 = fused proximally. The tibia and fibula are fused at their proximal ends in otariids (except *Callorhinus* and the fossil *Thalassoleon mexicanus*) and phocids (except "*Monachus*" *schauinslandi*). In walruses these elements are separate, even in old animals (King 1983:161). In *Callorhinus* the tibia and fibula are unfused (Lyon 1937). *Thalassoleon macnallyae* (in contrast to *T. mexicanus*) has a proximally fused tibia and fibula (Repenning and Tedford 1977). These elements are unfused in *Allodesmus* (Mitchell 1966), *Enaliarctos* (Berta and Deméré 1986), and terrestrial carnivorans. This distribution suggests that the ancestral pinnipedimorph condition is unfused (Berta and Ray 1990).

123. Calcaneal secondary shelf. 0 = absent, 1 = present. All living otariids possess a well-developed secondary shelf of the sustentaculum (Robinette and Stains 1970). According to Repenning and Tedford (1977:39), this shelf is not seen in *Imagotaria*. Nor have we seen it in *Odobenus*. It is "essentially lacking" in the fossil otariid *Thalassoleon mexicanus* and only slightly developed in *Hydrarctos lomasiensis* (Muizon 1978). Thus the derived condition is an autapomorphy of otariids above the level of *Thalassoleon*.

124. Calcaneal tuber. 0 = long, 1 = short. In terrestrial carnivorans, when the calcaneum is in articulation with the astragalus the calcaneal tuber extends far proximal of the astraglar head. This also tends to be the case in otariids, but in phocids the calcaneal tuber is shortened and projects posteriorly only as far as the process of the astragalus. Similarly, in odobenids and *Allodesmus* the calcaneal tuber is short and extends only slightly beyond the head (from Mitchell 1966: pls. 21, 22). In agreement with Wyss (1987), Berta and Ray (1990) identified the derived condition as a synapomorphy uniting odobenids, *Allodesmus*, and phocids.

125. Medial process on calcaneal tuber. 0 = absent, 1 = present. Repenning and Tedford (1977) noted that walruses are characterized by a prominent tuberosity on the medial side of the calcaneal tuber. This process is absent in other pinnipedimorphs and terrestrial carnivorans. Hence we interpret the derived condition as an odobenid synapomorphy.

126. Caudally directed process (calcaneal process) of astragalus. 0 = absent, 1 = present, 2 = well developed. The phocid astragalus is distinguished by a strong caudally directed process over which the tendon of the flexor hallucis longus passes. This arrangement prevents anterior flexion of the foot, resulting in seals' inability to bring their hindlimbs forward during locomotion on land. In the living walrus there is at least a tendency toward development of a calcaneal process (better developed in *Imagotaria*; Repenning and Tedford 1977), and *Allodesmus* appears to be similar (see Mitchell 1966: pls. 21, 22). A calcaneal process is absent in terrestrial carnivorans, *Enaliarctos*, and otariids (Howell 1930).

We interpret presence of a calcaneal process on the astragalus as a multistate character. An intermediate condition (1) occurs in walruses and *Allodesmus*; the second condition (2) is unique to phocids.

127. Baculum. 0 = unenlarged, 1 = enlarged. Scheffer and Kenyon (1963), Wyss (1987), and Berta and Ray (1990) showed odobenids, phocids, and *Allodesmus* to share the derived condition of large bacula; otariids retain the primitive unenlarged condition.

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128. Testes. 0 = scrotal, 1 = abdominal (i.e., inguinal). The testes of otariids and terrestrial carnivorans lie outside the inguinal ring. In contrast, in phocids and *Odobenus* the testes are inguinal (Harrison et al. 1952; Fay 1981, 1982; Davis 1964).

129. Copulation. 0 = terrestrial, 1 = aquatic. *Odobenus* and phocids (except *Mirounga*) copulate in the water, whereas otariids and other carnivorans copulate on land.

130. Pelage. 0 = abundant, 1 = sparse, 2 = secondary hairs absent. Berta and Deméré (1986) used lack of underfur as a derived condition to diagnose sea lions. Sparse underfur is also diagnostic of *Odobenus* and phocids (Scheffer 1958), in which it evolved independently from sea lions. Secondary hairs occur in otariids and the majority of phocids but are virtually absent in "*Monachus*," *Mirounga*, and *Odobenus* (Scheffer 1964; Fay 1982).

131. Natal coat. 0 = black, 1 = gray or white. Phocids exclusive of "*Monachus*" and *Mirounga* have a first pelage paler than that of otariids, odobenids, and most terrestrial carnivorans, a condition that Wyss (1988b) interpreted as a potential synapomorphy uniting phocines and lobodontines.

132. Primary hair. 0 = medullated, 1 = nonmedullated. Scheffer (1964) observed that the primary hairs of otariids have a medulla but those of phocids and *Odobenus* do not. Since medullated hair has been documented for *Canis* and *Mustela* (Noback 1951), the derived condition has been interpreted as a synapomorphy uniting phocids and *Odobenus* (Wyss 1987).

133. Mystacial whiskers. 0 = smooth, 1 = beaded. Beaded mystacial whiskers diagnose all phocids except "*Monachus*," *Erignathus* (Wyss 1988b), *Ommatophoca*, and *Hydrurga* (Ling, pers. comm.), which have retained or reverted to the primitive smooth condition.

134. Molt. 0 = cornified tissue and hair do not form sheets, 1 = cornified tissue and hair form sheets during molt. As noted by Wyss (1988b), an unusual pattern of molting characterizes *Mirounga* and "*Monachus*" *schauinslandi* (only species of that genus whose molt has yet been examined). In these seals, the primary hairs become fused to the stratum corneum so that when the pelage is shed it forms large continuous patches held together by this thin layer of cornified epidermal tissue. Wyss interpreted this feature as an apomorphy of these two species.

135. Pelage units. 0 = arranged alternately, 1 = spaced uniformly. Scheffer (1964) pointed out that in *Odobenus* and phocids the pelage units are arranged in groups of two to four or in rows. In otariids the pelage units are uniformly spaced. Because the pelage units of *Ursus* and *Canis* are arranged alternately (Meijere 1884), Wyss (1987:10) considered their uniform arrangement in otariids a synapomorphy of that family.

136. Subcutaneous fat. 0 = thin, 1 = thick. Tarasoff (1972) noted that walruses and phocids are characterized by thick layers of subcutaneous fat. These layers are less well developed in otariids and lacking in other terrestrial carnivorans, including lutrines.

137. Mammary teats. 0 = four, 1 = two. Ursids (Davis 1964), otariids, and *Odobenus* have two pairs of nipples, whereas phocids except "*Monachus*" and *Erignathus* have only one pair, thought to correspond to the posterior pair of other pinnipeds (King 1983).

138. Grooming. 0 = extensive, 1 = lacking. Associated with sparse pelage is the lack of grooming observed in walruses and phocids (Tarasoff 1972). Since grooming is recorded for lutrines we tentatively interpret lack of grooming as the derived condition.

139. External pinnae. 0 = present, 1 = absent. *Odobenus* and phocids lack external ear pinnae, the presence of which characterizes otariids and other terrestrial carnivorans.

140. Sweat-duct orifice position. 0 = distal, 1 = proximal. In the adult walrus and phocids sweat ducts open proximal to the opening of the sebaceous glands. By contrast, in otariids the sweat duct is more distal (Ling 1965, Fay 1982).

141. Venous system. 0 = hepatic sinus uninflated, caval sphincter absent, intervertebral sinus small, posterior vena cava single, 1 = hepatic sinus inflated, caval sphincter well developed, intervertebral sphincter large, posterior vena cava duplicate, route for hindlimbs gluteal. Walruses and phocids share the specialized venous system outlined above (Fay 1981). In contrast, otariids have a less specialized venous system that more closely approximates the typical mammalian pattern. Wyss (1987) used the derived condition to unite *Odobenus* and the phocids.

142. Pericardial plexus. 0 = poorly developed, 1 = well developed. Another structure of the venous system, a well-developed pericardial plexus, distinguishes phocids exclusive of "*Monachus*" *schauinslandi* from otariids and *Odobenus* (Harrison and Tomlinson 1956; King and Harrison 1961; King 1977; Fay 1981).

143. Trachea. 0 = bifurcation of bronchi anterior, 1 = bifurcation of bronchi posterior. Fay (1981) and King (1983: fig. 9.2) observed that in the walrus and phocids the trachea divides into the two primary bronchi immediately outside the lung. A similar condition occurs in ursids and canids. By contrast, in otariids the bifurcation is more anterior, at the level of the first rib, and the two elongated bronchi run parallel until they diverge to enter the lungs dorsal to the heart. Hence the derived condition represents one of the very few synapomorphies of the Otariidae.

APPENDIX 2

Diagnostic characters for the nodes and terminal taxa in Figure 2 are summarized below according to conventions used by Gauthier et al. (1988). These diagnoses were obtained from the consensus topology by means of the "describe-tree" option in PAUP version 3.0s (Swofford 1991). Synapomorphies are placed at the level(s) of generality at which they are observed. Some characters may be of a more general distribution; these are placed in brackets. Reversals are designated by a minus sign preceding the character number. Ambiguous character assignments (including convergences) are designated by an asterisk following the character number. Only terminal taxa that could be autapomorphously characterized are listed.

Pinnipedimorpha: [9], [10], 11, 15, 17*, 19*, 25, 27, [31], 40, 43, 47*, 48, [49], [54], [60], 65*, 66, 72, 80*, 85*, 87, 88, 90, 91*, 92, 96*, 98, 101*, 103*, 104*, 105, 110, 118, 120*
Enaliarctos: 50, 70*
Pinnipediformes: 3*, 9, 10, 14, 24, 64*, [81], 89*, [94], [95], 100*, 108*, [109], 113*, [115], [117], 119*
Pteronarctos: 69*
Pinnipedia: 7*, 8*, 16*, 30, 59, 63*, 64* (1 to 3), 71, 73*, 81, 94, 95, 115, 117, 119
Otariidae: 4, 12*, 17* (1 to 3), –80, 86, 135, 143
Thalassoleon: 64
Unnamed node (*Arctocephalus* + *Callorhinus* + Otariinae): 62*, 65* (1 to 2), 123
Unnamed node (*Arctocephalus* + Otariinae): –113, 122*
Callorhinus: 69*
Otariinae: 58*, 130*
Phocomorpha: 26*, 32, 34, 37*, 42, 46, 51, 57*, 76*, 77*, 79*, 96 (1 to 2), 107*, 114*, 116*, 124, 126, 127, 128, 129, 130* (0 to 2), 132, 136, 138, 139, 140, 141
Phocoidea: 1*, 2*, –3, 5, 6* (1 to 2), 13, –16, 22, 24 (1 to 2), 26 (1 to 2), 35, 39*, 45*, 52, 53*, 65* (1 to 2), 75, 133*, 137*, 142
Allodesmus: 26 (2 to 1), 39* (1 to 2), 62*, –73, –76, –77, –79, –114
Desmatophoca: 62*, 64 (3 to 2), 70*
Pinnarctidion: –7, –19, –63, 64* (3 to 0), 65* (2 to 1), 68*, –75
Phocidae: 6 (2 to 1), 12*, 17* (1 to 2), 20, 23, 28, 29, 33, 37* (1 to 2), 39* (1 to 2), 41, –45, –53, 56*, 68*, –102, 112, –113, –120, 122*, 126 (1 to 2)
Unnamed node (*Acrophoca* + *Homiphoca* + *Piscophoca* + "*Monachus*," *Mirounga* + Lobodontini): 55*, 58*, 78*, 84, 96* (1 to 2), 106*, 134*
Unnamed node (*Acrophoca* + *Homiphoca* + *Piscophoca*): –2, 36*, 53*, 64* (3 to 2)
Unnamed node (*Homiphoca* + *Piscophoca*): 82, –119, 121*
Piscophoca: 65* (2 to 1)
Homiphoca: 3, 16, –91, –114
Mirounga: 16
"*Monachus*": –137
Lobodontini: 16*, 36*, 82*, 84 (1 to 2), 96* (2 to 1), 130* (2 to 1), 131*, –134
Phocinae: (*Erignathus* + *Cystophora* + Phocini): –2, 21, 44, 82*, 83, –85, 88 (1 to 2), –89, –91, *93, *97, –100, –101, –103, –104, –105, –107, –108, 121, 130* (2 to 1), 131*
Unnamed node (*Cystophora* + Phocini): 18, 38, 43 (1 to 2), –56
Cystophora: 55*, –93, 106*
Erignathus: 16, –133, –137
Phocini: 111
Odobenidae: 17* (1 to 2), 58*, 93*, 96* (1 to 2), 99, 125
Imagotaria: 64* (3 to 2), 97*, –116, –120
Unnamed node (*Aivukus* + *Gomphotaria* + *Odobenus*): 55*, 61, 62*, 68*, 78*, 99 (1 to 2)
Unnamed node (*Gomphotaria* + *Odobenus*): 1*, –3, 12*
Odobenus: 3* (0 to 2), *65 (1 to 2)
Gomphotaria: 17* (2 to 0), –37, –113

Basicranial Evidence for Ursid Affinity of the Oldest Pinnipeds

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ABSTRACT.—Marine carnivorans of the genera *Pinnarctidion* and *Enaliarctos* (late Oligocene and early Miocene), acknowledged to be among the geologically oldest pinnipeds in the fossil record, are now known from crania that supply detailed information on basicranial structure. These fossils reveal that the basioccipital bone in these genera is deeply excavated on its lateral margins by large embayments that occupy 53.3 to 61.3% of the basioccipital width. Such embayments have not been reported in living pinnipeds but have been identified in ursid and amphicyonid carnivorans. The soft tissues that occupied these sinuses in fossil amphicyonids and ursids remain conjectural, but dissection of the embayed basioccipital in living ursids demonstrates that this pocket contains a loop of the internal carotid artery nested within a large venous (inferior petrosal) sinus. Nesting of the artery within the sinus may be a countercurrent heat-exchange mechanism to cool arterial blood flowing to the brain. Presence of these basioccipital sinuses in *Enaliarctos*, *Pinnarctidion*, and other early pinnipeds and their apparent absence in living pinnipeds suggest they have been lost or modified during evolution in Neogene marine environments. We speculate that during prolonged exercise there may be less need to cool the brain's blood supply in aquatic environments than in terrestrial habitats. The existence of the basioccipital embayment in the geologically oldest pinnipeds, coupled with the ursid morphology of their upper carnassial, supplements other evidence indicating that pinnipeds are derived from an ursid ancestor and does not support the view that pinnipeds are most closely related to mustelids.

INTRODUCTION

In their initial report on the pinniped *Enaliarctos*, Mitchell and Tedford (1973) described cranial material of three individuals referred to *Enaliarctos mealsi*: (1) the nearly complete holotype skull (LACM 4321), (2) a cranial endocast, and (3) a more poorly preserved skull comprising rostral and caudal parts. They also assigned three upper and three lower isolated cheek teeth to the genus. By the time Barnes (1979) reviewed the group, all *Enaliarctos* crania reported had been discovered on the southern and western slopes of Pyramid Hill, Kern County, south-central California, in marine rocks of late Oligocene to early Miocene age. The holotype skull was found in 1961 by Harold Meals, who, in company with Richard Bishop, also found the important isolated cheek teeth. The second (bipartite) skull and the endocranial cast were discovered a decade earlier in 1950 by paleontologist Chester Stock. Mitchell and Tedford (1973) created the pinniped subfamily Enaliarctinae for *Enaliarctos*, recognizing its significance as an important morphological link between aquatic pinnipeds and terrestrial arctoid Carnivora.

Since these early discoveries, new enaliarctine fossils have been found at a number of localities along the Pacific coast of the United States in Washington, Oregon, and California. The late Douglas Emlong collected enaliarctines now conserved in the National Museum of Natural History (Smithsonian Institution), Washington, D.C. (USNM); James and Gail Goedert and Guy Pierson have contributed new enaliarctines to the Natural History Museum of Los Angeles County (LACM). These fossils are primarily of early Miocene to early middle Miocene age (16.3 to 23.3 Ma, Harland et al. 1990), but some probably come from rocks as old as latest Oligocene. Recent publications on these new enaliarctines have described important fossils from the Pyramid Hill localities in California (Barnes 1979; Berta and Ray 1990) and new crania from the Oregon coast (Barnes 1989, 1990, 1992; Berta 1991). These discoveries demonstrate not only the diversity of latest Oligocene to early Miocene pinnipeds along the Pacific coast but also show that the postcranial skeleton of *Enaliarctos mealsi* had already evolved many aquatic specializations characterizing the skeletons of living otariids.

Although Mitchell and Tedford (1973) erected the subfamily Enaliarctinae for *Enaliarctos mealsi* only, Barnes (1979, 1989, 1992) placed additional genera (*Pinnarctidion*, *Pteronarctos*, *Pacificotaria*) in this subfamily, which he considered a basal otariid stock from which arose a number of otariid lineages. Recently, most authors have come to regard the subfamily Enaliarctinae (or its familial equivalent, Enaliarctidae) as a paraphyletic taxon (Wyss 1987; Barnes 1989; Berta 1991), and Berta (1991) has attempted to derive a cladistic scheme of relationships for these "enaliarctine" fossils. Despite the recent discovery and description of numerous early pinnipeds, disagreement as to whether a paraphyletic Enaliarctinae is an acceptable systematic category persists.

In this study we do not attempt to resolve the complex question of the phylogenetic relations of the "enaliarctine" pinnipeds. Our intent is to demonstrate the broad distribution of the embayed basioccipital in the oldest known pinnipeds, to present measurements of various taxa quantifying its size, to suggest the presence of a carotid loop within the embayment, and to argue that, when both dental and basicranial evidence is considered, a sister-group relationship of pinnipeds and ursids is highly probable. The taxonomic generality of the embayed basioccipital argues for its presence in the common ancestor of "enaliarctine" pinnipeds. Thus we employ the paraphyletic term "enaliarctine" in the sense of Barnes (1992) for the genera *Enaliarctos*, *Pinnarctidion*, *Pteronarctos*, and *Pacificotaria* without prejudging their phyletic relationships, to be determined by future cladistic studies.

Recent debate focusing on the derivation of pinnipeds from terrestrial carnivorans has generally agreed that pinnipeds must have evolved from an arctoid. There is less unanimity in the selection of the arctoid branch from which pinnipeds might have sprung. Mitchell and Tedford (1973) emphasized the multiple anatomical features of *Enaliarctos* that they interpreted as transitional between those of terrestrial arctoids and those of marine pinnipeds: the fissiped heterodont cheek teeth (particularly the upper and lower carnassials and upper molars), the pattern of convolutions on the anterior surface of the brain (based on cranial endocasts), and the structure of the basicranium (chiefly the auditory region). The form of the upper carnassial, the neuroanatomy of the endocasts, and the structure of the auditory bulla are in agreement, suggesting derivation of *Enaliarctos* from hemicyonine ursids within or near the genus *Cephalogale* (Mitchell and Tedford 1973). Although the placement of *Cephalogale* in the Hemicyoninae might be debated, most paleontologists familiar with basicranial anatomy and dentitions of arctoid carnivorans concur with this assessment of ursid

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
Proc. San Diego Soc. Nat. Hist. 29:57–67, 1994

affinities. Árnason and Widegren (1986), however, on the basis of molecular hybridization, claimed a mustelid ancestry for all living pinnipeds. Consequently, we wish to document a feature of the basicranial anatomy among the enaliarctine pinnipeds that bears importantly on this question and has largely escaped attention in previous analyses of these animals. This feature, termed the embayed basioccipital, was earlier noted by Barnes in *Enaliarctos mealsi* (Barnes 1979: 9), *Pinnarctidion bishopi* (Barnes 1979: 26), *Pteronarctos goedertae* (Barnes 1989: 13), and *Allodesmus packardi* (Barnes 1979: 9). He suggested on this basis a relationship between enaliarctines and ursids or amphicyonids. Hunt and Barnes (1991) surveyed and measured the basioccipital embayments in enaliarctines and pointed out that these structures are found in all enaliarctines known to date.

MATERIAL AND METHODS

We examined the original enaliarctine material described by Mitchell and Tedford (1973) as well as additional fossil crania discovered subsequently: (1) *Enaliarctos mealsi*, LACM 4321, genoholotype, nearly complete skull, Pyramid Hill Member of Jewett Sand, probably from the lower nodule-bearing "grit zone," LACM locality 1627, Kern Co., California; (2) *E. mealsi*, LACM 5303, bipartite skull (rostral portion and associated endocast), Pyramid Hill Member of Jewett Sand, exact stratigraphic level uncertain, LACM (CIT) locality 481, Kern Co., California; (3) *Pinnarctidion bishopi*, University of California, Berkeley, Museum of Paleontology (UCMP) 86334, genoholotype, nearly complete skull, Pyramid Hill Member of Jewett Sand, in place in the upper fossiliferous concretion-bearing bed on south face of Pyramid Hill, UCMP locality V6916 (= LACM locality 1628), Kern Co., California; (4) *P. bishopi*, LACM 5302, cranial endocast, Pyramid Hill Member of Jewett Sand, exact stratigraphic level uncertain, LACM (CIT) locality 481, Kern Co., California; (5) undescribed pinniped, LACM 128004, nearly complete skull, Pysht Formation, LACM locality 5561, Merrick's Bay, Clallam Co., Washington; (6) undescribed pinniped, LACM 134394 (J. L. Goedert 258), cranial endocast, Pysht Formation, LACM locality 5561, Merrick's Bay, Clallam Co., Washington; (7) cf. *Pteronarctos piersoni*, LACM 123817, posterior cranium, Astoria Formation, LACM locality 4851, Moloch Beach, Lincoln Co., Oregon; (8) *Pteronarctos goedertae*, LACM 123883, genoholotype, complete skull, basal part of Astoria Formation, LACM locality 5058, north end of Nye Beach, Newport, Lincoln Co., Oregon; (9) *Pteronarctos piersoni*, LACM 127972, holotype, complete skull, "Iron Mountain bed," Astoria Formation, LACM locality 4851, Moloch Beach, Lincoln Co., Oregon; (10) *Pteronarctos piersoni*, LACM 128002, paratype, complete skull, "Iron Mountain bed," Astoria Formation, LACM locality 4851, Moloch Beach, Lincoln Co., Oregon.

These fossils have been previously discussed and illustrated by Mitchell and Tedford (1973) and Barnes (1979, 1989, 1990), with the exception of numbers 5, 6, and 7, which have not yet been described in the paleontological literature. Number 5 is the subject of a manuscript in preparation by Barnes and Hunt; number 7 is illustrated for the first time in this report.

Preservation of some of these pinniped crania in a variety of indurated sedimentary matrices has conserved the three-dimensional geometry of the skulls, particularly the complex structure of the basicranium. The hardness of the rock, however, has also necessitated tedious, painstaking preparation to reveal details of the basicranial anatomy. A number of these skulls and endocasts experienced weathering as concretions in outcrops and/or on beaches prior to their collection. In some cases weathering has fortuitously removed basicranial bone in such a way as to reveal the extent of the basioccipital embayments better than normally could be seen in an undamaged skull.

Usually the basioccipital embayments have filled with sediment so that the volume and dimensions of the sinuses in life are preserved and can be measured. In some skulls, however, after the sinus filled with sediment, compression of the skull by the weight of overlying rock has compacted the basioccipital bone adjacent to the sinus to a greater degree than the bone enclosing the sediment-supported sinus itself. Hence the sinus protrudes from the skull, its surface expression slightly exaggerated by differential compaction. This should be kept in mind during viewing of the stereophotographs of pinniped basicrania. Dimensions of the sinuses were measured in millimeters with dial calipers.

BASIOCCIPITAL SINUSES IN EARLY MIOCENE PINNIPEDS

A deeply excavated lateral margin of the basioccipital bone is a characteristic feature of the basicranium of enaliarctines (*sensu* Barnes 1992) and primitive members of the subfamilies Desmatophocinae, Imagotariinae, and Allodesminae (all *sensu* Barnes 1989). Development of the sinuses is bilateral, one occurring on each edge of the bone. Each sinus is situated directly medial to the entotympanic ossification of the auditory bulla that transmits the internal carotid artery and anteromedial to the posterior lacerate foramen; they penetrate deeply into the basioccipital but do not reach the midline of the bone, hence they do not communicate.

Table 1 indicates the relative depth of penetration of the sinus into the basioccipital in various species. Depth of penetration is measured as the greatest transverse width of the sinus, at about the midpoint along the length of the entotympanic tube housing the internal carotid artery. In previously described enaliarctines the greatest transverse width approximates 1 cm in most animals.

To express depth of penetration of the sinuses relative to basioccipital dimensions, we combined the transverse width of both sinuses and expressed this value as a percentage of the total basioccipital width (Table 1). These values range from a low of about 45% in a small undescribed enaliarctine (LACM 128004) to a high of 61.3% in a referred specimen of *Enaliarctos mealsi* (LACM 5303). Included in this sample are not only enaliarctines but also early desmatophocines (*Desmatophoca*), allodesmines, and imagotariines (*Neotherium*). These values are similar to those measured for the same dimensions in living ursids (e.g., *Ursus arctos*, Univ. Nebr. State Mus. ZM-191, sinus width, 12.9 mm; basioccipital width, 50.4 mm; sinus width as percentage of basioccipital width, 51.2%. The same set of measurements in a young *Ursus americanus* is 6 mm, 26.3 mm, and 45.6%). Both pinnipeds and living ursids possess a wide basioccipital bone.

Figure 1 illustrates the surficial expression of the basioccipital sinuses in the basicranium of the bipartite skull referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973: 229). The pair of sinuses occupies 61.3% of the basioccipital width. Fine-grained dark gray quartz sand fills the sinuses and the posterior lacerate foramina. Thin (basioccipital) bone covers the ventral surface of the sinuses; the bone has been broken away from the posterior floor of the left sinus and the medial and posterior part of the right sinus, revealing the sediment plug within. However, the prominent ventral protrusion of the sinuses below the basicranium in LACM 5303 is the result of differential crushing of the basioccipital. The basicranium of the holotype of *Enaliarctos mealsi*, which is not crushed, fails to show this exaggerated bulging of the sinuses (Mitchell and Tedford 1979: 221, fig. 5). Nevertheless, the position and shape of the sinus in the holotype and LACM 5303 clearly correspond, as both display a swollen posterior terminus and a marked medial extension. The sinuses are shaped very like those in the basioccipital of the Aquitanian terrestrial ursid *Cephalogale gracile* (early Miocene, Allier Basin, France).

TABLE 1. Measurements (in mm) of maximum transverse width of the basioccipital sinus in enaliarctine and other archaic pinnipeds, and a comparison of relative development of the sinuses in various species.

Taxon and specimen[a]	Sinus width (SW)	Basioccipital width (BW)	Relative sinus width[b]
Enaliarctos mealsi			
LACM 4321, holotype	(10)[c]	37.5	53.3%
LACM 5303, referred	11.1	36.2	61.3%
Enaliarctos mitchelli			
USNM 175637, referred	9.4	34.4	54.6%
Enaliarctos emlongi			
USNM 250345, holotype	10.3	37.8	54.5%
Pinnarctidion bishopi			
UCMP 86334, holotype	(9.8)	35.1	55.8%
LACM 5302, referred	(8)	(30)	53.3%
Pacificotaria hadromma			
USNM 250320, referred	(8.4)	28.6	58.7%
Pacificotaria sp.			
USNM 250282, referred	(13.2)	46.0	57.4%
Desmatophoca oregonensis			
Univ. Oregon F735, holotype	(13.7)	57.5	47.6%
USNM 250283, referred	(11.2)	(46.8)	47.8%
Desmatophoca brachycephala			
LACM 120199, holotype	(13)	53.5	48.6%
undescribed desmatophocine			
Emlong Coll. 211	13.7	47.0	58.3%
G. Pierson 84-02-184	(12.3)	46.8	52.6%
Neotherium mirum			
LACM 131950, referred	13.6	47.6	57.1%
undescribed allodesmine			
LACM 133442	12.8	49.2	52.0%
undescribed enaliarctine			
LACM 128004	5.65.9	24.9	45–47.4%
LACM 134394	10.1	(39)	51.8%
LACM 123817	(1011)	(34.9)	57.3–63%

[a] LACM, Natural History Museum of Los Angeles County, Los Angeles; UCMP, University of California Museum of Paleontology, Berkeley; USNM, National Museum of Natural History, Smithsonian Institution, Washington.

[b] Calculated as the combined width of both right and left sinuses expressed as a percentage of total basioccipital width (2[SW]/BW).

[c] Parentheses denote estimated measurements.

To illustrate the internal structure of these basioccipital sinuses, we prepared carefully the cranial endocast (LACM 5302) referred by Barnes (1979: 17) to *Pinnarctidion bishopi* and previously assigned by Mitchell and Tedford 1973) to *Enaliarctos mealsi* (Fig. 2). Fine-grained sediment filling the sinus was removed, and the surrounding bones of the left auditory region were cleaned. Figure 2A provides a full view of the entire posterior cranium, showing that only a small amount of basicranial bone still adheres to the cranial endocast. Figure 2B, a closer view of the left auditory region, reveals the anatomical detail of the sinus and surrounding structures.

Although the petrosal promontorium has been broken, and much of it lost, the internal margin of the petrosal remains intact, displaying a shallow anteroposterior groove defining the lateral margin of the sinus. The medial limit of the sinus is defined by the basioccipital embayment. The roof of the sinus is without a bony covering because the petrosal margin is separated from the basioccipital by a wide gap filled with fine-grained sediment. In living ursids, this gap is likewise not covered by bone but is spanned by a thin but extremely strong sheet of connective tissue made up of the fused dura mater and endocranium (which separates the cranial cavity from the lumen of the inferior petrosal sinus). The lateral and medial walls and floor of the sinus are reinforced by periosteum of the basioccipital and petrosal. The lumen of the inferior petrosal venous sinus nested within this dense connective tissue tube is very difficult to dissect: a high-speed drill is required to cut away the basioccipital ventral to the sinus, exposing the floor of strong fibrous connective tissue. A scalpel can then be used to cut through the connective tissue to enter and open the sinus.

In extant ursids the interior of the sinus is lined by venous epithelium that is smooth and reflective, almost glassy in appearance, and contains a conspicuous elongated loop of the internal carotid artery. Upon exiting the auditory bulla at the anterior carotid foramen, the internal carotid makes a sharp, nearly 180° turn in order to enter the venous sinus. In ursid and amphicyonid carnivores the turning point is registered as a conspicuous depression in the basisphenoid bone immediately posterior to the foramen ovale; this depression is also found at the same location in the basisphenoid of the enaliarctine *Pinnarctidion* (LACM 5302, Fig. 2B). Although we cannot be certain whether the enlarged venous sinus of early pinnipeds contained an internal carotid loop, the depression in the basisphenoid of LACM 5302 suggests that it did because the depression demonstrates the 180° reversal in the direction of the artery necessary to create such a loop.

In June 1985, a small enaliarctine skull (basilar length approximately 10.2 cm), believed to be of latest Oligocene age, was discov-

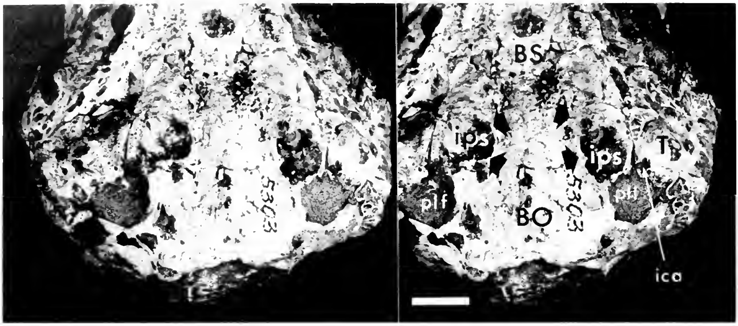

Figure 1. Ventral view of basicranium of *Enaliarctos mealsi*, LACM 5303, Pyramid Hill, Kern County, California. Crushing has accentuated the surface expression of sediment plugs filling the inferior petrosal sinus (ips), a subdural venous channel running between the basioccipital (BO) and petrosal bones that continues forward to become the cavernous sinus of the basisphenoid (BS). Black arrows mark the medial edges of these sinuses, demonstrating their maximum penetration into the basioccipital. The posterior entrance of the internal carotid artery (ica) into the auditory bulla identifies the tubular ossified entotympanic element in this early pinniped, fused to the medial edge of ectotympanic (T). Note the enlarged posterior lacerate foramen (plf). Scale bar = 1 cm.

ered by J. L. Goedert in the Pysht Formation, Clallam County, Washington (Fig. 3). This remarkable skull (LACM 128004) retains a well-preserved basicranium with an intact auditory region. Careful preparation of the basicranium revealed important details of the bulla and basioccipital sinuses. The bulla is made up of two unfused elements: the ectotympanic, covering the middle ear, and the entotympanic, which forms a tube surrounding the internal carotid artery. The nearly complete ectotympanic is preserved on the right side; a complete entotympanic tube is preserved on the left. Medial to the entotympanic ossification, the basioccipital is broken fortuitously to reveal a conspicuous sinus in the lateral part of the basioccipital. Figure 3A shows the bilateral development of the sinus within the basioccipital; both sinuses together occupy about 45–47% of the basioccipital width (Table 1). Figure 3B demonstrates that the sinus is large, two and a half times as wide as the arterial tube within the entotympanic. There appears to be a prominent depression situated in the anterointernal corner of the auditory region in the basisphenoid where the internal carotid artery, after exiting the anterior carotid foramen in the entotympanic tube, turns sharply backward to enter the basioccipital sinus; this is comparable in form and position to the same depression described above in *Pinnarctidion bishopi* (LACM 5302, see Fig. 2B).

Despite its small size, this skull belonged to an adult [based upon a suture age of at least 28 according to the method of Sivertsen (1954)]. Its size and distinctive morphology indicate that it represents a new taxon with auditory region and basioccipital sinuses configured in the same basic manner as the described Pyramid Hill enaliarctines. Thus, the shared presence of these basioccipital sinuses in several genera of early pinnipeds suggests they were present primitively within the Enaliarctinae and can be inferred to have existed in their common ancestor.

This hypothesis receives additional support from the discovery of a posterior cranium (Fig. 4) of an early middle Miocene pinniped (LACM 123817) found in 1983 by Guy Pierson in the Astoria Formation, Moloch Beach, Lincoln Co., Oregon. The fossil comes from LACM locality 4851, the same site that produced the holotype skull of *Pteronarctos piersoni* (Barnes 1990: 3) and the dome-headed chalicothere *Tylocephalonyx* (Munthe and Coombs 1979: 78–79). Barnes (1990) estimated the age of the concretion-bearing horizon (the "Iron Mountain bed") within the Astoria Formation that produced these fossils to be about 16 Ma.

It is difficult to assign this fossil to a taxon confidently because it is abraded and lacks the rostral part of the skull; however, it is similar in size and general structure to *Pteronarctos piersoni* and we tentatively identify it as cf. *Pteronarctos piersoni*.

Both auditory bullae have been lost from this basicranium, revealing the robust petrosal bones. Directly medial to these petrosals are large sediment-filled basioccipital sinuses that occupy 57.3 to 63% of basioccipital width. The sinuses appear to penetrate the basioccipital most deeply at the midpoint along the medial edge of the petrosal. The configuration of the sinus is particularly well displayed on the left side.

Barnes (1989) described the skull of *Pteronarctos goedertae* from near the base of the Astoria Formation (LACM locality 5058), Nye Beach, Lincoln Co., Oregon, estimating an early Miocene age of about 19 Ma for these sediments. The basioccipital of the holotype cranium (LACM 123883) has been cut open by Barnes, who reported (1989: 13) a small embayment for the sinus. Thus, the genus *Pteronarctos* provides evidence for basioccipital embayments over the approximately 3-million-year history of the lineage in Oregon (16 to 19 Ma).

Primitive members of other pinniped subfamilies also have an embayed basioccipital. The most primitive Imagotariinae, the earliest ancestors of dusignathines and odobenine walruses (Repenning and Tedford 1977), are the middle Miocene Japanese species of the genus *Prototaria* (see Barnes 1989; Kohno et al. 1992). The holotype cranium of *Prototaria primigena* has a large, convex protuberance on the surface of the basioccipital on each side medial to the auditory bulla. This specimen has not been dissected, so the presence of a vacuity filled with sediment cannot be demonstrated unequivocally. Another species in the same genus, however, *Prototaria* Kohno n. sp. (in press), also has similar protuberances in

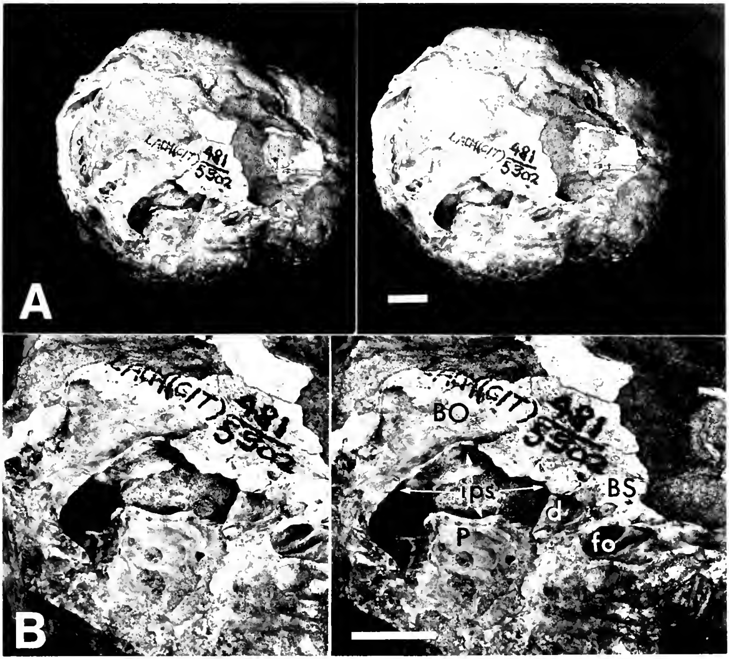

Figure 2. Cranial endocast and partial basicranium referred to *Pinnarctidion bishopi*, LACM 5302, Pyramid Hill, Kern County, California: A, ventrolateral view of complete endocast; B, detailed view of bone remaining in left auditory region. A deep embayment of the basioccipital (BO) houses an enlarged inferior petrosal venous sinus (ips) medial to petrosal (P). The venous sinus probably contained an elongated loop of the internal carotid artery, as implied by the form of a small depression (d) in the basisphenoid (BS), posterior to the foramen ovale (fo). In living ursids with the internal carotid loop, a similar depression is the location of a sharp 180° bend in the artery where it changes course to run posteriorly in the sinus, forming the carotid loop. Scale bar = 1 cm.

the same location. This cranium was sagittally sectioned by erosion prior to its discovery. The braincase has been cleaned of sediment, revealing a prominent deep embayment in the basioccipital medial to the petrosal. Thus the most primitive Imagotariinae retained the venous sinus within the basioccipital.

An embayed basioccipital is also present in a slightly more evolved imagotariine, *Neotherium mirum*, from the middle Miocene Sharktooth Hill Bonebed in California and long known only by postcranial bones (Kellogg 1931; Repenning and Tedford 1977). A virtually complete skull (LACM 131950) that undoubtedly represents this species, recently excavated from the Sharktooth Hill Bonebed, was fortuitously broken through the braincase. A deeply embayed basioccipital lies medial to the petrosal in this specimen (Fig. 5).

All later imagotariines for which we have data on the floor of the cranium have no embayment in the basioccipital. The floor of the braincase is smooth, and there is only a slight depression where the embayment exists in more primitive species. This is the case in the holotype of *Pontolis magnus* (see Repenning and Tedford 1977: pl. 10, fig. 2) and in a referred skull of *Imagotaria downsi* (see Repenning and Tedford 1977: pl. 10, fig. 1).

Data for any dusignathine or any fossil odobenine walrus do not exist. The floor of the basioccipital in the Recent *Odobenus rosmarus* lacks a typically developed basioccipital embayment but shows evidence of two small pockets that may represent vestiges of the embayed condition.

The braincase of the holotype of the early middle Miocene *Desmatophoca oregonensis* from the Astoria Formation in Oregon has been prepared, demonstrating a deeply embayed basioccipital very much like that of *Neotherium mirum*. *D. oregonensis* is the type species of *Desmatophoca* Condon, 1906. The only other species presently known in this subfamily is *Desmatophoca*

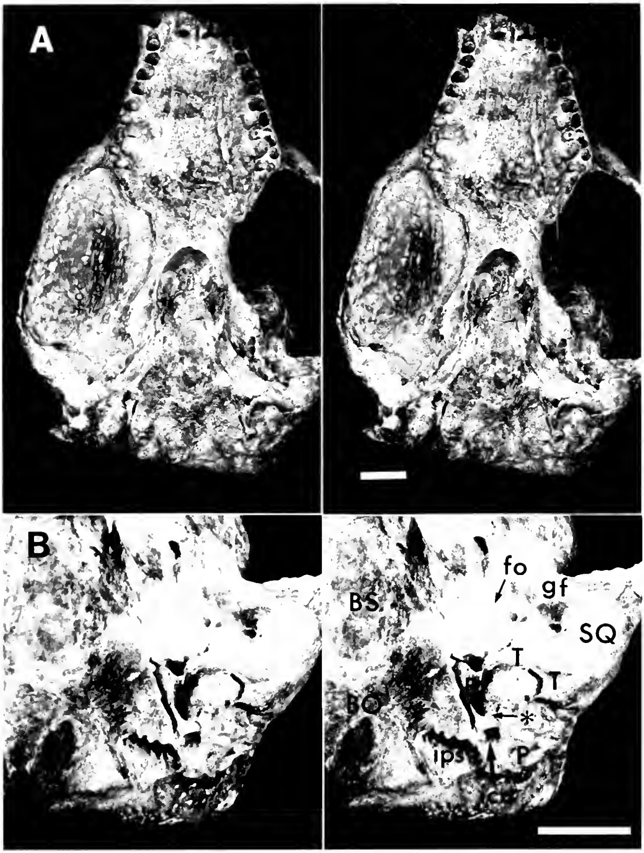

Figure 3. Nearly complete skull of an undescribed otariid pinniped, LACM 128004, Pysht Formation, Merrick's Bay, Clallam County, Washington: A, ventral view; B, detailed view of left auditory region showing the enlarged inferior petrosal sinus (ips) within the margin of basioccipital (BO). The sinus is enclosed by basioccipital (BO), entotympanic (E), and petrosal (P). Diameter of the sinus is more than twice that of the bony tube for the internal carotid artery (ica). Entotympanic (E) and ectotympanic (T) elements of the auditory bulla are both fully ossified but remain unfused where they are in contact (asterisk). BS, basisphenoid; fo, foramen ovale; gf, glenoid fossa; SQ, squamosal. Scale bar = 1 cm.

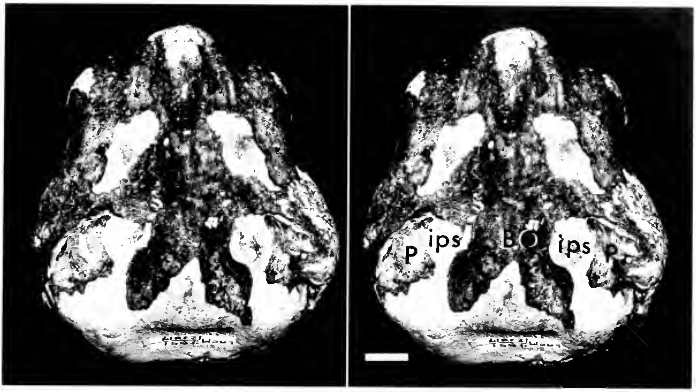

Figure 4. Ventral view of posterior cranium of cf. *Pteronarctos piersoni*, LACM 123817, Astoria Formation, Moloch Beach, Lincoln County, Oregon, ventral view. Weathering and erosion of the cranium prior to its collection abraded the basicranium, exposing the enlarged inferior petrosal sinuses (ips) situated between the petrosal (P) and embayed basioccipital (BO) bones. Scale bar = 1 cm.

brachycephala Barnes, 1987, from the late early Miocene Astoria Formation of Washington. In many features, this species is more primitive basicranially than *D. oregonensis*, and preparation of the holotype revealed a well-developed basioccipital embayment.

An embayed basioccipital is also present in the earliest known member of the subfamily Allodesminae. The evidence for this is an undescribed braincase (LACM 133442) from the early middle Miocene part of the Astoria Formation in Lincoln County, Oregon, the same horizon that produced *Pteronarctos piersoni* and *Desmatophoca oregonensis* (see Barnes 1987, 1989, 1990). This cranium has the following allodesmine features: cuboid mastoid process, large and posteriorly projecting paroccipital process, large lambdoidal and nuchal crests, well-developed sagittal crest, flat tympanic bulla, and facet for the tympanohyal in the tympanohyal pit. This specimen also has a deeply embayed basioccipital, very much as in the holotype of *Desmatophoca oregonensis* and the referred skull of *Neotherium mirum*.

The embayment appears to have been lost in later, more highly evolved Allodesminae. Evidence for this can be found in the middle Miocene *Allodesmus kernensis*, the type species of the genus *Allodesmus*. A cranium of a young adult male referred to this species (LACM 21097) has been found in the Sharktooth Hill Bonebed in California, the same horizon that produced the type material of this species and of *Neotherium mirum*, the primitive imagotariine. The braincase is open dorsally and reveals the detailed internal structure of the endocranium. Where the other pinnipeds discussed above have a deeply embayed basioccipital, this specimen has only a broad, flat, and slightly concave sulcus, suggesting that the basioccipital embayment was lost in the *Allodesmus* lineage by middle Miocene time.

BASIOCCIPITAL SINUSES IN LIVING URSIDS

From analogy with living ursids, the basioccipital embayments of extinct ursid and amphicyonid Carnivora are believed to have contained in life an artery nested within a subdural venous sinus that functioned as a countercurrent heat-exchange device to cool arterial blood flowing to the brain (Hunt 1974, 1977). This interpretation is based upon dissections of the basioccipital embayments of extant ursids (Hunt and Joeckel 1989; Hunt 1990), in which the internal carotid artery becomes greatly lengthened by doubling back on itself within the subdural inferior petrosal venous sinus situated in the lateral margin of the basioccipital bone (Fig. 6). Histological study of the internal carotid artery both within and outside the sinus has supported the heat-exchange hypothesis (Hunt 1990).

The carotid loop of ursids was originally identified by Tandler (1899) in his classic investigation of mammalian cranial arteries. Many years later, Davis (1964) drew attention to Tandler's discovery in his description of a similar convoluted internal carotid in the cavernous sinus of the giant panda, *Ailuropoda melanoleuca*. Davis also found a carotid loop in the American black bear, *Ursus americanus*. Subsequently, injection of radio-opaque material into the cranial arteries of 107 species of mammals representing 49 families allowed Boulay and Verity (1973) to produce a series of radiographs of representative species of the major carnivoran families, permitting a preliminary survey of the morphology of the internal carotid artery in arctoid, aeluroid, and cynoid Carnivora. Although they made no mention of the elongated and looped carotid of ursids, their radiographs plainly show an enormous internal carotid loop in the sloth bear, *Melursus ursinus*, a probable loop in the Asiatic black bear, *Selenarctos thibetanus*, and a well-defined loop in the giant panda, confirming the earlier work of Davis (1964). These initial descriptions of the looped carotid gave no attention to its probable function.

Tandler's (1899: 721–722) initial description of the loop formed by the internal carotid artery in the polar bear, *Thalarctos maritimus*, corresponds to our current observations in other living ursids (Hunt 1990). He wrote, "After the [internal] carotid has perforated the bony basicranium, it lies subdurally in the wide, caudally extended cavernous sinus. Here the artery takes the form of a double loop, whose individual legs appear to be twisted about their long axis. By

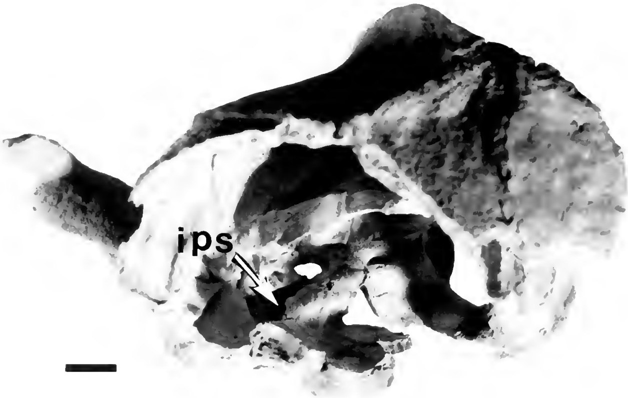

Figure 5. Internal view of the posterior cranium (LACM 131950) of the early imagotariine *Neotherium mirum*, Sharktooth Hill Bonebed, Kern County, California. Note the large embayed basioccipital bone housing the inferior petrosal venous sinus (ips).

means of this characteristic pattern, the subdural portion of the carotid attains considerable length; in the case that I investigated, the length of the vessel from its entrance through the bony basicranium to its exit through the dura at the sella turcica amounted to about 16 cm."

From Tandler's description, it is more likely that in the polar bear the carotid loop in fact lies primarily within the inferior petrosal venous sinus (between the basioccipital and petrosal), extending anteriorly from there into the cavernous sinus on the dorsal surface of the basisphenoid. The inferior petrosal venous sinus and cavernous sinus together form a single linear channel running from the posterior lacerate foramen forward to the sella turcica of the basisphenoid. Such an enormous loop of necessity requires access to the full length of this subdural sinus. Tandler reported that the internal carotid loop had been illustrated prior to 1899, but implied that it had not been discussed: "Barkow no doubt perceived this somewhat complicated relationship [of the arterial loop], based upon an obvious figure (Plate 4) of this feature given in Part 4 of his Comparative Morphology."

Davis (1964: 252) described and illustrated clearly a similar convoluted vessel in his detailed anatomical study of the giant panda: "Emerging from the carotid canal, the [internal carotid] artery enters the cavernous sinus. Immediately after entering the sinus it forms a tight knot by arching first posteriorly, then anteriorly upon itself. This is followed in the vicinity of the sella turcica by a tight S-loop, all of which greatly increases the length of the vessel; while the distance traversed within the sinus (from the carotid foramen to the anterior border of the sella) is only 22 mm., the length of the vessel is 68 mm." Davis (1964: 277) also identified an internal carotid loop in the American black bear, mentioning Tandler's earlier description of the artery in the polar bear: "A striking example of the close agreement between *Ailuropoda* and the Ursidae is the elongation and looped arrangement of the subdural part of the internal carotid. In all other carnivores the carotid passes straight through the sinus cavernosus, but in a specimen of *Thalarctos* described by Tandler the vessel immediately arched caudad in the sinus, forming a long U-shaped loop twisted around its own long axis, along the medial border of the petrosal. I found an identical situation in a specimen of *Ursus americanus*, in which the subdural part of the carotid measured 60 mm while the linear distance traversed by this part of the vessel was only 12 mm, a ratio of 1:5."

A radiograph of the basicranium of the sloth bear in Boulay and Verity's (1973: 162) catalogue shows an artery particularly elongated in the auditory region. Using their scaling for this radiograph, we estimated the length of the carotid loop to be 7.7 cm, measured from the entrance of the artery into the inferior petrosal sinus to its exit from the cavernous sinus. The same measurement is difficult to determine for their radiograph of the Asiatic black bear because the arterial path is obscured, although looping of the vessel is evident. Radiographs of the giant panda clearly demonstrate a convoluted arterial path just as Davis (1964) described: the internal carotid loop lies primarily within the cavernous sinus; its subdural length is about 8.5 cm (Boulay and Verity 1973: 168, 171).

Hunt (1990) dissected the basioccipital sinus in the American black bear and the sun bear, *Helarctos malayanus*, and discovered a similar anatomical arrangement in which an elongated loop of the internal carotid, twisted upon itself, is nested within the large saclike inferior petrosal venous sinus. The subdural length of the carotid loop in the former species measured 7.6 cm, in the latter about 8.6 cm. These measurements of the subdural length of the internal carotid are compared in Table 2, where they are also presented as a percentage of the basilar length of the skull in various living ursids.

Thus, an internal carotid loop nested within a venous subdural sinus is now known in five of the seven species of living bears and in the giant panda. Because the basioccipital embayment has been identified in dried skulls of all of the remaining living ursids, the

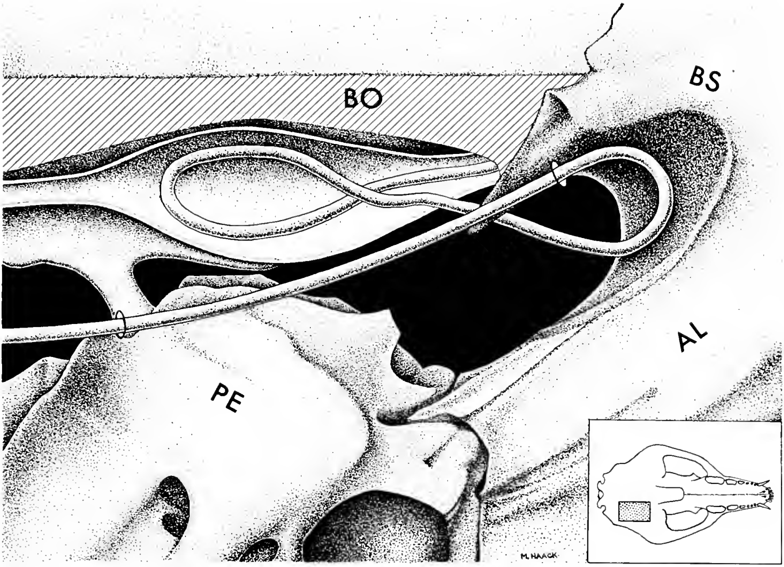

Figure 6. Left auditory region of a living ursid, showing the looped internal carotid artery nested within the inferior petrosal venous sinus. The sinus is emplaced in the lateral margin of the basioccipital bone. In the illustration the side of the basioccipital has been removed to show the artery–vein complex, and the venous sinus has been opened to show the arterial loop within. Small circles around the artery show the location of the anterior and posterior carotid foramina: the segment of the carotid between the circles lies within the medial wall of the auditory bulla (from Hunt 1977). BO, basioccipital; BS, basisphenoid; AL, alisphenoid; PE, petrosal.

presence of the carotid loop in all living members of the family Ursidae is probable. All living ursids in which the internal carotid arterial loop has been dissected or identified in a radiograph show the loop resting within the inferior petrosal venous sinus; in fact, the most posterior extent of the loop reaches to the posterior termination of the sinus. In *Ailuropoda melanoleuca*, however, the internal carotid loop is contained primarily in the cavernous sinus, hence anterior to its location in other living ursids.

A SUBDURAL INTERNAL CAROTID LOOP IN OTHER CARNIVORA

The radiographs published by Boulay and Verity (1973) make possible a survey of the subdural internal carotid in 31 carnivoran species. Not all radiographs clearly portray the artery during its entire course en route to the Circle of Willis, owing to failure of the injected medium to penetrate the artery or to an unfavorable orientation of the head during radiography. The aeluroid Carnivora, however, lack a looped carotid, many having an artery reduced and nearly nonfunctional. Aeluroids are well known for their tendency to bypass the internal carotid and to rely upon an external carotid blood supply, in which an orbital rete is interposed between the orbit and the brain (Davis and Story 1943; Hunt 1974).

Table 3 indicates the state of the subdural internal carotid in the cynoid and arctoid carnivorans injected by Boulay and Verity. There is no evidence of a carotid loop in canids. Neither do we find a carotid loop in *Procyon lotor*; Story (1951) found no internal carotid loop in any of the living procyonids.

Boulay and Verity were able to inject a large number of mustelids, including species of *Mustela*, *Martes*, *Meles*, *Lutra*, and *Gulo*. In *Mustela* and *Martes*, there is no evidence of a looped carotid artery. In both *Meles meles* and *Lutra lutra*, however, although no loop occurs in the inferior petrosal sinus, the artery displays a sinuous bend or small loop within the cavernous sinus just before reaching the Circle of Willis. These loops appear to be analogous to the loop of the internal carotid developed in the same position in *Ailuropoda*, but are not as developed.

Most interesting of all these cranial radiographs of mustelids, however, is that of the wolverine, *Gulo gulo*, which has a remarkably well-developed loop of the internal carotid. Careful comparison of landmarks on the radiograph with dissected wolverine skulls demonstrates that the carotid loop is within the cavernous sinus (Fig. 7), developed in the same location and having the same configuration as in the giant panda. There is no carotid loop in the

TABLE 2. Lengths (in cm) of and ratios between the subdural internal carotid artery and basilar length of the skull in living ursids.

Taxon	Internal carotid length within the subdural venous sinuses (ICL)	Basilar length of skull (BLS)	ICL/BLS
Ursus americanus[a]	7.6	19.15	39.7%
Helarctos malayanus[a]	~8.6	~21	40.9%
Melursus ursinus[b]	~7.7	~19–21	36.7–40.5%
Ailuropoda melanoleuca[c]	6.8	~23–24	28.3–29.6%
Ailuropoda melanoleuca[b]	8.5	~24	35.4%

[a] Measured during dissection by R. M. Hunt.
[b] Measured from radiograph (Boulay and Verity 1973:162, 168, 171).
[c] Data from Davis (1964:252).

basioccipital's inferior petrosal sinus nor is there any deep embayment of that bone of the ursid type. The condition in *Meles* and *Lutra* is possibly an initial stage in the development of a subdural internal carotid loop within the cavernous sinus like that of the wolverine. We regard the hypothesis that an internal carotid loop was present primitively in the Mustelidae and was subsequently lost in many living mustelid lineages as improbable and without basis; furthermore, a carotid loop in the cavernous sinus does not appear to register in bone and hence cannot be detected in fossils.

These observations have important implications: (1) The carotid loops of mustelids and ursids must have been independently derived—they occur in different subdural locations in the basicranium and so cannot be derived from a common ancestral condition. Many living mustelids entirely lack such a loop and, we presume, never possessed one. (2) The similar carotid loops of the giant panda (Ursidae) and wolverine (Mustelidae) are surely parallelisms and indicate that arctoid carnivorans may independently develop such loops in the cavernous sinus of the skull. (3) Only ursid and amphicyonid Carnivora and archaic pinnipeds share the same type of deep basioccipital embayments in their skulls and therefore are presumed to possess subdural carotid loops within the inferior petrosal sinus. Despite Tandler's description, we doubt that the polar bear has a significant carotid loop in its cavernous sinus—its loop is probably always within the basioccipital, as it is in all other ursine bears. (4) Arctoid Carnivora appear to have the potential to develop convoluted internal carotid arteries within the subdural sinuses that lie along the sides of the basicranial axis of Huxley. Such convoluted arteries may have evolved in various lineages in parallel, hence the similarity of the basioccipital in ursids and amphicyonids may exemplify convergence, or it may indicate relationship between the two families (a determination will require additional evidence). The similar basioccipital embayments and their contained arteries found in the living ursine bears are probably all derived from a common ancestral taxon, probably the Miocene European *Ursavus*, and do not represent parallel evolution within the modern Ursidae, as implied by the high degree of similarity among the species so far studied.

TABLE 3. Status of the internal carotid artery within the inferior petrosal and cavernous sinuses of arctoid and cynoid Carnivora, from radiographs published by Boulay and Verity (1973).

Group A: Carotid follows a straight course within subdural venous sinuses: *Canis latrans, Canis familiaris, Nyctereutes procyonoides, Procyon lotor, Mustela erminea, Mustela putorius, Martes flavigula.*

Group B: Carotid follows a straight course with slight sinuous bend in cavernous sinus: *Meles meles, Lutra lutra, Zalophus californianus, Pusa sibirica.*

Group C: Carotid does not follow a straight course: elongate loop developed either in inferior petrosal (*Melursus ursinus, Selenarctos thibetanus*) or cavernous sinus (*Ailuropoda melanoleuca, Gulo gulo*).

It is probably no accident that these looped carotids occur in the two families of large-bodied arctoid Carnivora, the Ursidae and Amphicyonidae. Dissipating heat is more difficult for larger mammals (Taylor 1980), and these large terrestrial carnivorans could well have benefited from a device to cool the blood flowing to the brain. It is interesting that among the mustelids a looped carotid artery, although of a different nature, occurs in the largest terrestrial representative of the family living today, the wolverine. We do not expect to find carotid loops in large aquatic mustelids such as *Pteronura* and *Enhydra*, because of the amount of time these animals spend in the water, but we anticipate that such a loop may have been present in the large extinct terrestrial mustelid *Megalictis*, an early Miocene carnivore that attained the size of a small bear.

SUMMARY

The presence of embayed basioccipital sinuses (associated with a common basicranial anatomical pattern) in the late Oligocene to early middle Miocene enaliarctine pinnipeds of California, Oregon, and Washington indicates the taxonomic generality and wide geographic distribution of this anatomical trait among the earliest known pinnipeds of the eastern North Pacific margin. All enaliarctines of late Oligocene to early middle Miocene age for which basicrania are known have the basioccipital embayment. All primitive members of subfamilies (Imagotariinae, Desmatophocinae, Allodesminae) believed to have evolved from enaliarctines also have an embayed basioccipital. These include the three most primitive middle Miocene imagotariines (*Prototaria primigenia, P.* n. sp., and *Neotherium mirum*), the earliest known allodesmine (a cranium from the early middle Miocene Astoria Formation), and the holotypes of the early middle Miocene desmatophocines *Desmatophoca oregonensis* and *D. brachycephala*. None of the later, more derived otariid pinnipeds has an embayed basioccipital like those of archaic fossil pinnipeds and living ursids. The structure is absent in the modern fur seals and sea lions (Otariinae) and modern walrus (Odobeninae), in which we

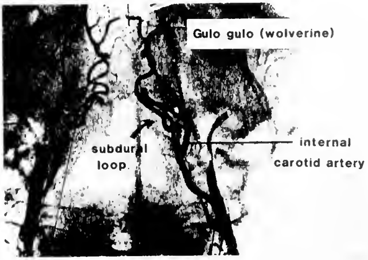

Figure 7. Radiograph of the subdural loop of the internal carotid artery within the cavernous sinus of the wolverine, *Gulo gulo* (from Boulay and Verity 1973).

noted that unusual unidentified depressions on the basioccipital margin may be vestiges of the embayment.

Among living pinnipeds the embayed basioccipital must have been lost or so altered that it is not easily recognized. Presumably the venous sinus and its carotid arterial loop have been modified through time. The usefulness of a cranial mechanism to cool arterial blood flowing to the brain seems limited in aquatic mammals. We think it significant in this regard that living pinnipeds subjected to high temperatures quickly become uncomfortable and return to the water (King 1983:146–149).

The only other Carnivora in which this basioccipital sinus is conspicuous are the terrestrial ursids and extinct amphicyonids. The ursid (not amphicyonid) upper carnassial teeth (Mitchell and Tedford 1973), type A (plesiomorphic arctoid) auditory bullae (Hunt 1974, 1977), and embayed basioccipital sinuses of enaliarctines strongly suggest ursid ancestry. Among known terrestrial fossil carnivorans, the most probably ancestral taxa are small species of the Eurasian ursid *Cephalogale* and *Amphicynodon*. Both hemicyonine and ursine ursids, as well as pinnipeds, appear to have originated within the amphicynodontine radiation. The basicranial evidence makes a sister group between pinnipeds and mustelids implausible, if enaliarctines are the ancestors of otariids or particularly if they are considered broadly representative of the basal pinniped stock from which both otariids and phocids were derived.

An internal carotid loop, within either the inferior petrosal or cavernous subdural venous sinuses of the basicranium, has evolved in parallel in several arctoid lineages. Extant ursids possess a subdural carotid loop nested in the inferior petrosal sinus. Extinct ursids and amphicyonids are believed to have had similar loops because they possess deep basioccipital embayments like those found in living bears. The giant panda and wolverine have independently evolved a subdural carotid loop within the cavernous sinus; these loops' being located differently from those of ursids and amphicyonids indicates that they must be parallel developments. The function of these carotid loops nested within a subdural venous sinus seems best explained as a device to cool warm arterial blood flowing to the brain in large exercising mammals.

No living pinniped insofar as we can determine possesses an embayed basioccipital or a carotid loop within the inferior petrosal venous sinus. Some extant pinnipeds (*Zalophus californianus*, *Pusa sibirica*, *Phoca vitulina*; Tandler 1899; Boulay and Verity 1973) do show a slightly sinuous bend of the internal carotid artery within the cavernous sinus; however, this sinuosity is not as pronounced as in the mustelids *Meles* and *Lutra*. Yet the basioccipital embayment of enaliarctines is pronounced.

We conclude from this character's taxonomic distribution that pinnipeds lost these brain-cooling devices early in their history, for most lineages in middle Miocene time, and that their subdural carotids and sinuses returned, by evolutionary reversal, to a more normal configuration.

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The Evolution of Body Size in Phocids: Some Ontogenetic and Phylogenetic Observatons

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ABSTRACT.—Large body size is generally regarded as having arisen relatively late in phocid history. Evaluation of the question of the size of the ancestral phocid in a phylogenetic context reveals, however, that large size is most likely the ancestral condition, and small size among some members of the subfamily Phocinae is best regarded as secondary. A pattern of widespread character reversal in phocid evolution coincides roughly with this inferred decrease in size. Several features diagnostic of the family Phocidae and subfamily Phocinae appear at least partly attributable to ontogenetic juvenilization.

INTRODUCTION

Extant phocids vary widely in size, from *Pusa sibirica*, with a nose-to-tail length of 1.3 m, to the two species of *Mirounga*, whose adult males measure 4–5 m (King 1983). This degree of diversity raises the question of the size of the ancestral phocid, a topic rarely addressed rigorously. Large body size among marine mammals is generally considered an adaptive response to the physiological demands imposed by a heat-dissipating aquatic environment ("large" applies to species whose adult females are 2.3 m long). The widely held notion that large size among pelagic taxa represents an evolutionary advancement follows directly from this view and finds strong support in the fossil record of certain marine Carnivora. The trend among otariids and odobenids, for example, seems to be toward increasing body size (Repenning 1976). Thus a similar shift in size during the evolution of phocids also seemed likely. Alternatively, were phocids primitively large, some members of the group only secondarily attaining more diminutive proportions? The comments presented below have a dual aim; first, to determine which of these two alternatives is supported by phylogenetic evidence, and second, to evaluate the conclusion in relation to known patterns of character evolution within the group, taking into account possible ontogenetic modifications.

The currently most widely held view of phocid systematics recognizes two subfamilies: the Phocinae, including the tribe Phocini, together with *Erignathus* and *Cystophora*, and the "Monachinae," including the monk, elephant, and Antarctic seals (Fig. 1). As a result of their presently nearly disjunct geographic distributions, phocines and "monachines'" have been informally dubbed "northern" and "southern" phocids, respectively. Because the monophyly of the "monachine" assemblage is questionable (Wyss 1988), I place its name in quotation marks, as above.

The notion that phocids were small primitively has considerable historical precedent. Most arguments favoring this view and having more than a simply intuitive basis do not, however, fare well under scrutiny.

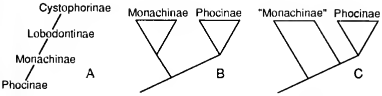

Figure 1. History of thought on phocid interrelationships. A, Laws' (1959) depiction of phocines as representing an early stage in phocid evolution; B, bipartite division of phocids recognized by most workers since King (1966); C, scheme proposed by Wyss (1988) in which one of these divisions, the "Monachinae," is considered paraphyletic. Triangles denote monophyletic groups with unspecified internal branching arrangements.

Comments by Kellogg (1922: 98) both reflect the consensus view and give an impression of its imprecise foundation: "It has been stated by Williston (1914) that 'it seems to be a law of evolution that no large creatures can give rise to races of small creatures,' and that 'the largest sea animals have been the final evolution of their respective races.' As the history of the animals in the past appeared to confirm this, it was assumed by some that the sea lions, walruses, and elephant seals therefore represent a higher degree of specialization than do smaller seals and that the latter approximate more nearly in size the ancestral group." Although Kellogg did not go on to state whether he agreed with this assumption, other workers have been more forthright in expressing their opinion on the question of primitive phocid size.

Flower (1881: 156) considered *Mirounga* to combine "in itself in the fullest degree all the characters by which the Seals are distinguished from the terrestrial Carnivora." Barrett-Hamilton (1902) echoed this view, considering the Phocinae to represent the least, the Cystophorinae (a formerly recognized association of *Mirounga* and *Cystophora*) the most "specialized" phocid subfamilies.

This interpretation was carried over into the more recent literature by Laws (1959: 430–431), who argued—partially on the basis of prior acceptance of progressive increase in body size—that "the series Phocinae–Monachinae–Lobodontinae–Cystophorinae shows increasing specialization to an aquatic life, with *Phoca* the most primitive and *Mirounga* the most specialized genera" (Fig. 1A). Laws did, however, provide additional anatomical information in support of his phylogenetic series; that evidence will be considered below.

In his influential consideration of pinniped biogeography, McLaren (1960: 20) likewise argued that the smaller species of the subfamily Phocinae are "anatomically the most primitive and *least* aquatically adapted," (emphasis in original) but offerred no morphological evidence in support of this contention.

King (1965) considered *Pagophilus* and *Cystophora* (the only phocines she treated) to represent "less adapted phocids" and later reaffirmed this view, considering the smallest phocids to be generally "less advanced" and "presumably closer to the ancestral phocid" (King 1972: 111). Finally, Mitchell (1966: 1) judged *Mirounga* "the most specialized and advanced phocid," subsequently advancing the view (Mitchell 1967) that *Pusa* (the smallest phocid) represents the "most logical" phocid structural ancestor, because of its highly generalized morphology. He did not indicate, however, whether size was part of this qualification. Other workers have regarded *Pusa* (and the other constituents of the tribe Phocini) as a rather late-diverging phocid clade but have not considered the implications of this as they relate to size change (Ray 1976; Muizon 1982b).

Much of the impetus for construing phocines to be "basal" phocids derives from the earlier incorrect paleontological practice of allocating fragmentary fossil phocids of uncertain affinities to the genus *Phoca*. This procedure may have been the outgrowth of a nomenclaturally bound preconception that *Phoca* somehow

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
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represents an "archetypal" or "average" phocid (an assessment inconsistent with recent studies), or it may have been a holdover from the Linnaean practice of lumping all pinnipeds under this name. Whatever its motivation, this practice was commonly employed at the end of the last century, when much fossil phocid material was first being described. The systematics and nomenclature of the living taxa have since been variously updated, but information concerning fossils failed to keep pace. The result has been, as discussed by Ray (1976), a paleontological literature now badly out of date. Thus it is not true (though it is often stated) that material properly referable to the genus *Phoca* itself is known from the middle Miocene. Nevertheless, the impression that an extant genus (whose living members are small) has ancient representatives, combined with the view (widespread until recent years) that phylogenetic relationship is virtually dictated by evidence from the fossil record, strongly shaped notions of phocid evolution. Paleontological hegemony in systematics has ended, and in the case of phocids comparative studies indicate that some living forms (species of the genus *Monachus*) actually represent the most persistently conservative and earliest diverging members of the family (Ray 1976; Repenning and Ray 1977). Indeed, the earlier view that *Phoca* "typified" the family significantly hindered attempts to elucidate relationships among phocids and the relationship of phocids to other carnivorans.

One additional factor contributing to acceptance of the "small equals primitive" concept of phocid evolution merits attention. During the past three decades it has been widely supposed in anatomically based studies that the Pinnipedia represent an unnatural phylogenetic assemblage, comprising on one hand otariids and odobenids, thought to be related to ursids, and, on the other, phocids, thought to be related to mustelids (*Potamotherium*, an enigmatic late Oligocene through Miocene otterlike taxon, and *Semantor*, a closely related Pliocene form, in particular) (Orlov 1933; McLaren 1960; Tedford 1976; Muizon 1982a,b).

PHYLOGENETIC CONSIDERATIONS

If the pinnipeds had multiple origins, the presumption that phocids were small ancestrally seems credible given the size of their perceived close relatives. The body weight of *Potamotherium* (based on regression of dental dimensions in living carnivorans) has been estimated as 7.3 kg (Legendre and Roth 1988); typical mustelids are several times less massive than even the smallest phocids. It is generally acknowledged, however, that support for the diphyletic ancestry of pinnipeds has eroded significantly during the past several years. Consensus is growing that the pinnipeds share an exclusive common ancestor, on the basis of morphology (Flynn et al. 1988), karyology, (Fay et al. 1967), immunology (Sarich 1969, a,b), and biochemistry (Jong 1982; Árnason and Widegren 1986). The weight of present evidence argues against the venerable notion of a phocid–mustelid alliance (Wiig 1983; Wyss 1987), with broad implications for theories of relationship within and between the major lineages of pinnipeds. At the intrafamilial level, the acceptance of pinniped monophyly is perhaps most disruptive of conventionally accepted views of relationships among phocids (Wyss 1988).

I have assumed the monophyly of pinnipeds and a close relationship among odobenids, two Miocene lineages that include *Desmatophoca* and *Allodesmus*, and the phocids. Odobenids, allodesmids, and desmatophocids have traditionally been considered closely allied to the otariids *sensu stricto* (e.g., Repenning and Tedford 1977). The conclusions of this study, however, are not strictly dependent on acceptance of either these assumptions, supported in detail by Wyss (1987, 1988).

Because their precise usage is critical to much of the discussion that follows, some of the descriptors used in the preceding text, in particular such terms as "primitive," "derived," and "advanced," bear comment. As highlighted by attempts such as Laws' (1959) to place taxa within linear arrays, elements of such outdated notions as the scala naturae or great chain of being still influence current evolutionary thought (Queiroz 1988). In the contemporary literature one still frequently sees reference to taxa as "advanced" or "highly evolved," the implication being that these are "direct line" descendants of groups occupying a "lower" evolutionary rung. Because evolution is not a process of sequential progression or linear advancement, and because an organism may be progressive in some respects and conservative in others, attributes of organisms rather than the organisms themselves are properly regarded as primitive or advanced. Thus the question is not whether "primitive" phocids were small, but whether being small was primitive for phocids.

Three lines of evidence have been used previously to assess ancestral phocids' body size. First, for reasons of presumed physiologic advantage, large body size is assumed to represent a derived condition. Despite its intuitive appeal, this proposal remains difficult to evaluate critically in the absence of corroboration from independent lines of evidence.

Second, evidence from the fossil record has been considered to support the notion of small size in the ancestral phocid. Beyond the inadvisability of interpreting the oldest known member of a group as necessarily representing the ancestor of that group or its earliest offshoot (Schaeffer et al. 1972), the fossil record implies the nearly simultaneous appearance of disparate lineages of phocids (Ray 1976). Thus the stratigraphic record documenting the early history of true seals is either highly incomplete, or the appearance of the group was marked by a rather rapid pulse of morphologic change. Beyond indicating that the earliest known phocids are similar in size to such large modern forms as the monk seals (see Ray 1976), fossils shed little light on the question of ancestral size.

Third is independent anatomical information, particularly of the appendicular skeleton. Laws (1959) cited the apparent coincidence of the assumed increase of size with changes in flipper morphology. He noted that the phocine hindflipper bears large nails, that of other phocids, vestigial or no nails. The digits of the phocine foreflipper are nearly equal in length; in other phocids the first is markedly longer and the succeeding four are progressively reduced. Using a similar anatomical basis but arguing by analogy, King (1964) hypothesized that the "trend in the Phocidae is towards the development of a 'flipper,' like that of otariids[s] and cetaceans[s], from a 'paw.'" She noted the elongated first digit, reduced fifth digit, and reduced claws as contributing to a "specialized" flipper shape as in *Ommatophoca* (a large Antarctic form).

The pedal features cited by Laws and King as occurring in the generally larger nonphocine phocids are indeed structurally advanced relative to the conditions seen in terrestrial carnivorans, and those characterizing phocines (the smaller phocids) are by all appearances more conservative. Critical to determining the possible phylogenetic implications of these features, however, is an evaluation of their generality of distribution. The seemingly "specialized" architecture of the foreflipper of *Ommatophoca* may be primitive at a more general level. Indeed, enlargement of the first digit, reduction of the fifth, and reduction of claws lose their systematic importance among the phocids when it is recalled that very similar conditions prevail in otariids, odobenids, and in all fossil pinniped lineages for which adequate material is known. These attributes are diagnostic of a more inclusive group, the Pinnipedia, and therefore do not represent advanced features of the phocids. Phocines are progressive among pinnipeds in secondarily reacquiring such otherwise terrestrial carnivoran attributes as an entepicondylar foramen, a distinct supinator crest on the humerus, strong claws, and more typically developed first and fifth digits of the manus—including a strongly produced intermediate phalanx on the fifth (Wyss 1988).

The only remaining seemingly advanced pedal character ascribed by Laws and King to the larger phocids is reduction of the third digit of the hindflipper. This feature characterizes "monachine" phocids (the largest members of the Phocidae) and in itself appears to support monophyly of this assemblage. This feature also occurs in *Cystophora*, however, a taxon generally regarded as a phocine (Wyss 1988). Nonetheless, the shortened third digit represents a potential synapomorphy of the "Monachinae," monophyly of which in turn implies that large size likely appeared at some time subsequent to the origin of phocids. Broader comparisons do not substantiate this view, however. Rather, a comparative review of 39 osteological and soft anatomical features (Wyss 1988) revealed that shortening of the third digit is more reasonably interpreted as primitive for phocids, with a reversal to a more typically carnivoran form occurring among phocines. The earlier determination that reduction of claws and enlargement of the first and reduction of fifth digits on the hand represent generalized phocid conditions is also supported independent of the question of a single versus multiple pinniped origin(s). In summary, apart from an insubstantial functional rationalization, we are left without published evidence to suggest that phocids are secondarily large.

Notions of character evolution are predicated on notions of phylogeny, theories of transformation for any given feature (size, for instance) being determined by superimposing its distribution on a branching diagram derived from unrelated comparative information. A key element of formulating such an independent phylogeny is the assessment of character polarity, a procedure involving the census of features in taxa outside the immediate group of concern (Maddison et al. 1984). However, this process, outgroup comparison, may become problematic for taxa such as phocids, where there is disagreement about higher-level affinities. Since opinion on the question of the phocids' closest allies differs as widely as mustelids and odobenids, I shall initially sidestep the controversy and attempt to demonstrate that ancestral phocid size may be securely inferred without recourse to comparison with any particular outgroup. In addition, the question of phocid size change may be resolved unambiguously irrespective of which of the currently debated internal arrangements of the group is adopted.

Acceptance of the two commonly recognized subfamilies of phocids as monophyletic groups does not permit unequivocal assessment of primitive phocid size. As depicted in Figure 2a, the phocines' size varies, but "monachines" are uniformly large. It may be argued equally parsimoniously that (1) phocids were small ancestrally and large size has originated among "monachines" and some phocines independently, or (2) large size is primitive for phocids and small size represents a secondary innovation among some phocines.

As alluded to earlier, however, a dichotomy between the Phocinae and "Monachinae" may be unjustified phylogenetically, as it appears that the "Monachinae" are paraphyletic. Note that if "monachines" are taken to be even minimally paraphyletic (i.e., divisible into two monophyletic subgroups as in Fig. 2b), the primitive condition for phocid size is most economically interpreted as large. The logic of outgroup analysis (see Maddison et al. 1984) implies that this decision is not sensitive to the pattern of relationship accepted for phocines. A "Monachinae" more highly paraphyletic than the one depicted in Figure 2b would argue even more persuasively for this interpretation.

Acceptance of even a limited degree of phylogenetic resolution among phocines dispenses with the need for "monachine" paraphyly as the basis for inferring large size as the ancestral phocid condition. It is generally agreed that *Cystophora* and *Erignathus* are successively more distant from the tribe Phocini (i.e., *Phoca*, *Pusa*, *Halichoerus*, *Histriophoca*, and *Pagophilus*). Anatomical and cytological evidence supporting this branching pattern, from King (1966), Fay et al. (1967), Burns and Fay (1970), and Muizon (1982a), were summarized by Wyss (1988). That *Erignathus* and *Cystophora* fall within the size range of "monachines" (although *Cystophora* less centrally so) establishes with reasonable assurance that phocines are characterizable as primitively large. Thus, irrespective of whether "monachines" are paraphyletic, if *Erignathus* is acknowledged as the sister taxon of other phocines (a concept having strong anatomical and karyological support) the ancestral phocid must have been large and the smallness of some phocines must be secondary.

Acceptance of either "monachine" paraphyly or the placement of *Erignathus* as the sister taxon of other phocines (two premises supportable even in the context of pinniped diphyly) conflicts with the judgment that phocids were ancestrally small. Acceptance of both premises makes the case for size decrease even more secure. Similarly, acceptance of pinniped monophyly increases confidence in this conclusion. Pinnipeds exclusive of phocids are, in general, rather large, particularly those here regarded as closely associated with phocids: odobenids, desmatophocids, and allodesmids. Figure 3 presents observed ranges of standard lengths of adult females and neonates for most living species of phocids and *Odobenus*. As for extinct lineages, the standard length of a single male specimen of *Allodesmus kernensis* has been estimated as 260 cm (Mitchell 1966), clearly placing this species within the cluster of large-bodied pinnipeds (Fig. 3). Standard lengths for other closely related but less well known species probably differed only slightly from this figure. Condylobasal length of *Desmatophoca oregonensis* is reported as 32.5 cm; that of *D. brachycephala*, 28.3 cm (Barnes 1987). Correspondingly, *Desmatophoca* was presumably shorter than *A. kernensis*; nevertheless *Desmatophoca* represents a large pinniped, clearly excluded from the cluster of small phocines formed in the lower left half of Figure 2.

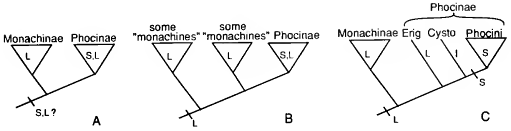

Figure 2. Alternative interpretations of ancestral phocid body size. Recognition of two monophyletic subfamilies (A) precludes unambiguous assessment of primitive phocid condition. Admittance of either "monachine" paraphyly (B) or recognition of some resolution of phocine interrelationships (C) results in acceptance of primitive condition as large. L, large; I, intermediate; S, small; *Erig*, *Erignathus*; *Cysto*, *Cystophora*.

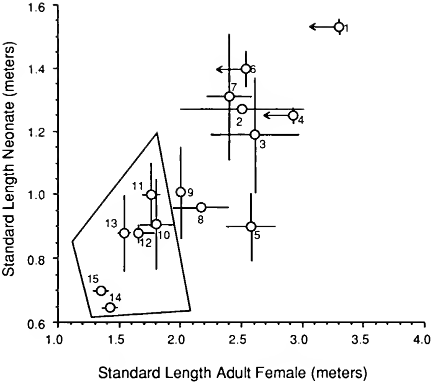

Figure 3. Ranges of adult female standard length versus neonatal standard length for most Recent phocid species and *Odobenus*. 1, *Hydrurga leptonyx*; 2, *Mirounga* (range encompasses both species); 3, *Odobenus rosmarus*; 4, *Leptonychotes weddelli*; 5, *Monachus* (range encompasses both surviving species); 6, *Erignathus barbatus*; 7, *Lobodon carcinophagus*; 8, *Ommatophoca rossi*; 9, *Cystophora crista*; 10, *Halichoerus grypus*; 11, *Pagophilus groenlandica*; 12, *Histriophoca fasciata*; 13, *Phoca vitulina*; 14, *Pusa hispida*; 15, *Pusa sibirica*. Polygon separates members of the Phocini. Arrows indicate species of which only maximum adult female size has been reported. Data from Ridgway and Harrison (1981), Fay (1981), and King (1983).

DISCUSSION

Several phylogenetic grounds, therefore, favor the hypothesis of phocid size decrease. Given this, we may consider whether the decrease is correlated with any other known patterns of character evolution. In the Phocidae there is evidence of massive character reversion (Wyss 1988). Examples of this phenomenon in phocines, in addition to lengthening of the third digit of the pes, a relatively unabbreviated fifth digit on the manus, de-emphasis of the first digit of the manus, and development of strong claws, include trochleated interphalangeal articulations, development of strong keels on metapodial heads, presence of an entepicondylar foramen and salient supinator crest on the humerus, strong scapular spine with emphasis of the infraspinous fossa, and large hook-shaped insertion of the teres major, and perhaps the resumed development of a third upper incisor and lateral compression of the upper incisors (Wyss 1988). None of these features characterized phocids ancestrally and none is found elsewhere among pinnipeds, yet all except the last are widely distributed among terrestrial arctoid carnivorans.

Could these character reversals be related to changes in size, which in turn might be related to general shifts in timing during ontogeny? Modes of such shifts have been the subject of much commentary (e.g., Albrecht et al. 1979). If patterns of character change among phocids are indeed related to ontogenetic perturbations, they are not related in any straightforward manner. The distribution of observed character change in phocid phylogeny does not seem easily accommodated by any single heterochronic trajectory discussed by Albrecht et al. and other authors. Several anatomical features illustrate these points.

One well-known uniquely derived phocid attribute is the lack of fusion (even in maturity) between the paroccipital (jugular) process of the exoccipital and the mastoid region of the petrosal (Burns and Fay 1970), a fusion common to adult terrestrial carnivorans and otariids (Fig. 4). Other phocid cranial sutures also appear to be late in closing or never close tightly, for example, the one between the basioccipital and the medial margin of the auditory region—a pattern carried to extreme among phocines (see below). As in most pinnipeds, but in contrast to terrestrial carnivorans, the anteroventral part of the orbital wall in phocids fails to ossify, resulting in the persistence into adulthood of large vacuities. Similar morphology may be seen in the fetal stages of some terrestrial carnivorans. As discussed by Burns and Fay (1970), the basicranial region of phocines is distinctive for the variability of numerous perforations, including one or two pairs in the presphenoid, a large vacuity just posterior of center in the basioccipital, and one or more on each exoccipital between the condyle and paroccipital process. These vacuities are most persistently developed among the Phocini but are not uncommon among juvenile "monachines." Likewise, pterygoid canals are often very large, even in fully mature individuals, particularly in *Monachus*, *Leptonychotes*, *Lobodon*, and *Halichoerus* (Fig. 4), whereas in other pinnipeds and terrestrial carnivorans these are by adulthood reduced to minute openings.

Two additional conditions of the phocid auditory region seem to indicate developmental juvenilization. Embryologically in mammals, the round window (fenestra cochlea) and the canal housing the cochlear aqueduct (cochlear canaliculus) arise from a common aperture on the posterior surface of the pars cochlearis of the petrosal. During development, growth of a cartilaginous eminence on the posteromedial rim of this aperture, the processus recessus, delimits separate openings into the scala tympani for both of these structures. In phocids, however, the growth of this structure is suppressed, and an osseous division between the entrance of the perilymphatic duct and the round window does not develop (Kummer and Neiss 1957; Fleischer 1973). Similarly, embryonic phocids fail to develop a prefacial commissure (= suprafacial com-

Figure 4. Ventral view of skull of "*Monachus*" *albiventer* displaying several anatomical features discussed in text. Note lack of fusion between the paroccipital process and mastoid region of the petrosal, and perforations in the presphenoid, pterygoid, and basioccipital. From Gray (1874), reversed left to right from original.

missure), a cartilaginous rod typical of mammals (including terrestrial carnivorans) that bridges the facial nerve on the dorsal surface of the petrosal and contributes to the formation of the internal auditory meatus.

The apparent loss of cartilaginous extensions of the digits in most adult phocids also seems to be readily accounted for by some relatively "simple" ontogenetic truncation. Cartilaginous extensions are otherwise present in all pinnipeds, including *Enaliarctos*, the sister taxon of the remaining pinnipeds (Wyss 1987; Berta et al. 1989). Confidence in this assessment would be enhanced by detailed ontogenetic and histologic investigation of the ends of the digits, particularly among phocines. To date, such studies have been carried out only on two lobodontines, *Lobodon* and *Leptonychotes* (Leboucq 1904a,b).

Together, these features suggest that the origin of phocids may have involved neotenic retention of embryonic traits in a group stemming from a more generalized pinniped ancestry. Enthusiasm for such an all-encompassing notion of developmental transformation is tempered, however, by the realization that other aspects of phocid morphology represent products of a uniquely accelerated ontogeny. One outstanding example of this concerns the development of the auditory region. In otariids, at birth, the elements constituting the auditory bulla remain unexpanded and unfused (as is typical of eutherian mammals possessing an ossified auditory bulla). At this ontogenetic stage the ectotympanic maintains its primitive crescentic form, and the entotympanics remain in initial stages of ossification. In phocids, in contrast, the auditory region is essentially fully formed at birth, the bulla being completely fused. Even at this early stage the deposition of thick layers of pachyostotic bone in the temporal region—a diagnostic phocid attribute—is highly advanced. Also, the massive ear ossicles of phocids appear extremely early in ontogeny, having been noted, for example, in an embryo of *Leptonychotes* 27 mm long (Fawcett 1918). Thus, if the origin of phocids did involve neoteny, the effects of such a shift clearly failed to extend to several components of their morphology, most notably details of the auditory region. Other indications of a developmental acceleration in phocids include the suppression or early replacement of the deciduous dentition and an extremely short period of lactation (King 1983).

In the subfamily Phocinae, neoteny of certain features is carried even further than in the family Phocidae as a whole. Most obvious, of course, is the dramatically smaller size of members of this subfamily, previously discussed. Also, as noted above, the lack of closure during ontogeny of several vacuities of the basi- and exoccipital bones is most marked among the Phocinae, as is the degree of separation between the auditory complex and the basioccipital. Typically (and primitively in mammals, including pinnipeds) the posterior lacerate foramen becomes defined during ontogeny as a roughly circular aperture between the posteromedial border of the auditory region and the exoccipital. Earlier in ontogeny the presumptive "foramen" is confluent anteriorly with the petrobasilar fissure, effecting a broad unossified region between the auditory complex and its medially bordering bones; subsequent obliteration of the petrobasilar fissure results in the typical adult configuration of the foramen. As first noted by King (1966) and confirmed by Burns and Fay (1970), the petrobasilar fissure rarely closes among the Phocini. The latter authors found that the fissure closed in less than 25% of their sample of any species of the tribe Phocini, in 50% of their sample of *Cystophora*, in 2% of their sample of *Erignathus*, and in 0% of their sample of other phocids.

King (1972) presented morphometric evidence interpretable as indicating the juvenilized form of the phocine cranium. Comparing the changes in size of the cranium, snout, and orbits of younger (smaller) and older (larger) skulls of a single species (*Mirounga leonina*), King noted the proportionally larger (longer, wider, and higher) crania, shorter snouts, and larger orbits of the smaller skulls. Proceeding to the comparison of skull shape among adults of different species, King (1972: 96) found that "changes in proportions of cranium, snout and orbit between the smaller and larger skulls are just those that would be evident if young and adult skulls of the same species were being compared. Thus the skulls of the smaller seals of the Family, although adult, present a more juvenile appearance than do skulls of larger animals." Recent proposals of phocid interrelationships and the probable patterns of size change imply that the juvenile appearance of the adult skulls of smaller species (Fig. 5) more likely represents a secondary derivation, as King (on the basis of incorrect paleontological evidence) had gone on to suggest.

These data might suggest that the smallest phocids (*Pusa*, *Phoca*, *Histriophoca*, and *Pagophilus*) are neotenic derivatives of a group (other phocids) that in some respects is itself already neotenic. It is difficult to reconcile, however, such a simple developmental scenario for the origin of small phocids with the known distribution of other characters within the group. Why should the origin of phocines appear to coincide with an episode of widespread character reversal, and why are these reversals maintained in taxa (small phocines) whose ontogeny is apparently truncated?

At present it seems unrealistic to attempt to explain the origin and early diversification of phocids in terms of any absolute, cohesive, or unidirectional model of developmental transmutation. Rather it appears that phocid morphology is best viewed as the product of a complex interplay between multiple, seemingly incongruent patterns of developmental modification, including both acceleration and retardation.

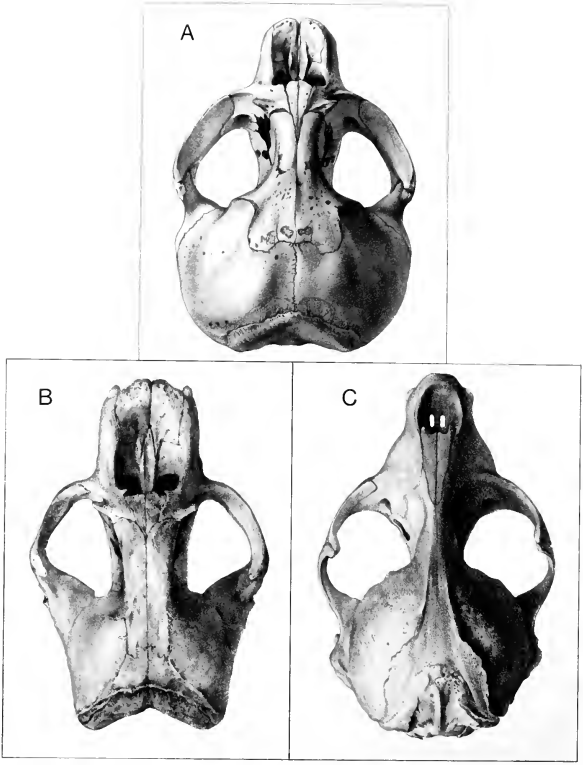

Figure 5. Comparative dorsal views of phocid skulls. A, *Mirounga leonina*, juvenile. From Gray (1874), reversed left to right. B, *Mirounga leonina*, adult. From Turner (1888), reversed top to bottom. C, *Phoca vitulina*, adult. From Blainville (1839–64), reversed top to bottom. Changes made on negative and print of C to make lighting appear to be from upper left. Note close resemblance in overall cranial proportions, particularly with respect to size of orbits and "swollenness" of cranial vault.

ACKNOWLEDGMENTS

I thank Annalisa Berta and Thomas Deméré, organizers of this symposium, for the generous offer to participate. To them and to an anonymous reviewer I owe numerous improvements to the final manuscript. Francis H. Fay provided, as is his custom, an extremely thorough and helpful commentary on the manuscript, for which I am most grateful. For their superb efforts with Figures 4 and 5, I thank Lorraine Meeker and Chester Tarka.

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Two New Species of Fossil Walruses (Pinnipedia: Odobenidae) from the Upper Pliocene San Diego Formation, California

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ABSTRACT.—Two new species of fossil walruses (Family Odobenidae) from the San Diego Formation (upper Pliocene; Blancan correlative) of San Diego County, California, are referred to the extant Odobeninae and the extinct Dusignathinae. The humerus of the new odobenine taxon shares several apomorphies with the type humerus of *Valenictus* from the late Miocene of southeastern California and is assigned to this formerly problematic genus. *Valenictus chulavistensis*, n. sp., is a tusked walrus closely related to modern *Odobenus* but more derived in possessing an entirely edentulous mandible and lacking all postcanine maxillary teeth. The toothlessness of *V. chulavistensis* is unique among known pinnipeds but parallels the condition seen in modern suction-feeding beaked whales (family Ziphiidae) and the narwhal (*Monodon*). The new dusignathine is assigned to the genus *Dusignathus* primarily because of synapomorphies of the lower jaw. *Dusignathus seftoni*, n. sp., possesses enlarged upper and lower canines and a shortened rostrum. The co-occurrence of these taxa in the San Diego Formation indicates that odobenid diversity in the eastern North Pacific continued to be greater than at present at least into late Pliocene time.

INTRODUCTION

The discovery and description of new species of fossil and living organisms is always an illuminating event, as it supplies new data points in the "history of life." Such discoveries are especially important to researchers attempting to reconstruct the phylogeny of groups as divergent as walruses, whose lack of modern diversity contrasts with their greater fossil diversity (Repenning and Tedford 1977). Not only do these discoveries fill out the taxonomic membership of known branches, they may supply the first evidence of previously unknown but related groups. Moreover, they provide insights into the morphological diversity within a clade and help define the taxonomic distribution of specific character states.

This report describes two new species of fossil walruses (family Odobenidae, *sensu* Repenning and Tedford 1977) from the marine upper Pliocene San Diego Formation of San Diego County, California. The new taxa are assignable to two monophyletic (*sensu* Hennig 1966) lineages of odobenids, one to the extinct Dusignathinae (*sensu* Barnes and Raschke 1990), the other to the Odobeninae (*sensu* Repenning and Tedford 1977), the clade that includes the living arctic walrus, *Odobenus rosmarus*.

This report is part of a more general study of the higher systematic relationships of odobenids (Deméré 1994, this volume) and builds upon the earlier work of Repenning and Tedford (1977). A rapidly improving fossil record for odobenids has contributed much to this study.

GEOLOGY

The majority of the new fossil material reported here was collected from marine sandstones of the San Diego Formation (Deméré 1983; Domning and Deméré 1984) as exposed at various localities in the eastern portion of the city of Chula Vista, southwestern San Diego County, California. The San Diego Formation in this area consists of approximately 50 m of interbedded pebble conglomerates, fine-grained massive sandstones, fine-grained laminated sandstones, and shelly sandstones. This sequence of sedimentary rocks was deposited in shoreface to middle-shelf environments (Deméré 1983).

The San Diego Formation has produced abundant and well-preserved remains of marine invertebrates and vertebrates. The marine invertebrate assemblage includes foraminifers, brachiopods, molluscs, crustaceans, and echinoderms (Hertlein and Grant 1960, 1972). The marine vertebrate assemblage includes sharks and rays, bony fishes, sea birds (Howard 1949, 1958; Chandler 1990), cetaceans (Barnes 1973; Deméré 1986), pinnipeds (Berta and Deméré 1986), and sirenians (Domning and Deméré 1984). Remains of terrestrial mammals have also been collected from this rock unit (Table 1).

The co-occurrence of *Stegomastodon* sp., *Titanotylopus* sp., *Equus* sp., *Platygonus* sp., and *Megalonyx* sp. in the San Diego Formation indicates correlation with the Blancan North American Land Mammal Age (NALMA), late Pliocene. In addition, the associated marine invertebrate assemblage indicates correlation with the "San Joaquin" molluscan stage of Addicott (1972), provincial late Pliocene, estimated to be 2–3 million years old (Deméré 1983).

METHODS AND MATERIALS

The fossil material described in this report is housed at the San Diego Natural History Museum, San Diego, California (SDSNH). Comparisons were made with specimens at other institutions including the Natural History Museum of Los Angeles County, Los Angeles, California (LACM) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Of special note is new undescribed material of *Neotherium mirum* examined at the LACM and undescribed material of *Pontolis magnus* examined at the USNM. Additional specimens cited in this report are housed at the Museum of Paleontology, University of California, Berkeley, California (UCMP); Department of Geological Sciences, University of California, Riverside, California (UCR); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); and Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB).

Cranial measurements follow Siversten (1954) and Barnes (1979), mandibular measurements follow Repenning and Tedford (1977), and postcranial measurements follow Kellogg (1931).

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Odobenidae Allen, 1880

Subfamily Odobeninae Mitchell, 1968

Valenictus Mitchell, 1961

Type species.—Valenictus imperialensis Mitchell, 1961.

Emended diagnosis.—An odobenine walrus distinguished from other taxa by the following apomorphies of the humerus: greatly

In A. Berta and T. A. Deméré (eds.)
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enlarged entepicondyle, short and robust shaft, large lesser tuberosity, and narrow bicipital groove.

Distribution.—Late Miocene to late Pliocene of southern and central California.

Included species.—*V. imperialensis* Mitchell, 1961; *V. chulavistensis*, n. sp.

Valenictus chulavistensis n. sp.

Figures 1–7

Diagnosis.—A species of *Valenictus* distinguished from *V. imperialensis* by the following features of the humerus: larger overall size, more sigmoidal posterior profile, sharply keeled supinator ridge, more robust and rectangular entepicondyle, and more obtuse angle between the shaft and the axis of the distal trochlea. Also diagnosed by the following autapomorphies: edentulous dentary, edentulous premaxilla and postcanine maxilla, osteosclerotic long bones, astragalus with broad sulcus calcanei, very reduced collum tali, and coalesced navicular and sustentacular facet. Shares the following apomorphies with tusked odobenines: enlarged, evergrowing upper canines with three layers (globular orthodentine, orthodentine, and cementum), palate narrow and arched longitudinally as well as transversely, enlarged mastoid processes as widest part of skull, shortened temporal fossa with blunt zygomatic arches, and dorsoventrally expanded postorbital process of jugal.

Type material.—Holotype: SDSNH 36786, a partial skeleton preserving the left side of the skull (maxilla, jugal, squamosal, mastoid, occipital condyle), nearly complete mandible, partial vertebral column (5 cervical, 12 thoracic, 2 lumbar, 4 sacral, and 5 caudal vertebrae), partial right and left scapulae, left humerus, radius, ulna, and manus, partial right manus, left femur, right pes, and partial left pes. Collected by Richard A. Cerutti.

Paratype: SDSNH 38227, a nearly complete skull with both canines but lacking the nasals, premaxillae, and middle ear ossicles. Collected by Richard A. Cerutti.

Etymology.— The specific name is for the city of Chula Vista, San Diego County, California, where the remains of this, and many other Pliocene marine mammals, have been found.

Holotype and paratype locality.—SDSNH locality 3551, Rancho Del Rey, city of Chula Vista, San Diego County, California.

Horizon and age.—San Diego Formation, "lower member" (Deméré 1983); late Pliocene (Blancan NALMA correlative).

Referred material.—The following SDSNH specimens were all collected from the San Diego Formation (complete locality information is available to interested researchers upon request): 38228, partial rostrum preserving the left maxilla and premaxilla; 15162, partial left C^1; 38225, right C^1; 38226, partial right C^1; 35284, partial left C^1; 25180, partial right C^1; 30796, fragmentary right C^1; 35276, partial atlas vertebra; 36796, fused sacral vertebrae (3); 38676, fused sacral vertebrae (3); 38394, left scapula; 38308, partial left humerus; 38307, right humerus, distal end; 38286, left humerus, distal end; 35263, partial left humerus; 38315, left humerus; 35275, right humerus; 38312, left humerus; 38300, partial left humerus; 38230, right ulna; 32790, right radius; 38288, left radius; 38324, right radius; 38650, right radius; 36799, left scapholunar; 36800, left unciform; 38201, left magnum; 38208, left metacarpal I; 42694, left metacarpal I; 38206, left metacarpal IV; 38339, associated right and left innominates and partial baculum; 38310, left innominate; 25145, partial left innominate; 38291, partial right innominate; 38325, partial left innominate; 32770, fragmentary right innominate; 36798, right innominate; 42751, partial left hindlimb with femur, tibia, fibula, calcaneum, navicular, mesocuneiform, and metatarsals I, II, and III; 25394, left femur; 25074, left femur; 25076, left femur, distal end; 42690, right femur; 38245, right femur, proximal end; 32767, left femur, distal end; 32777, left fibula, distal end; 42654, right fibula; 42655, right fibula; 22290, right tibia; 25087, left tibia, distal end; 35296, right tibia, distal end; 33935, left tibia, distal end; 38633, partial left tibia; 35273, left astragalus; 21130, right calcaneum; 22412, right calcaneum; 32765, left calcaneum; 25179, associated ribs and hindlimb bones with right patella and navicular, and left entocuneiform and metatarsal II; 38209, left metatarsal I; 38261, left metatarsal I.

Cranium.—The holotype partial skull (SDSNH 36786) is from a mature adult male, as indicated by closure of all preserved sutures and the narrowing of the proximal end of the upper canine (Rutten 1907).

In contrast, the paratype skull (SDSNH 38227, Figs. 1A, B; 2A, B) is from an immature male (F. H. Fay, pers. comm.). The tusks in this skull taper continuously from the root to the distal end, and many sutures are distinct. This skull was shortened anteroposteriorly by lithostatic load, with the palate displaced against the auditory bullae and beneath the basioccipital. Portions of the zygomatic arches and braincase were partially etched by root action and soil acidity. The premaxillae were largely destroyed by a bulldozer at the time of their discovery.

A referred left rostral fragment (SDSNH 38228, Figs. 2C, D) is from an immature female (F. H. Fay, pers. comm.) and of the three cranial specimens preserves the smallest canine alveolus (Table 2). The maxillary portion of SDSNH 38228 is nearly complete (surfaces are preserved for the maxilla/jugal, maxilla/frontal, maxilla/palatine, and maxilla/nasal sutures) and occurred with the only premaxilla known for this taxon.

The cranium of *V. chulavistensis* preserves many features characteristic of the tusked odobenines, including a narrow longitudinally and transversely arched palate (as in *Odobenus rosmarus* and *Alachtherium cretsii*), mastoid processes as the widest part of the skull, diagonally oriented orbitosphenoid with small, funnel-shaped optic foramen, lack of a sagittal crest, telescoping of palate beneath anterior portion of basicranium, and posterior elongation of the hard palate to the level of the glenoid fossae. In addition, the skull of this new species also preserves more generalized odobenid features including lack of supraorbital processes and large antorbital processes constructed from both maxilla and frontal.

In lateral aspect the premaxilla of SDSNH 38228 is shaped roughly like an acute right triangle, the hypotenuse being the external narial border. Anteriorly the premaxillae terminate in a conspicuous nasal process, as in *Zalophus californianus* (see Howell 1929) and most fossil odobenids (e.g., *Neotherium mirum* and *Imagotaria downsi*). The nasal process is elevated above the canine alveolus as in *Odobenus* and *Alachtherium*; however, the vertical dimension between the nasal process and the incisive border of the premaxilla is short. In *Odobenus* the nasal process is very reduced (in adults) and the narial opening is elevated well above the incisive margin. The incisive region of the premaxilla in the new taxon is edentulous, lacking all traces of alveoli (Figs. 1B, 2C). The incisive foramina are distinct and oriented nearly horizontally as they extend posterodorsally into the narial opening. The external narial opening in SDSNH 38228 would have been a transversely compressed oval, measuring approximately 38 mm high by 29 mm wide. In lateral aspect the narial opening makes an angle of approximately 40° with the horizontal axis of the skull. In *Odobenus* this angle is approximately 70° and in *Alachtherium* approximately 55°.

Unlike the derived condition in *Odobenus*, the ascending processes of the premaxillae of *Valenictus chulavistensis* overlapped the nasal bones externally for approximately one-half the length of the nasals. This assessment is based on the configuration of the sutures, as the nasals themselves are not preserved.

The maxillae of all three rostral specimens are conspicuously swollen in the region of the canine root (Fig. 3). However, this

TABLE 1. Composite faunal list of mammals from the San Diego Formation.

- Rodentia
  - Heteromyidae
    - Heteromyidae sp.
  - Cricetidae
    - *Neotoma* sp.
- Lagomorpha
  - Leporidae
    - Leporidae sp.
- Artiodactyla
  - Tayassuidae
    - *Platygonus* sp.
  - Camelidae
    - *Titanotylopus* sp.
    - cf. *Hemiauchenia* sp.
  - Cervidae
    - Cervidae sp.
- Perissodactyla
  - Equidae
    - *Equus* sp.
  - Tapiridae
    - *Tapirus* sp.
- Carnivora
  - Felidae
    - *Felis* sp. cf. *F. rexroadensis*
  - Mustelidae
    - *Spilogale* sp.
  - Canidae
    - Caninae sp.
  - Otariidae
    - *Callorhinus gilmorei* Berta and Deméré
    - Otariidae sp.
  - Odobenidae
    - *Valenictus chulavistensis* n. sp.
    - *Dusignathus seftoni* n. sp.
- Cetacea
  - Mysticeti
    - "Cetotheriidae"
      - *Herpetocetus* sp. 1
      - *Herpetocetus* sp. 2
    - Balaenopteridae
      - *Balaenoptera davidsonii* Cope
      - Balaenopteridae sp. 1
      - Balaenopteridae sp. 2
      - Balaenopteridae sp. 3
      - Balaenopteridae sp. 4
    - Balaenidae
      - Balaenidae sp. 1
      - Balaenidae sp. 2
  - Odontoceti
    - Pontoporiidae
      - *Parapontoporia sternbergi* Gregory and Berry
    - Phocoenidae
      - Phocoenidae sp. 1
      - Phocoenidae sp. 2
    - Monodontidae
      - Delphinapterinae sp.
    - Delphinidae
      - Delphinidae sp. 1
      - Delphinidae sp. 2
- Sirenia
  - Dugongidae
    - *Hydrodamalis cuestae* Domning
- Proboscidea
  - Gomphotheriidae
    - *Stegomastodon* sp.
- Edentata
  - Megalonychidae
    - *Megalonyx* sp.

swelling is not as great as in *Odobenus* and is expressed more anteroposteriorly than transversely. In *Odobenus*, the maxillae are so swollen that the infraorbital foramina are almost completely hidden when the skull is viewed in anterior aspect. The inclination of the canine root in relation to a vertical transverse plane (Fay 1982:111) is more procumbent (Fig. 2B) than that of *Odobenus* (36°–56° in *V. chulavistensis*, compared with 9°–20° in *Odobenus*, and 25°–48° in *Alachtherium*). As in all pinnipeds, the maxillae form the anterior walls of the orbits (Wyss 1987). The infraorbital foramen is large (19 mm wide by 33 mm high in SDSNH 38227; 12 by 28 mm in SDSNH 36786; 19 by 20 mm in SDSNH 38228), with a delicate dorsal strut and more robust ventral strut. The ventral surface of the latter is marked by a conspicuous fossa, which opens posteroventrally to accommodate the sharply keeled dorsal margin of the dentary. The ventral margin of the maxilla, posterior to the large canine alveolus, is keeled between the lateral and palatal surfaces, and is continuous with the lateral keeled margin of the ventral strut of the infraorbital foramen (Fig. 3). In lateral aspect, the ventral margin of the maxilla in *Odobenus* is continuous lingually with an alveolar shelf, and is continuous labially with the ventral strut of the infraorbital foramen as in *V. chulavistensis*. This is unlike the condition in *Neotherium*, *Imagotaria*, *Pontolis*, *Dusignathus*, *Aivukus*, and *Gomphotaria*, in which the ventral strut of the infraorbital foramen is conspicuously elevated above the ventral (alveolar) margin of the maxilla.

The jugal is relatively longer and more transversely compressed in *V. chulavistensis* than in *Odobenus*. However, as in *Odobenus*, the jugal in the new species contacts the maxilla in a transversely compressed peg-and-socket joint. The postorbital process of the jugal of *V. chulavistensis* is large and dorsoventrally expanded as in *Odobenus*. The orbit (i.e., diameter between the maxillary border of the orbit and the postorbital process of the jugal) is small as in *Odobenus*, relatively smaller than in *Aivukus*, *Pontolis*, *Imagotaria*, and *Neotherium*.

The zygomatic portion of the squamosal is robust and shortened as in *Odobenus* and *Alachtherium*, not slender and elongated as in all other fossil odobenids (including *Aivukus*). The squamosal fossa at the root of the zygoma is short and narrow and continuous posteriorly with a narrow shelf above the external auditory meatus. The external auditory meatus is open broadly externally and not restricted by the closeness of the mastoid and postglenoid processes, as it is in adult crania of *Odobenus*.

In dorsal aspect, the temporal fossae are oval openings anteroposteriorly shortened relative to those of *Neotherium*, *Imagotaria*, *Gomphotaria*, and *Aivukus*. They are not as shortened, however, as those of *Odobenus*.

The squamosal/parietal suture is horizontal and positioned near the base of the broadly convex braincase. The cranial vertex is broadly rounded transversely (as in *Odobenus*) and marked by a weakly raised interparietal suture. There is no indication of the sagittal sulcus described by Rutten (1907) for the holotype cranial fragment of *Alachtherium antverpiensis* (= *A. cretsii*), nor of the parasagittal cristae seen on adult crania of *Odobenus*.

The parietal/frontal suture is partially preserved on the right side of SDSNH 38227 at the level of the intertemporal constriction. The suture indicates that the frontals extended posteriorly between the parietals at the midline, as in *Odobenus*. Anterior to the intertemporal constriction the frontals widen dramatically, terminating anterolaterally in large antorbital processes. The frontal/maxilla suture is obscure but seems to have been transversely oriented. It is clear, however, that the suture bifurcates the antorbital processes, so both maxilla and frontal form the processes.

Near the midline, the lambdoidal crest is developed medially as a distinctive, anterodorsally inclined, transverse crescentic shelf (convex border anteriorly placed) that joins with its more lateral

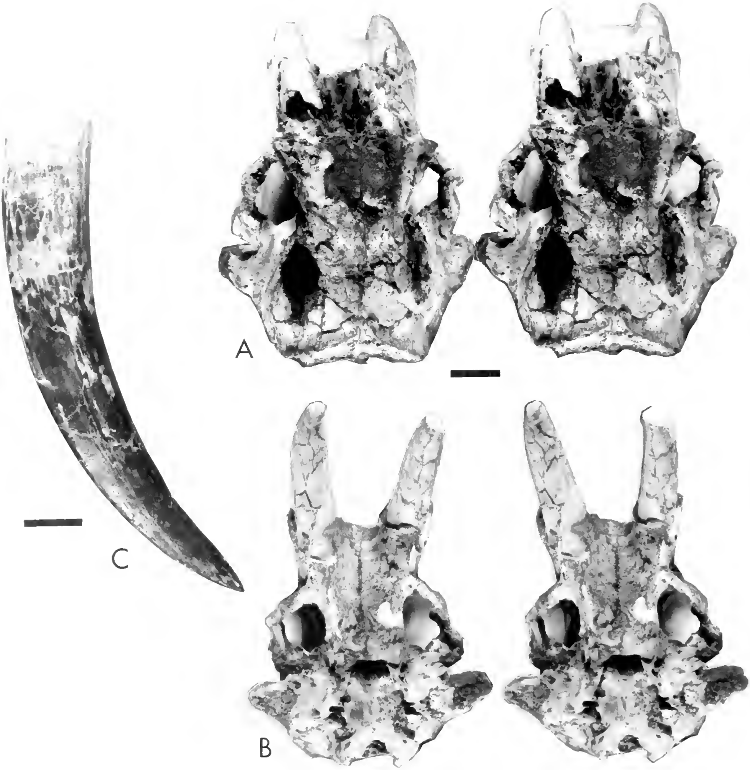

Figure 1. *Valenictus chulavistensis*, new species. A, B, SDSNH 38227, paratype skull. A, dorsal view (stereophotographs); B, ventral view (stereophotographs). C, SDSNH 38225, referred right C^1, medial view. Scale bar, 5 cm.

portions as they descend toward the mastoid processes. This inclined shelflike crest (the site of insertion of neck extensor muscles) is also seen in *Odobenus*, the holotype of *Alachtherium antverpiensis* (Rutten, 1907), the holotype of *Alachtherium antwerpiensis* Hasse, 1910, and the referred skull of *Alachtherium antverpiensis* (Rutten 1907) described by Erdbrink and van Bree (1990). The lambdoidal crest does not project posterodorsally to overhang the occipital shield as in *Neotherium*, *Imagotaria*, *Pontolis*, and *Gomphotaria*. The occipital shield is vertically oriented with a distinct sagittal crista as in *Odobenus* and *Alachtherium*. In posterior aspect (Fig. 2A) the occiput is hemispherical as in *Odobenus* and differs from the rectangular shield characteristic of *Alachtherium* (see Hasse 1910). The occipital condyles are widely separated dorsally, do not reach the roof of the foramen magnum, and are not exceptionally large.

The basioccipital is broad and roughly pentagonal (Figs. 1B; 3). The posterior portion of the basioccipital bears a strong sagittal ridge, bounded anterolaterally on either side by rugose circular areas for insertion of the rectus capitis ventralis muscles. A portion of the basioccipital/basisphenoid suture is preserved at the anterolateral corners of the basioccipital.

The auditory bulla completely fills the portion of the basicranium between the basioccipital, mastoid, and postglenoid pro-

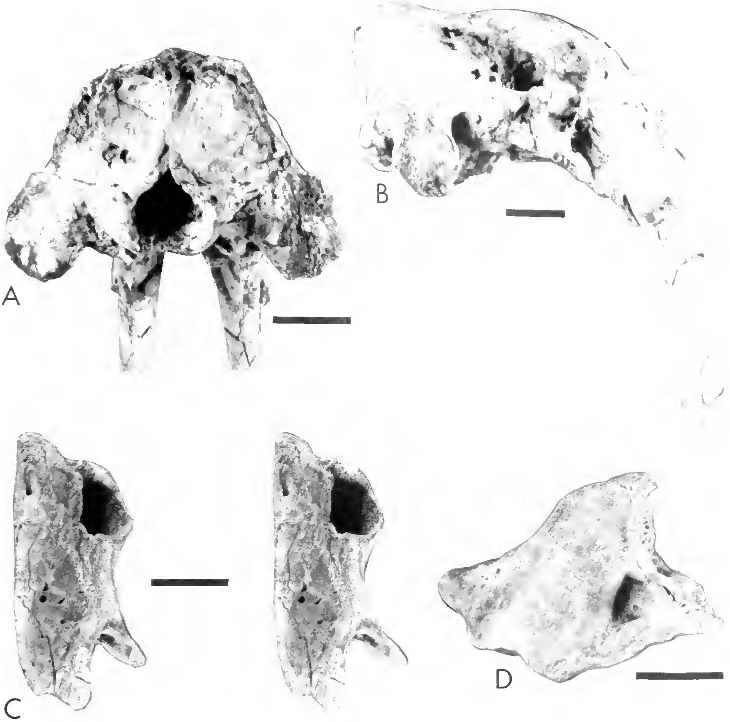

Figure 2. *Valenictus chulavistensis*, new species. A, B, SDSNH 38227, paratype skull. A, posterior view; B, lateral view. C, D, SDSNH 38228, referred left maxilla and premaxilla. C, ventral view (stereophotographs); D, lateral view. Scale bar, 5 cm.

cess. The bulla is not inflated except near the posterior opening of the carotid canal. This opening is rather steeply inclined anterodorsally as in adult crania of *Odobenus* and is closely appressed to a small posterior lacerate foramen. There is no clear distinction between the entotympanic and ectotympanic. Anteriorly, the bulla is closely appressed to, and overrides, the posterior portion of the postglenoid process. Several distinct and irregular bullar processes lie anterior to the hyoid fossa and stylomastoid foramen. The latter foramen is a large cylindrical opening well separated from the large, slitlike hyoid fossa by a smooth continuous surface extending from the bulla laterally out onto the ventromedial surface of the mastoid process. This condition is like that in *Odobenus* and *Alachtherium* and unlike that in *Imagotaria* and *Pontolis*, in which the two openings are connected by a continuous groove, or *Neotherium*, in which the two openings lie very close to one another.

The foramen ovale and alisphenoid foramen are closely appressed and recessed in a common fossa, which is directed ventrally as in *Odobenus*. The anterior opening of the carotid canal and bony eustachian tube are obscured by the diagenetically telescoped basicranium.

The palate is narrow and arched both longitudinally and transversely (Figs. 1B, 2C) as in *Odobenus*. There is no alveolar shelf along the lingual border of the upper canines, as the entire postcanine portion of the maxilla is edentulous, without any trace of alveoli. The maxilla/palatine suture on the palate meets the margin of the temporal fossa at the apex of a small but distinct pterygoid process. Together the horizontal laminae of the palatine bones form

TABLE 2. Skull measurements of *Valenictus chulavistensis* and *Dusignathus seftoni* (in mm).

	Valenictus chulavistensis			*Dusignathus seftoni*
	SDSNH 36786[a]	SDSNH 38227[b]	SDSNH 38228	SDSNH 38342[a]
Total length (condylobasal length) (0)[c]	410[d]	222[d]		
Rostral tip to middle of occipital crest				320
Length of tooth row, P^1–M^2				83
Width of rostrum across canines (12)	152[e]	146	112[e]	140[e]
Width of rostrum across base of I^3				56
Width of palate at P^4				94[e]
Depth of greatest palatal arch		56	45	
Width across antorbital processes (5)		147[d]	116[e]	108[e]
Width between infraorbital foramina		127	96[e]	118[e]
Width across intertemporal constriction		82		51
Width of braincase (8)				106
Zygomatic width (17)	232[e]	206		222[d]
Auditory width (19)		171		
Mastoid width (20)	306[e]	247		
Paroccipital width		154		
Greatest width across occipital condyles	110[e]	95		
Greatest width of anterior nares (3)		46[d]	30[e]	50
Greatest height of anterior nares			36[e]	52
Greatest width of nasals			26[e]	40
Greatest length of nasals (4)				73
Width of zygomatic root of maxilla (14)	38	29	21	21
Greatest width of foramen magnum	42[e]	48		
Transverse diameter of infraorbital foramen	26	29	23	28

[a] Holotype.
[b] Paratype.
[c] Numbers in parentheses refer to measurements in Siversten (1954).
[d] Estimate based on bilaterally symmetrical feature.
[e] Estimate on broken features.

a broad trapezoid, the longest side represented by the internal narial opening and the palatine/pterygoid sutures. The hamular processes of the pterygoids are constructed as in *Odobenus* (i.e., dorsoventrally compressed and transversely expanded flanges that hook laterally at their flattened distal extremities) and are unlike the delicate transversely compressed processes of *Imagotaria*. The medial wall of the pterygoid is preserved within the narial passage, with a clearly defined pterygoid/basisphenoid suture. The hard palate is elongated, extending to the postglenoid fossae as in *Odobenus* and *Alachtherium*, and lacks any hint of the horizontal pterygoid strut (Barnes 1989) that characterizes the lateral borders of the internal narial opening in almost all other pinnipeds. In this configuration the site for origination of the internal pterygoid muscle is moved to the temporal fossa.

The mastoid processes are greatly enlarged, constructed internally from cancellous bone, and extend ventrally to a level below the hamular processes and auditory bullae, as in *Alachtherium* and *Odobenus*. In lateral aspect, the mastoid process presents a broad "teardrop" form that is more convex posterolaterally than in *Odobenus*. The ventral portion of the mastoid is slender and anteroposteriorly compressed to produce a transversely elongate process. In *Odobenus*, the ventral portion of the mastoid is more of a swollen knob, with a conspicuously roughened area for origination of the digastricus muscle. In *V. chulavistensis* the mastoid and paramastoid processes are closely appressed, with the latter forming the thin, delicate process characteristic of odobenids. As in *Odobenus*, the mastoid/paramastoid suture is not fused.

The right orbital wall of SDSNH 38227, although damaged, provides details on the structure of this region. The optic foramen is funnel-shaped and positioned dorsally within a diagonally oriented orbitosphenoid that lacks a conspicuous horizontal plate of bone anterior to the foramen. This unusual configuration is also seen in *Odobenus*. In other pinnipeds, the optic foramen is typically a vertical slot positioned ventrally within a horizontally oriented orbitosphenoid that has a relatively long plate of bone anterior to the foramen. As in *Odobenus*, the orbitosphenoid in *V. chulavistensis* appears to be bounded anteriorly by a relatively large and posteriorly placed orbital vacuity unlike the more anteriorly placed vacuities seen in extant otariids and at least one fossil odobenid (*Imagotaria* sp., USNM 335599). In *Odobenus* the palatine bone forms the entire ventral border of the orbital vacuity, including both the anteroventral and posteroventral portions (i.e., the maxilla/palatine suture meets the maxilla/frontal suture anterior to the vacuity). In otariids (e.g., *Zalophus*, *Eumetopias*, and *Otaria*) and at least one fossil odobenid (*Imagotaria* sp., USNM 335599) the anteroventral border of the vacuity is formed from the maxilla (i.e., the maxilla/palatine suture does not reach to the maxilla/frontal suture but instead contacts the vacuity directly).

A portion of the left petrosal was recovered with SDSNH 38227 and is odobenidlike in its relatively large size, enlarged apex anterior to the promontorium, and broad internal auditory meatus. This meatus has passages for the facial and vestibulocochlear nerves separated by a low transverse crest. The roof of the meatus is not preserved, and much of the promontorium and all of the cochlea

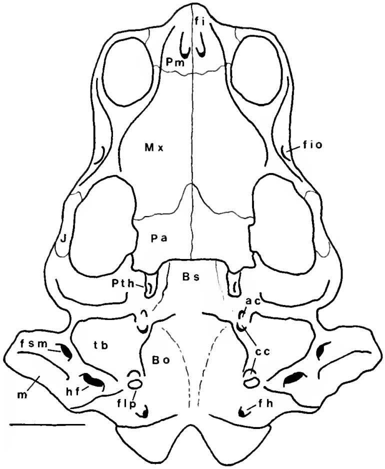

Figure 3. Reconstruction of *Valenictus chulavistensis*, new species, ventral aspect. Based largely on SDSNH 38227. ac, alisphenoid canal; Bo, basioccipital; Bs, basisphenoid; cc, carotid canal; fh, hypoglossal foramen; fi, incisive foramen; fio, infraorbital foramen; flp, posterior lacerate foramen; fsm, stylomastoid foramen; hf, hyoid fossa; J, jugal; m, mastoid; Mx, maxilla; Pa, palatine; Pth, hamular process of pterygoid; Pm, premaxilla; tb, tympanic bulla. Scale bar, 5 cm.

and floccular fossa are missing. Thus the fenestra ovale can not be measured. The petrosal apex is anteriorly elongated as in *Aivukus* and not shortened as in *Odobenus*.

Dentition.—The dentition of *Valenictus chulavistensis* consists solely of the upper canines, which are elongated, curved, evergrowing tusks constructed as in *Odobenus rosmarus* and *O. huxleyi* (see Ray 1960). Internally, the tusks of *Odobenus* and *V. chulavistensis* consist of three layers, a central column of globular orthodentine, a surrounding ring of dense compact orthodentine, and a thin outer layer of cementum (Ray 1960). The thicknesses of these layers as measured on a referred partial tusk (SDSNH 38226) are 7.6, 8.9, and 1.5 mm, respectively, for the globular orthodentine (radius), compact orthodentine, and cementum (see Table 3 for additional measurements). This specimen has a bluntly rounded crown and well-worn anterior border. The cementum layer is well preserved proximally and thins toward the anterodistal edge, probably because of wear. The medial surface has two broad longitudinal grooves, the more anterior being more prominent and extending nearly to the distal tip of the tooth. The lateral surface is faintly fluted, with one particularly strong longitudinal groove near the posterior margin. The cementum layer is completely worn away on the tip of the crown and in a longitudinal band running proximally along the anterior margin from the tip back toward the proximal end, where the wear band rolls medially. In a few places where the cementum layer has been broken away, a pattern of very fine transverse lines (growth lines) is preserved in the compact orthodentine layer, as noted by Ray (1960) for *O. huxleyi*.

SDSNH 38225 is a beautifully preserved complete right canine (Fig. 1C). In contrast to the broadly rounded anterior margin of SDSNH 38226, this specimen has a sharply beveled margin (averaging about 10 mm wide) extending from the distal end 235 mm up the anterior circumference of the tooth. Another beveled surface occurs along the distolateral surface from the tip proximally for a distance of 162 mm. Preserved along the medial border of the anterior half of the tooth, a conspicuous wear surface is bounded by cementum on its margins but lacks cementum itself. This large wear surface is irregularly concave proximally and distally. An intact cementum layer is preserved along the entire posterior margin of the tusk. The intralveolar portion of the tusk is characterized by numerous closely spaced fine longitudinal grooves that terminate abruptly distal to where they encounter the extralveolar surface. This specimen does not preserve any of the broad longitudinal grooves on its medial surface as seen in SDSNH 38226. A faint groove, however, is preserved on the lateral surface within 20 mm of the anterior margin. A second, more conspicuous longitudinal groove occurs just lateral to the posterior margin but does not continue onto the extralveolar surface. On this tusk, cementum is preserved only on the proximolateral surface, the posterior margin, and the distomedial surface. These wear patterns (i.e., abraded and worn anterior surfaces at the distal ends of the crowns) are similar to those reported by Fay (1982) for tusks of *O. rosmarus*. The wear on the distal end of SDSNH 38225 is so extensive that the dense orthodentine layer has been abraded away on the anterior surface to reveal the central globular orthodentine core (a condition also seen in tusks of *O. rosmarus*). The medial surfaces of the tusks of *V. chulavistensis* have broad longitudinal grooves as in *Odobenus* and in contrast to the more numerous and distinct longitudinal grooves preserved on the fluted tusks of *Gomphotaria pugnax* (see Barnes and Raschke 1991).

The tusks in the paratype skull (Fig. 2B) as well as in two nearly complete referred tusks (SDSNH 38225, 38284) are arched in the parasagittal plane (Table 3), as in *Odobenus*. Radii of this arc as measured along the posterior surface of the two referred tusks are 403 and 398 mm, respectively; in a fossil tusk of *O. rosmarus*, 270 mm (Rutten 1907). Fay (1982:111) noted that in living walruses the radius of the longitudinal arc is variable, with ranges of 456 to >5000 mm for males and 226 to 1425 mm for females. The fossil tusks from Chula Vista fall within these ranges and point out the taxonomic weakness of this feature as discussed by Erdbrink and van Bree (1990).

Mandible.—A nearly complete mandible (Fig. 4) was collected with the holotype skeleton (SDSNH 36786) and consists of a left mandibular ramus (lacking only the coronoid process) strongly fused at the symphysis to a partial right horizontal ramus (Table 4). In lateral aspect, the mandible presents a slender profile unlike that of any known pinniped. A slender and strongly upturned symphyseal region forms an angle between the anterior margin and the ventral margin of the horizontal ramus of about 125°. The posterior margin of the upturned symphysis forms an angle of about 130° with the ventral margin. In *Alachtherium* (IRSNB M.170) the symphyseal portion is also upturned but more massive, with the anterior margin of the symphysis forming an angle of only about 112° with the ventral margin and about 143° with the posterior (alveolar) margin.

The ascending, symphyseal portion of the mandible (right and left rami) of *V. chulavistensis* is slender and triangular in cross section (not swollen and massive as in *Odobenus*), with the apex of the triangle corresponding to the anteroventral margin of the symphysis. In *Alachtherium* the ascending symphyseal portion of the mandible is also somewhat triangular. The "incisive" border of the

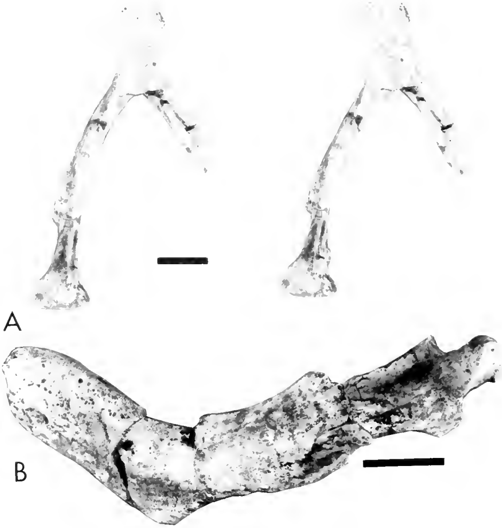

Figure 4. *Valenictus chulavistensis*, new species, SDSNH 36786, holotype mandible. A, dorsal view (stereophotographs); B, lateral view. Scale bar, 5 cm.

mandible is characterized by a highly vascularized, laterally expanded bony pad (as in *Prorosmarus* and *Odobenus*). This bony pad is continuous posteriorly with a broad trough that runs posteroventrally to the point of divergence between the right and left rami. The ridges that form the dorsolateral borders of this symphyseal trough run down and out onto the horizontal rami to become the sharply keeled dorsal margins of the rami. Both rami are entirely edentulous, with no trace of alveoli or alveolar shelves. The horizontal rami are transversely compressed and dorsoventrally shallow (Table 4), in contrast to the deep rami of *Alachtherium*.

On the lateral surface of the horizontal ramus, at the point of divergence of the rami, are a pair of opposing mental foramina, one opening posteriorly, the other anteriorly. Both are set in a deeply excavated and elongated oval fossa. *Alachtherium* possesses a similar pair of mental foramina within an open oval fossa. In *Prorosmarus* and *Odobenus* a single nearly circular mental foramen penetrates deeply into the ramus. At the back of this foramen are a pair of opposing smaller foramina. A pair (right and left) of large longitudinal nutrient foramina lie at the extreme anterior tip of the mandible, just below the bony pad. Similar foramina are seen on the mandibles of *Prorosmarus*, *Alachtherium*, and *Odobenus*.

In lateral aspect, the ventral margin of the ramus between the rugose inferior genial tuberosity and the marginal process is concave. The marginal process (Davis 1964) is well developed and divisible into dorsal and ventral components. The ventral portion of the process is a keeled ridge, set off from the ventral margin of the ramus as a posteriorly directed pointed process. In ventral aspect, the axis of this process diverges medially from that of the ramus. The dorsal portion of the marginal process lies immediately above the posterior end of the ventral portion and is a conspicuous, anteroposteriorly elongated, knoblike eminence. The two portions of the marginal process are separated by an anteroposteriorly oriented sulcus. Dentaries of mature individuals of *Otaria byronia* display a similar divided marginal process (personal observation), while dentaries of immature individuals of *Otaria* display intermediate conditions, from a single conspicuous flangelike marginal process to one that shows incipient division. *Prorosmarus*, *Alachtherium*, and *Odobenus* also possess well-developed marginal processes, although without any obvious division into dorsal and ventral components. The structure of the marginal process in *V. chulavistensis* suggests a large digastricus muscle with an anteriorly placed insertion on the ramus. The horizontal ramus is widest at the level of the marginal process.

TABLE 3. Measurements of upper canines (tusks) of *Valenictus chulavistensis* (in mm).

	SDSNH 36786[a]	SDSNH 38225	SDSNH 38226	SDSNH 38227[b]
Radius of curvature, anterior surface	265	355	351	
Radius of curvature, posterior surface	312	403	520	
Total length, arc of anterior surface		485		340[c]
Total length arc of posterior surface		419		320[c]
Length, tangent of arc of posterior surface		405		311[c]
Length, base of root to intra-alveolar margin	136	145		125[c]
Anteroposterior diameter, base of root	74	71		64
Transverse diameter, base of root	36	44		34
Anteroposterior diameter, intra-alveolar margin	81	69		53–54
Transverse diameter, intra-alveolar margin	49	47		36–39
Anteroposterior diameter, mid-crown	68	64		49–49
Transverse diameter, mid-crown	45	42		31–33

[a] Holotype.

[b] Paratype (two tusks).

[c] Estimate on broken feature.

The pterygoid process is large and robust, ventromedially directed, hooklike, and well separated from the marginal process. In *Alachtherium* and *Odobenus* the two processes are positioned close together, with the pterygoid process as a low, anteroposteriorly elongated knoblike projection closely appressed to the ramus and not medially extended.

The mandibular condyle is a robust and transversely elongated cylinder, similar in size and thickness to that of an *Odobenus* of comparable size. The coronoid process is not preserved, but its broken base indicates it was slender and anteroposteriorly elongated. In this respect the coronoid process was probably similar in form to that of *Alachtherium cretsii* and quite different from the short, stout, and broad-based coronoid process of *Odobenus*. In dorsal (occlusal) aspect the mandible has a "wish-bone" or furcula shape, with the left mandibular ramus preserving a distinctive sigmoidal outline, laterally concave between the tip of the jaw and the posterior border of the symphysis and laterally convex from there to the posterior border of the condyle. This sigmoidal outline is also characteristic of mandibles of *Alachtherium*, *Prorosmarus*, and *Odobenus* (see Berry and Gregory 1906) and serves to accommodate the greatly enlarged upper canines (tusks).

Postcrania.—The holotype includes all major portions of the postcranial skeleton except the tibia and innominate. Fortunately, these elements are represented in additional, referred material. It is beyond the scope of this report to describe each of these skeletal elements. The unique morphology of the humerus, calcaneum, and astragalus, however, calls for discussion of these elements.

Humerus.—The current sample includes five complete and five partial humeri (Table 5). The following description focuses primarily on the holotype (Fig. 5).

The humerus of *Valenictus* is striking in its overall stockiness relative to the more slender and elongated humeri of *Odobenus* and *Alachtherium*. Stockiness, expressed as the ratio of proximal width (measured at the widest part of the lesser tuberosity) to total humeral length, is significantly greater ($p > 0.05$) in *Valenictus* than in other odobenids.

In *V. chulavistensis* the humerus is constructed from very dense osteosclerotic bone, as in sirenians. In other marine mammals, it consists of spongy, cancellous bone. This greater bone density also characterizes all other limb bones of the holotype, including carpals, tarsals, and metapodials. Interestingly, in contrast to sirenians, osteosclerotic bone does not occur in the axial skeleton (i.e., vertebrae and ribs) of *V. chulavistensis*. The nature of the internal structure of the holotype humerus of *V. imperialensis* is unknown.

TABLE 4. Mandibular measurements of fossil odobenids (in mm).

	Valenictus chulavistensis SDSNH 36786	*Alachtherium cretsii* IRSNB M.168	*Dusignathus seftoni* SDSNH 20801	*Dusignathus santacruzensis* UCMP 27131
Greatest length	310	364	344	215[a]
Length of tooth row, P_{1-4}		98	107	72
Depth of horizontal ramus at P_2		117	76	64
Width of horizontal ramus at P_2		30	39	17
Depth of horizontal ramus at P_4		93	86	55[a]
Width of horizontal ramus at P_4		35	39	17
Width of horizontal ramus at shallowest point along ramus	20	31	35	17
Minimum depth of horizontal ramus	50	76	87	53
Height, pterygoid process to coronoid process		157	145	83
Length of symphysis	135	184	135	70
Minimum width of symphysis	45	58	61	29
Greatest width of condyle	58	75	75	

[a] Estimate on broken feature.

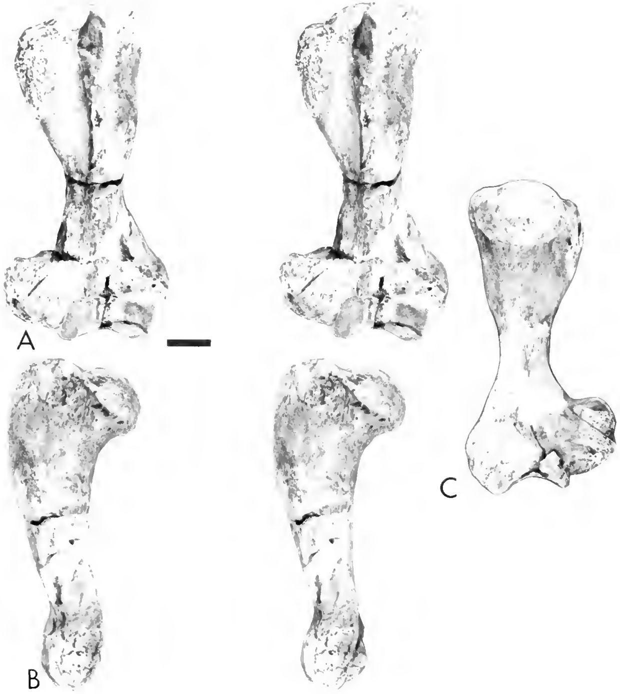

Figure 5. *Valenictus chulavistensis*, new species, SDSNH 36786, holotype left humerus. A, anterior view (stereophotographs); B, lateral view (stereophotographs); C, posterior view. Scale bar, 5 cm.

The proximal end of the humerus of *V. chulavistensis* is characterized by a relatively large and well-rounded capitulum (head) positioned only slightly below a thickened greater tuberosity. In *V. imperialensis*, *O. rosmarus*, and a humerus (USNM 187328) referred by Repenning and Tedford (1977: pl. 17) to the problematic odobenid *Pliopedia pacifica*, the greater tuberosity is also low relative to the head. In *V. imperialensis* the head is relatively larger than in the new species. The lesser tuberosity of both taxa is distinctly thickened and, with the greater tuberosity, encloses a narrow and proximally inset bicipital groove. The lesser tuberosity is positioned only slightly below the proximal capitulum. In *Odobenus* the lesser tuberosity is relatively smaller and placed more distally and the bicipital groove is broader and less inset. In the transverse plane, the greater tuberosity of both species of *Valenictus* is distinctly elongated, deflected medially, and of nearly constant width to its anterior extremity. This medial deflection of the lesser tuberosity provides the proximal end of the humerus with a very broad profile in anterior aspect. This feature also characterizes the humeri of *V. imperialensis* and *Pliopedia pacifica* (USNM 187328).

The pectoral crest of the humerus of *V. chulavistensis* is elongate, like that of *Odobenus*, and extends as a broad ridge distally almost to the trochlea. By contrast, in *Imagotaria*, *Gomphotaria*, and *Aivukus*, the pectoral crest is strongly developed as a keeled ridge. In *Valenictus*, *Odobenus*, *Alachtherium*, and *Pliopedia* the pectoral crest gradually joins with the anterodistal surface of the humerus. In *Aivukus* and *Gomphotaria*, the pectoral crest displays an abrupt distal deflection and descends sharply to the anterodistal surface of the humerus. The deltoid tuberosity in *V. chulavistensis* is separate from the pectoral crest and positioned posterolateral to the

TABLE 5. Measurements of humeri of fossil odobenids (in mm).

	Valenictus chulavistensis					*Valenictus imperialensis*	*Dusignathus seftoni*
	SDSNH 36786[a]	SDSNH 38312	SDSNH 38315	SDSNH 35275	SDSNH 38300	LACM (CIT) 3926[a]	SDSNH 43873
Greatest length, greater tuberosity to radial capitulum	326	315	306	263	300	253	346
Length, proximal capitulum to radial capitulum	325	306	310	270	296	252	321
Length, lesser tuberosity to radial capitulum	313	300	396	254	288	245	295
Transverse width across tuberosities	120	120	119	109	112	102	96
Greatest transverse width of proximal capitulum	91	88	85	77	79	69	86
Transverse width at narrowest part of shaft	56	55	56	61	63	51	62
Anteroposterior width at midshaft	75	94	86	76[b]	74[b]	88	97
Greatest width across epicondyles	162	159	168	137	153	125	
Greatest anteroposterior diameter of medial edge of trochlea	58[b]	68	61	60	59	53	65
Greatest anteroposterior diameter of radial capitulum	50[b]	52	42	52	46	39	
Greatest width of distal articulation	84	74	74	68	85	67	75[b]
Transverse width of entepicondyle	53	50	63	38	59	47	34

[a] Holotype.
[b] Estimate on broken feature.

crest on the lateral surface of a convex shaft. This configuration is like that of *Odobenus*, *V. imperialensis*, and *Pliopedia* (USNM 187328) and unlike that of *Imagotaria*, *Gomphotaria*, *Pontolis*, and otariids, in which the insertion for the deltoid muscle appears as a ridge confluent with the pectoral crest. An intermediate condition is seen on humeri of *Alachtherium cretsii* (van Beneden 1877: pl. 3, fig. 1) and *Prorosmarus alleni* (MCZ 7713 in Repenning and Tedford 1977), in which, the deltoid insertion, although still on the pectoral crest, is more posterolaterally placed (i.e., the crest is transversely broadened).

The distal end of the humerus of both species of *Valenictus* is very broad, primarily because of the greatly enlarged entepicondyle. In the holotype of *V. chulavistensis* the width of the entepicondyle is 16% of the total length of the humerus. This measure varies from 14 to 20% ($N = 4$) in the referred humeri. A least-squares regression analysis revealed no significant correlation between enlargement of the entepicondyle and body size ($R^2 = 0.31$, $p > 0.05$). In *V. imperialensis*, the entepicondyle falls within the range of *V. chulavistensis* at 19% of the total humeral length. In *Odobenus* the measure is only 8%, in *Alachtherium* about 8%, and in *Imagotaria* approximately 10%. In *V. chulavistensis*, the entepicondyle is extremely large and robust (Fig. 5C) and anteroposteriorly compressed with an outline roughly rectangular in both medial and anterior aspects. The proximodistal axis of this rectangular process is rotated posteriorly at its distal end. The entepicondyle of *V. imperialensis* is also enlarged but more distally placed, rounded, and knoblike, rather than rectangular and rotated posteriorly. A partial humerus (USNM 13643) collected from the lower Pliocene San Joaquin Formation, Kettleman Hills, California, shares many features with humeri of *V. chulavistensis*, including the large and robust rectangular entepicondyle rotated posteriorly and the osteosclerotic internal bone structure. Repenning and Tedford (1977) illustrated this specimen (pl. 16, fig. 7) and referred it to *V. imperialensis*. From the features discussed above, however, I tentatively refer USNM 13643 to the new species from Chula Vista.

The ectepicondyle of *V. imperialensis* is conspicuously reduced relative to the more enlarged condition in *V. chulavistensis*, *Odobenus*, and *Alachtherium*. The humerus of *Valenictus chulavistensis* also differs from that of *V. imperialensis* in possessing a distinctly embayed olecranon fossa set medial to a distinctly keeled supinator ridge. In *V. imperialensis*, the olecranon fossa has a more convex surface adjacent to a broadly rounded supinator ridge. In fact, the entire posterior profile of the shaft of *V. imperialensis* is planar, that of *V. chulavistensis*, sigmoidal.

As in all odobenids, the greatest anteroposterior diameter of the medial lip of the trochlea of *V. chulavistensis* is greater than that of the distal radial capitulum. However, the distal trochlear axis forms an angle of 90° ($N = 5$) with the humeral shaft's axis. In *V. imperialensis* ($N = 1$) and *Alachtherium* ($N = 1$) this angle is 83°, while in *Odobenus* ($N = 2$) the angle is even more acute at 77°. This suggests that the antebrachium of the new species was not as medially directed as in *Odobenus*.

The important differences that distinguish the humerus of *V. chulavistensis* from that of *V. imperialensis* include larger size, sigmoidal posterior profile, sharply keeled supinator ridge, robust and rectangular entepicondyle, more prominent ectepicondyle, and more obtuse angle between the shaft axis and distal trochlear axis.

Calcaneum.—The calcaneum of *V. chulavistensis* is unique. It is much broader distally than proximally. In *Odobenus* and *Imagotaria* (USNM 23862) these two dimensions are nearly equal. In dorsal or astragalar aspect (Fig. 6A), the sulcus calcanei between the sustentacular and ectal facets is broad and unlike the narrow sulcus of *Imagotaria* and *Odobenus*. Correlated with this broadening is a sustentacular facet that is positioned well distad, almost parallel with the distal cuboid facet. This distal placement of the sustentacular facet coupled with a well-developed lateral trochlear process (peroneal tubercle of Kellogg 1931) gives the calcaneum of *V. chulavistensis* its extremely broad distal end. The cuboid facet is an elongate rectangle, in contrast to the quadrate cuboid facet of *Odobenus* and the short rectangular cuboid facet of *Imagotaria downsi* (Repenning and Tedford 1977, USNM 23862). As in *Imagotaria* (USNM 23862), and in contrast to *Odobenus* and *Prorosmarus* (USNM 215236), the sustentaculum lacks a secondary shelf (Robinette and Stains 1970). The ectal facet is nearly planar, not convex as in *Odobenus*, *Imagotaria*, and otariids. The calcaneal tuber is long, with a prominent medial tuberosity (Fig. 6B) similar in size and form to that of *Odobenus* but less medially elongated than that of *Imagotaria* (USNM 23862). The cuboid facet forms an angle of between 14° and 21° with the longitudinal calcaneal axis. In *Imagotaria* this measure is between

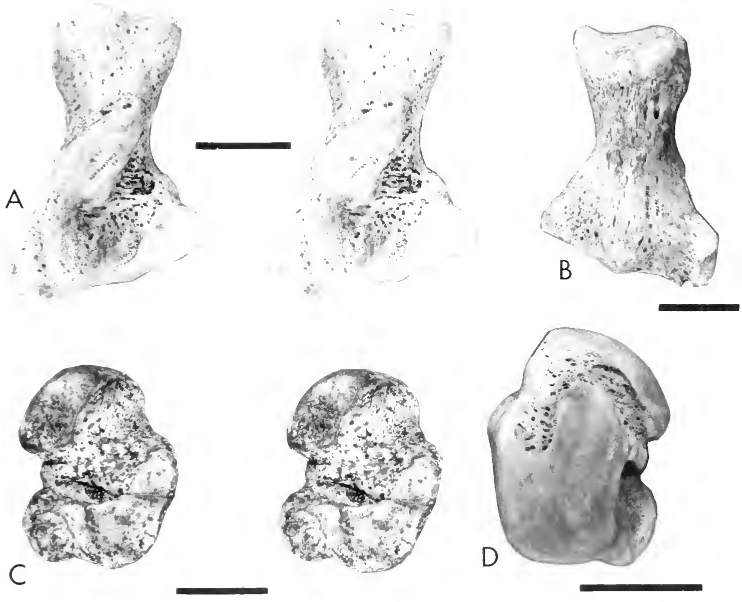

Figure 6. *Valenictus chulavistensis*, new species. A, B, SDSNH 36786, holotype right calcaneum. A, astragalar view (stereophotographs); B, palmar view. C, SDSNH 36786, holotype left astragalus, calcanear view (stereophotographs). D, SDSNH 35273, referred left astragalus, proximal view. Scale bar, 5 cm.

10° and 15°, while in *Odobenus* it is between 30° and 35°. Like other skeletal elements, the calcaneum is constructed of osteosclerotic bone.

Astragalus.—This element also has an extremely unusual morphology (Figs. 6C, D). The capitulum is *not* set off from the stocky trochlear portion of the astragalus by a distinct neck as is in all other pinnipeds. The medial trochlear ridge (maleolar tibial facet) is distinctly longer than the lateral trochlear ridge (trochlear tibial facet), not shorter or of equal length as in *Odobenus* and *Imagotaria* (USNM 23867). In fact, the medial trochlear ridge extends so far proximally that it meets the medial plantar tuberosity. In *Odobenus* and *Imagotaria* both tibial articular trochlea are well separated from the medial plantar tuberosity by a distinct sulcus for the flexor hallucis longus tendon. In *V. chulavistensis*, the medial side of the medial trochlear ridge has a well-developed sulcus and there is no prominent lateral process (collum tali), only a flexure in the lateral outline of the astragalus (Fig. 6C). In *Odobenus* and otariids the lateral process is prominent and well separated from the capitulum. The capitulum of *V. chulavistensis* is directed medially at an angle of approximately 40° to the long axis of the astragalus. In plantar aspect (Fig. 6C), the medial sustentacular facet is confluent with the navicular facet, in sharp contrast to the distinct and well-separated navicular and sustentacular facets of other pinnipeds. In *V. chulavistensis*, the region between the sustentacular and ectal facets is a very broad sulcus calcanei, correlated with the corresponding broad sulcus of the calcaneum. The ectal facet is broadly J-shaped and extends laterally to meet the plantar border of the vertical fibular facet (i.e., there is no proximolateral shelf between the ectal facet and the fibular facet as is seen in other pinnipeds). As in all odobenids, the astragalus of *V. chulavistensis* has a posteromedial calcaneal process (medial plantar tuberosity); however, the process in this taxon is a broadly rounded structure, less distinct than the prominent process of *Imagotaria*, as discussed by Repenning and Tedford (1977).

Phylogenetic relationships.—*Valenictus chulavistensis* is an odobenine walrus closely related to modern *Odobenus rosmarus* and the fossil walruses *Alachtherium cretsii*, *Prorosmarus alleni*, and *Pliopedia pacifica* (Fig. 7). Odobenine synapomorphies (numbers refer to characters as discussed by Deméré 1994, this volume) supporting this relationship include (1) external narial opening elevated above incisive margin, (9) palate narrow and arched transversely and longitudinally, (10) hard palate elongated, (11) palatine

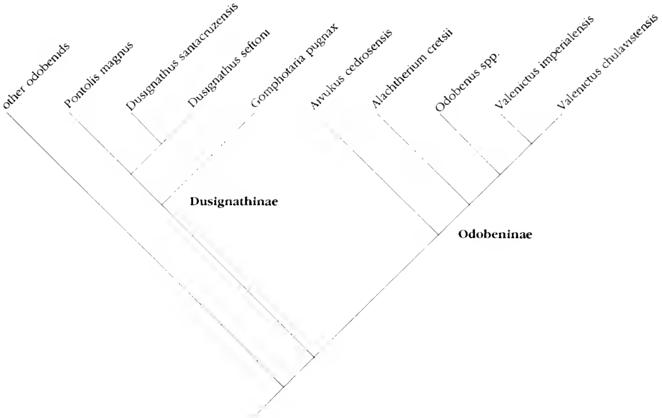

Figure 7. Phylogenetic relationships of dusignathine and odobenine walruses.

telescoped beneath alisphenoid, (12) hamular processes broad, (13) pterygoid strut lost, (17) mastoid processes as widest part of cranium, (19) cranial vertex with distinct flattened traction surface, (20) sagittal crest lost (also seen in some phocids), (21) zygomatic arches blunt and robust, (23) temporal fossae shortened, (24) optic foramen funnel-shaped, (25) orbital vacuity posteriorly placed, (29) upper canine with well-developed globular orthodentine column, (43) vesicular mandibular terminus, and (47) deltoid tubercle of humerus posterior to pectoral crest.

The humeri of *Alachtherium* and *Prorosmarus* possess features more plesiomorphic than those of *Odobenus* and *Valenictus*. Several autapomorphies of the new fossil species (e.g., edentulous lower jaw and nearly edentulous upper jaw, osteosclerotic long bones, and numerous features of the humerus, astragalus, and calcaneum) suggest that *V. chulavistensis* diverged from its common ancestor with *Odobenus* prior to pursuing its own unique evolutionary path toward its derived edentulous condition.

Recognition of *Valenictus chulavistensis* as a tusked odobenine walrus settles a long-standing question about the relationships of *Valenictus imperialensis*. When Mitchell (1961) first described this species he considered it to be a specialized odobenid. Later, he (Mitchell 1968) implied that *V. imperialensis* was distantly related to the Odobeninae. Repenning and Tedford (1977) and Barnes (1989) assigned this species to the Dusignathinae, with reservations.

Functional morphology.—A complete discussion of the functional aspects of the skeleton of *Valenictus chulavistensis* is beyond the scope of this report. Three aspects, however, are discussed here: development and function of elongated ever-growing canines (tusks), feeding behavior as it relates to tooth loss, and locomotor implications of the humerus.

Tusks and behavior.—Possession of homologous enlarged upper canines in *V. chulavistensis*, *Alachtherium*, *Odobenus*, and probably also *Prorosmarus* suggests that the common ancestor of these odobenine taxa had tusks and that modern *Odobenus* inherited them. In this light, adaptational scenarios explaining tusk evolution in *Odobenus* must also explain the development of tusks in all fossil walruses of temperate latitudes. The tusks of *Odobenus* must be considered not solely as adaptations for an arctic existence but as structures with a history. Fay (1982) showed that walruses do not use their tusks directly in benthic feeding, as erroneously suggested by other workers. The wear patterns noted by Fay (1982) on tusks of *Odobenus*, also preserved on tusks of *V. chulavistensis*, are the product of incidental abrasion during benthic feeding. As a walrus forages with its muzzle against the substrate, it drags its tusks passively through the bottom sediments, wearing their anterior margins. The anatomical and behavioral data of Fay (1982:137), when combined with the phylogenetic data presented here, suggest that tusks are not the product of viability selection but rather evolved for social display, most probably under the pressures of sexual selection. Walrus tusks, like cervid antlers, are structural adaptations for social interactions (e.g., intraspecific dominance) rather than as sea-floor "plowshares" or arctic "ice tongs." Presumably, *Valenictus chulavistensis* used its tusks for social display as does the living *Odobenus rosmarus*.

Jaws and feeding.—Possession of an edentulous lower jaw and nearly edentulous upper jaw begs the question, "how did *Valenictus chulavistensis* feed?" Fay (1982) has shown that modern walruses are suction-feeders, specializing on soft-bodied and thin-shelled benthic invertebrates (e.g., polychaetes, tunicates, and molluscs). According to Fay (1982) *Odobenus* does not use its peglike cheek teeth to crush prey but rather relies on a strong oral suction to ingest prey whole. He suggested that any function the cheek teeth retain is related to aquatic communication, supported by the observation that submerged walruses produce a loud clacking sound by percussive tooth occlusion. When feeding on thin-shelled pelecypods

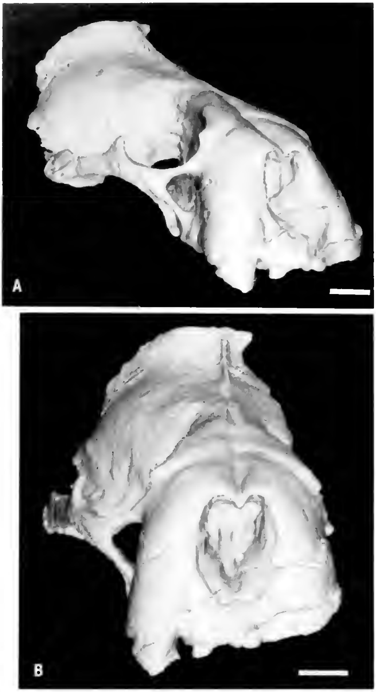

Figure 8. *Dusignathus seftoni*, new species, SDSNH 38342, holotype skull, computer tomography scan three-dimensional images. A, oblique lateral view; B, oblique anterior view. Scale bar, 3 cm.

Odobenus rosmarus sucks the mollusks from their shells before ingesting them (i.e., shells are not crushed by the teeth) (Fay 1982). With a strategy of feeding by oral suction, teeth are vestigial, implying that their loss in *V. chulavistensis* is not a "preadaptation" for starvation but a derived condition related to a unique feeding strategy. A test of this hypothesis is provided by the bearded seal, *Erignathus barbatus*, which as a strong suction-feeder and part-time benthic browser, frequently loses its teeth in old age (F. H. Fay, pers. comm.). In addition, the living monodontid, *Monodon monoceros*, and ziphiid odontocetes (e.g., *Mesoplodon* spp.) have lost all postcanine teeth and are oral-suction feeders, specializing on squid and small schooling fishes. Thus tooth loss following adoption of suction feeding is a derived condition at which several different groups of suction-feeding marine mammals have arrived independently. Since the common ancestor of *V. chulavistensis* and *Odobenus rosmarus* obviously had postcanine teeth, the edentulous condition of *V. chulavistensis* is more derived than the retention of teeth by *Odobenus* and represents the first case among pinnipeds of loss of all teeth but tusks.

Humerus and locomotion.—The humerus of *V. chulavistensis* preserves an interesting mosaic of characters. Most conspicuous is the overall stockiness of the humerus and the greatly enlarged entepicondyle. Enlargement of the entepicondyle is correlated with an increase in the mass of the forelimb's flexor and pronator musculature (English 1980) and suggests that *V. chulavistensis* relied more on forelimb flexion and pronation during swimming than does *Odobenus*. As discussed by English (1980), however, the strong muscles suggested by the large entepicondyle might have served to oppose supination and passive forelimb extension rather than to impose pronation and flexion actively. This opposition to supination and extension are important actions in maintaining a rigid pectoral "rudder."

Gordon (1981) divided extant pinnipeds into three general groups by mode of aquatic locomotion: forelimb swimmers (i.e., otariids), hindlimb swimmers (i.e., phocids), and forelimb/hindlimb swimmers (i.e., odobenids). Forelimb-swimming otariids rely primarily on adduction and abduction of the forelimb rather than on flexion and extension (Howell 1929; English 1980; Gordon 1981), suggesting that pronation and supination are important muscle actions. Hindlimb-swimming phocids rely primarily on abduction and adduction of the hindlimb (Howell 1929). The forelimb/hindlimb swimming mode proposed for odobenids may be misleading, as walruses' primary source of aquatic propulsion is supplied by the hindlimbs; they use the forelimbs only for steering and stabilization (F. H. Fay, pers. comm.).

Berta and Ray (1990) suggested that forelimb/hindlimb aquatic locomotion is the primitive condition for pinnipeds, as presumed in *Enaliarctos*. Whether or not the condition in *Odobenus* is homologous with that in *Enaliarctos* requires further analysis. It does seem, however, that *V. chulavistensis* adopted a locomotor strategy involving more forelimb pronation, or suppression of pronation, than that of *Odobenus*. This implies a greater degree of forelimb involvement in aquatic locomotion in *Valenictus*.

Giffin (1992) independently assessed the swimming behavior of *Valenictus chulavistensis*, including 10 vertebrae from the holotype, in her analysis of pinniped locomotion. Assuming a correlation between neural canal anatomy and locomotor ability, she concluded that *V. chulavistensis* was a forelimb/hindlimb (hindlimb-dominated) swimmer like modern *Odobenus* and not primarily a forelimb swimmer like modern otariids. Importantly, Giffin found a close similarity between *Odobenus* and phocids in terms of axial innervation and correlated muscle activity.

The humerus of *Alachtherium*, like that of *Odobenus*, does not have an enlarged entepicondyle (van Beneden 1877: pl. 3, fig. 1), suggesting that the condition in *Valenictus* is uniquely derived, while that of *Odobenus* is a shared primitive feature retained from the common ancestor of all tusked odobenines.

The osteosclerotic nature of the limb bones of *V. chulavistensis* is unique among known fossil and living pinnipeds and is convergent with the condition in sirenians. Functionally, this may have reduced buoyancy for the species' presumed benthic feeding in temperate latitudes. The fact that *Odobenus rosmarus* lacks osteosclerotic bone is a puzzle but may be related to its arctic habitat of cold, dense bottom waters.

Discussion.—*Valenictus chulavistensis* is possibly the most completely known fossil odobenine, represented by essentially every major skeletal element. This species was relatively large, similar in overall size to modern *Odobenus rosmarus*, but smaller than the great fossil walrus *Alachtherium cretsii* from the early Pliocene of the eastern North Atlantic.

The genus *Valenictus* has long been considered a problematic taxon, in large part because the type species is based on a single postcranial element not readily comparable with other more completely known taxa. Referral of the new San Diego Formation species to this genus offers a solution to this taxonomic problem by supplying important new information that confirms the odobenine relationships of *Valenictus*.

Valenictus imperialensis is also unusual because it occurs in the Imperial Formation of the Colorado Desert, Imperial County, California. The Imperial Formation was deposited during the late Miocene and early Pliocene in the proto-Gulf of California. As now, the Gulf had no direct connection with the temperate eastern North Pacific but instead extended south into tropical latitudes along a tectonic lineament characterized by crustal thinning and extension (Mammerickx and Klitgord 1982). The occurrence of tropical and subtropical molluscan taxa in the Imperial Formation, some with Caribbean affinities (Kew 1914; Vaughan 1917; Hanna 1926; Schremp 1981; Kidwell 1988), and their total absence in the well-studied marine Neogene deposits of coastal southern California, supports a strictly tropical connection and also implies an equatorial connection between the Caribbean and eastern tropical Pacific before the raising of the Isthmus of Panama. The invertebrate *and* vertebrate faunas of the proto-Gulf and temperate eastern Pacific were rather isolated from each other, implying a certain degree of endemism for the Imperial Formation faunas. Thus *V. imperialensis*, possibly confined to the subtropical proto-Gulf of California, may have been the result of late Miocene allopatric speciation. Furthermore, *V. chulavistensis* may represent a secondary late Pliocene dispersal of this clade into the temperate eastern North Pacific following emergence of the Isthmus of Panama.

The holotype humerus and only known specimen of *Valenictus imperialensis* shares several apomorphies with the humerus of *V. chulavistensis*. Although the possibility that the two species are conspecific cannot be ruled out altogether, the morphological differences presented above coupled with the late Miocene age of *V. imperialensis* and its apparent restriction to the proto-Gulf of California suggest that synonymy is unlikely. If all of the features shared by the two taxa represent synapomorphies inherited from a common ancestor and the additional apomorphies of *V. chulavistensis* represent uniquely derived features, *V. imperialensis* may not be diagnosable at the species level (i.e., it may represent a *nomen dubium*). This is a problem inherent in the questionable practice of describing fossil taxa from isolated skeletal elements of dubious diagnostic value. The discovery of additional material of *Valenictus imperialensis* and/or new material of other related odobenine species with the same synapomorphic features will help to resolve these questions.

Subfamily Dusignathinae Mitchell, 1968

Dusignathus Kellogg, 1927

Type species.—Dusignathus santacruzensis Kellogg, 1927.

Distribution.—Late Miocene and late Pliocene of California and Baja California.

Included species.—D. santacruzensis Kellogg, 1927, and *D. seftoni*, n. sp.

Emended diagnosis.—Dusignathine walruses distinguished from other taxa by the following apomorphies: mandibular symphysis narrowly V-shaped in occusal aspect, lower canines closely appressed to each other, left and right dentaries forming acute angle of 60° at symphysis, rostrum shortened, and mandibular rami deep (relative to *Gomphotaria*).

Dusignathus seftoni n. sp.

Figures 8–11

Diagnosis.—A species of *Dusignathus* distinguished from *D. santacruzensis* by the following autapomorphies: upper and lower cheek teeth forming a laterally convex arch in occlusal aspect, postcanine teeth in upper and lower jaws with medially rotated anteroposterior axes of roots, roots of all cheek teeth closely appressed, and dentary with deeply excavated masseteric fossa. Shares the following apomorphies with other dusignathines: nasal/frontal suture posteriorly directed and V-shaped; upper and lower canines enlarged as tusks.

Type material.—SDSNH 38342, a skull lacking the basicranium. Collected by Richard A. Cerutti and Matthew W. Colbert, 12 May 1989.

Etymology.—The species is named in honor of Thomas W. Sefton, who has generously supported the collection and study of fossil marine mammals from San Diego County.

Type locality.—SDSNH locality 3468, city of Chula Vista, San Diego County, California.

Horizon and age.—San Diego Formation, "lower member" of Deméré (1983), late Pliocene (Blancan NALMA correlative).

Referred specimens.—SDSNH 20801, right dentary preserving part of the symphyseal region of the left dentary; SDSNH 38256, damaged left humerus; SDSNH 43873, left humerus (all collected from the San Diego Formation). Complete locality information is available to interested reserachers upon request.

Cranium.—The holotype cranium was damaged by earth-moving equipment. The left side of the braincase is missing, as is the left zygomatic arch. Also missing is the entire basicranium, including both auditory regions, mastoids, and postglenoid fossae. The majority of the occipital shield, including the paramastoid processes, is also missing. Anteriorly, the left tooth row is obliterated, and with it the posterior border of the palate and internal narial opening. The right I^3, C^1, and P^{1-2} are sheared off just distad of the alveoli. The pattern of suture closure (see Sivertson 1954) indicates a subadult individual.

The cranium (Figs. 8, 9, 10A, B) preserves many general features characteristic of odobenids, including a low sagittal crest (as in *Neotherium* and *Imagotaria*), lack of supraorbital processes of frontals (as in *Neotherium*, *Imagotaria*, *Gomphotaria*, cf. *Pontolis*, *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus*), prominent antorbital processes (as in *Imagotaria*, *Gomphotaria*, *Pontolis*, *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus*), and enlarged infraorbital foramen (as in *Imagotaria*, *Pontolis*, *Gomphotaria*, *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus*).

The rostrum is short and broad relative to that of *Gomphotaria* (Table 2) and houses a pair of enlarged canines (tusks). The inclination of the canine root in relation to a vertical transverse plane is 33°, which is more vertically inclined (Figs. 8A, B) than the canines of *Gomphotaria pugnax* and approaches the condition in tusked odobenines. The frontal/maxilla suture forms an acute angle (approximately 60°) with the sagittal plane of the skull and is continuous with the nasal/frontal suture (Fig. 10B). The antorbital processes are split by the frontal/maxilla suture and are thus constructed from both frontal and maxilla. The nasals project posteriorly to form a wedge between the frontals (as in *Gomphotaria* and *Pontolis*, USNM 314300) and, anteriorly, are roughly rectangular (Figs. 9A, 10B). Thin ascending processes of the premaxillae overlap the nasals along 68% of their lateral margins. The anterior narial opening is more vertically oriented than that of *Gomphotaria* and ends in a prominent nasal process of the premaxillae. The floor of the narial opening is only slightly elevated (25 mm) above the level of the incisive margin. In contrast to *D. santacruzensis*, the maxillae are swollen to accommodate the roots of the enlarged canines, but not to the extent that they obscure the infraorbital foramina when the skull is viewed in anterior aspect (Fig. 8B).

The maxillary root of the zygomatic arch is delicately constructed, with a very slender dorsal strut. The ventral strut is directed dorsolaterally, in contrast to the more horizontally directed struts seen in *Imagotaria* and *Gomphotaria*. The effect of this is to

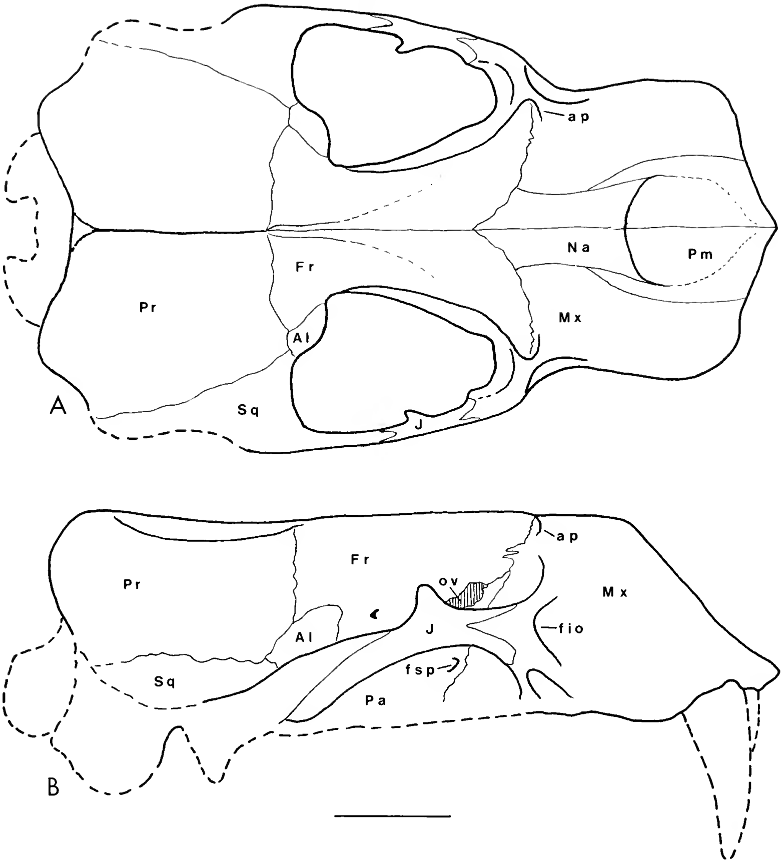

Figure 9. Reconstructions of *Dusignathus seftoni*, new species. A, dorsal view; B, lateral view. Al, alisphenoid; ap, antorbital process; fio, infraorbital foramen; fsp, sphenopalatine foramen; Fr, frontal; J, jugal; Mx, maxilla; Na, nasal; ov, orbital vacuity; Pa, palatine; Pr, parietal; Pm, premaxilla; Sq, squamosal. Scale bar, 5 cm.

give the infraorbital foramen a rounded triangular shape and a long axis inclined dorsolaterally, in contrast to *Imagotaria* and *Gomphotaria*, in which the long axis is directed horizontally. The ventral surface of the ventral strut is marked by a distinctive fossa (origin of the maxillo-naso-labialis muscle; Howell 1929) that is more prominent than that in *Aivukus*. The dorsal and ventral struts are positioned one above the other, in contrast to the condition seen in *Gomphotaria*, whose the dorsal strut lies anterior to the ventral.

The jugal is also delicately constructed, and has a small triangular postorbital process (Fig. 8A). The orbit is large relative to that of *Gomphotaria*. The squamosal fossa forms a shelf over the missing external auditory meatus but is narrower than in *Gomphotaria*. The zygomatic portion of the squamosal is long and slender and forms a splintlike suture with the jugal.

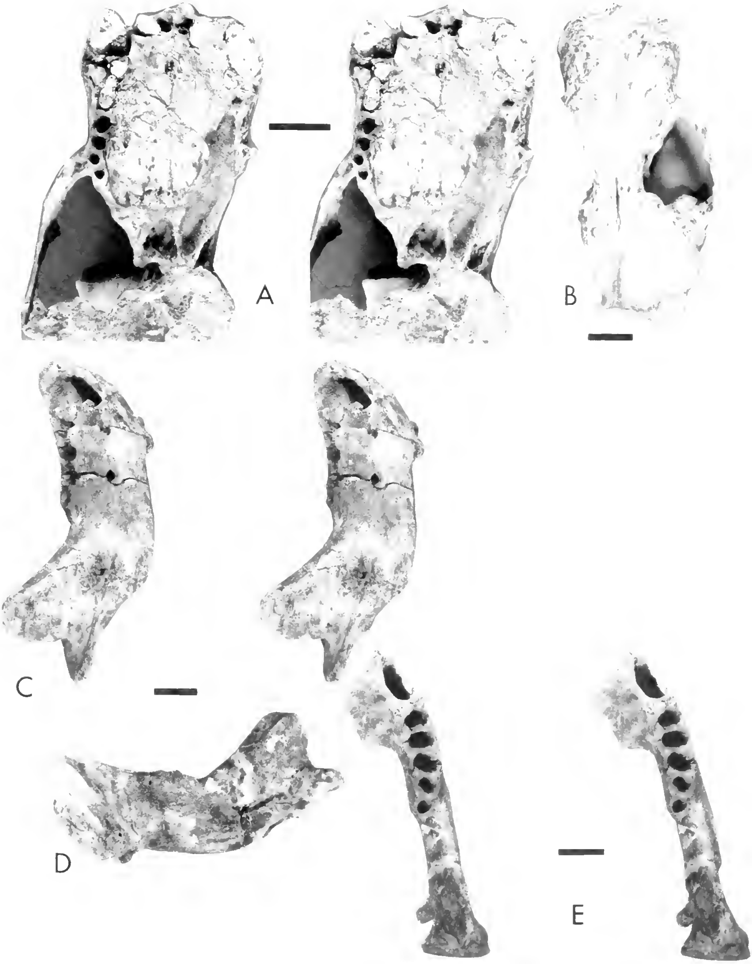

Figure 10. *Dusignathus seftoni*, new species. A, B, SDSNH 38342, holotype skull. A, ventral view (stereophotographs); B, dorsal view. C, D, E, SDSNH 20801, referred right dentary. C, lateral view (stereophotographs); D, medial view; E, occlusal view (stereophotographs). Scale bar, 5 cm.

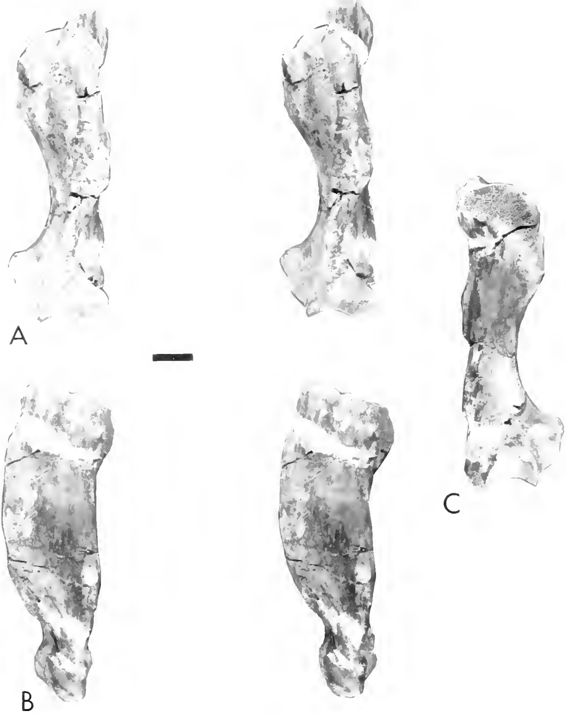

Figure 11. *Dusignathus seftoni*, new species, SDSNH 43873, referred left humerus. A, anterior view (stereophotographs); B, lateral view (stereophotographs); C, posterior view. Scale bar, 5 cm.

The palate is broad and not obviously arched. A pair of large incisive foramina are positioned 15 mm posterior to the lateral incisors (Fig. 10A). The palatine foramina lie 30 mm anterior to the palatine/maxilla suture. The posterior border of the palate is not preserved.

The anterior margins of the frontals along the midline are elevated slightly above the level of the maxillae and nasals. This elevation is even more pronounced in *Gomphotaria*. The anterior portion of the interfrontal suture is slightly depressed and becomes obscured posteriorly in a fine median sulcus that continues posteriorly into the interparietal suture. Farther posteriad the interparietal suture is marked by a low but distinct sagittal crest that merges posteriorly with the elevated right and left portions of the lambdoidal crest. The lambdoidal crest flares posteriorly, overhanging the largely missing occipital shield, which preserves no evidence of an occipital crista. The lateral walls of the braincase are broadly convex (as in *Neotherium*, *Imagotaria*, *Alachtherium*, and *Odobenus*), not concave (as in *Pontolis* and *Gomphotaria*). The interorbital constriction is prominent and positioned posteriorly against the anterior border of the braincase.

The orbital wall, on the right side, preserves much of the frontal/maxilla suture as it descends from the antorbital process to meet the palatine where the suture bifurcates into the frontal/palatine and palatine/maxilla sutures. There is no lacrimal bone, and thus the maxilla forms the entire anterior border of the orbit. The frontal/palatine suture is present for a short distance anteriorly but is lost posteriorly in a narrowly elongated orbital vacuity. A thin plate of palatine separates the orbital vacuity from the maxilla and thus the palatine/maxilla suture has a broad exposure on the orbital wall as it descends to the sphenopalatine foramen. From here the suture continues ventrally to the broken palatal margin. The orbitosphenoid is difficult to interpret because of breakage but seems to extend posteriorly from the posterior border of the orbital vacuity to the alisphenoid. The dorsal border of the orbitosphenoid is marked by a distinct ethmoidal foramen. A large arcuate opening marks the region of the missing optic foramen and orbital fissure. The dorsal portion of the alisphenoid is well preserved and broadly exposed on the anterolateral border of the braincase. The parietal/squamosal suture is well preserved and runs horizontally from the enlarged alisphenoid back to the broken lambdoidal crest. The pterygoids are not preserved.

Within the brain case, the cribriform plate is preserved as a teardrop-shaped structure, widest ventrally. A portion of the bony tentorium is preserved on the right side of the braincase, and has no expression externally.

Upper dentition.—Only the intra-alveolar portions of six teeth (right and left C^1, right and left I^3, P$^{1-2}$) are preserved in the holotype cranium. The empty alveoli of I^2, P$^{3-4}$, and M$^{1-2}$ indicate only single-rooted teeth. There is no I^1 alveolus. Alveolar diameters for the right upper dental arcade I^2–M^2 are as follows (anteroposterior length/transverse width in mm): 11.8/6.7; 14/20; 22/29.5; 13/12.5; 11/11; 14/10; 10/9; 8/7.4; 8.4/6.4.

The lateral incisor has an oval cross-section, with the long axis of the cross-section directed somewhat transversely. The right I^3 preserves a thin (1 mm) outer cementum layer surrounding a dense orthodentine core. The right C^1 of the new species is greatly enlarged relative to P^1 and has a large open pulp cavity (visible in computerized tomography images), suggesting either immaturity or continuous growth. The cross-sectional shape of this tooth is oval proximally (intra-alveolar), becoming roughly triangular distally. The distal cross-section approximates a right triangle, with the right angle placed medially and the hypotenuse corresponding to the labial surface of the tooth (Fig. 10A). In the holotype of *D. santacruzensis*, C^1 is oval throughout and has a closed root. In the rostral fragment (UCR 15244) from the Almejas Formation, Baja California, referred to *D. santacruzensis* by Repenning and Tedford (1977:46), C^1 has an oval cross-section and is approximately equal in size (alveolar diameter) to P^1. The canines of *D. seftoni* consist of a thin outer cementum layer and an inner massive orthodentine core, as in *Gomphotaria*. There is no evidence of a central globular orthodentine column as in the tusked odobenine walruses. No traces of enamel were observed on the narrow remnant of crown. The anterolateral surface of the canine has a single shallow longitudinal groove quite different from the regular longitudinal fluting seen in *Gomphotaria* (see Barnes and Raschke 1991) and the three or four shallow longitudinal grooves of *Odobenus* (see Ray 1960).

There are alveoli for six postcanine teeth. The alveolus for P^3 is a deep oval opening with the long axis of the cross-section rotated medially 36° to the sagittal plane. One wall of this alveolus is marked by a faint vertical ridge, presumably corresponding to an incipient bifid root. This alveolus extends at least 26 mm into the maxilla. The walls of this and all cheek-tooth alveoli continuously taper to the root, quite unlike the bulbous peglike roots of *Gomphotaria*. The alveolus for P^4 is also relatively deep (15 mm) but nearly circular in cross-section. Alveoli for M$^{1-2}$ are shallow (6 and 4 mm, respectively) and also circular in cross-section. In occusal aspect, the postcanine tooth row forms a broad, laterally convex arc aligning with I^3. The canine is positioned slightly outside of this arc. I^3 lies somewhat medial to C^1, not entirely anterior to it as in *Neotherium*, *Imagotaria*, and *Pontolis*. All of the postcanine alveoli are closely appressed to each other, with no intra-alveolar spaces. A conspicuous diastema 10 mm wide separates C^1 from I^3. This incisor–canine diastema is too narrow to accommodate an enlarged C$_1$, suggesting that the lower canine occluded with the upper lateral incisor as suggested for *D. santacruzensis* [see Repenning and Tedford (1977); both the holotype and the referred partial rostrum from the Almejas Formation, UCR 15244].

Dentary.—SDSNH 20801 is a complete right dentary (Table 4) with empty alveoli for a reduced incisor (possibly I$_3$), enlarged canine, and five postcanine teeth (presumably P$_1$–M$_1$). Although the specimen was damaged, a good cast of the specimen, made before the damage occurred, is available at the USNM.

The horizontal ramus is deep dorsoventrally (Fig. 10C) as in *D. santacruzensis* and thick transversely as in *Gomphotaria*. Two large mental foramina are located midway along the lateral surface of the dentary, one each below P$_1$ and P$_3$. The anterior mental foramen is oriented dorsoanteriorly, while the larger and more posterior mental foramen is oriented dorsomedially. In *D. santacruzensis* there are also two mental foramina, one each below P$_2$ and P$_3$. In medial aspect, the mandibular symphyseal surface is a narrow oval (as in *D. santacruzensis* and *Pontolis*, USNM 335563) and not a broad oval (as in *Gomphotaria*). A portion of the medial wall of the left canine alveolus is preserved indicating a fused symphysis. The posteroventral portion of the symphysis is marked by a large globular and deeply excavated genial tuberosity, which contrasts with the more slender, ridgelike tuberosity of *D. santacruzensis*. The coronoid process is large and rises at an angle of about 55° from the tooth row. In *Gomphotaria* and *Pontolis* (USNM 335563) the coronoid rises at a shallower angle (40° and 35°, respectively). The masseteric fossa in *D. seftoni* is more deeply excavated than in any living or fossil odobenid. The fossa is divided into upper and lower portions by a conspicuous horizontal masseteric ridge. The base of the fossa is marked anteriorly by a deep depression that is continuous posteriorly with a sharply margined shelf that extends as a horizontal surface to the mandibular condyle. A similar sharply margined masseteric shelf was described for a gigantic proximal mandibular fragment (UCR 15245) collected from the Almejas Formation and questionably referred to *D. santacruzensis* by Repenning and Tedford (1977:47). The mandibular condyle of UCR 15245 measures 107 mm in width; that of SDSNH 20801, 75 mm. The condyle of *D. seftoni* is broad, slender, and spindle-like.

As mentioned, the symphysis is fused, and preserves a portion of the medial wall of the left canine alveolus. The region between the two lower canines is narrow and in occulsal aspect is shaped like an isosceles triangle, with the most acute angle pointing forward. The medial walls of the right and left canine alveoli come to within 20 mm of each other, leaving no area for dorsally placed incisors. Although badly damaged, a small alveolus for an incisor is closely appressed to the anterior border of the canine. This alveolus, best seen on the USNM cast, is approximately 38 mm below the canine alveolar margin. The canine alveolus is large and deep and extends to a point below the alveolus for P$_2$. The canine's root (as determined from the alveolus) has an oval cross-section. The alveolar portion of the horizontal ramus in occlusal aspect is broad and laterally convex. The lingual borders of the cheek-tooth alveoli are higher than those on the labial border.

The pterygoid process (angular process) is large and projects medially approximately 20 mm as a hooklike flange as far as the medial border of the mandibular condyle. Anterior to this process, in lateral aspect, the ventral border of the ramus makes an abrupt flexure at the level of the distinct marginal process (Davis 1964). The marginal process itself is laterally swollen and rugose, marking the insertion for the digastricus muscle. The marginal process on the type right dentary of *D. santacruzensis* is slender and not enlarged. In lateral aspect, the ventral border of the ramus, between the marginal process and the globular genial tuberosity, is broadly sigmoidal, as in *D. santacruzensis*.

The medial surface of the coronoid process is marked by a distinct and curving strutlike ridge that is inset from, but parallel to, the anterior coronoid crest.

Lower dentition.—Although no teeth are present in the referred dentary, the alveoli are well preserved. Postcanine alveoli 1–4 (presumably P$_{1-4}$) are transversely elongate ovals at the level of the tooth row. In *Dusignathus santacruzensis* P$_1$ has a circular alveolus, while P_2–M_1 are elongated ovals. In *D. seftoni* the cross-sectional alveolar diameters for P_{1-4} (length/width in mm) are as follows: 23/19; 28/19; 29/22; 21/16. The conical alveolus for M_1 is circular at the level of the tooth row (13 mm diameter). The canine alveolus measures 48 by 34 mm. Alveolar depths for C_1–M_1 are as follows: 109 mm; 48 mm; 51 mm; 51 mm; 40 mm; 26 mm, respectively. Morphological details of the canine alveolus suggest that the root was open and had shallow widely spaced longitudinal grooves. Preserved on the alveolar walls of P_{1-4} are delicate vertical septa suggestive of vestigially bifid roots. In occlusal aspect, the entire tooth row (canine through M_1) forms a laterally convex arch.

Perhaps the most unusual feature of the lower tooth row is the orientation of the alveoli in occlusal aspect, specifically the angle made between the greatest cross-sectional dimension of the alveolus and a parasagittal plane. From back to front the roots undergo a progressive torsion, which in the right dentary is expressed as a successive counterclockwise rotation of the greatest cross-sectional dimension relative to a parasagittal plane: P_4 has rotated 52°, P_3 67°, P_2 96°, and P_1 130° (Fig. 10E).

Referral of the dentary (SDSNH 20801) to this new species is made on the basis of the comparably shortened tooth rows, laterally convex arching of the tooth rows, rotation of alveoli, and large size, features also observed in the holotype cranium.

Humerus.—A nearly complete left humerus (SDSNH 43873) and a partial left humerus (SDSNH 38256) are here referred to the new taxon (Fig. 11). SDSNH 38256 consists of the diaphysis and distal epiphysis, with the proximal epiphysis (including the capitulum and tuberosities) missing. SDSNH 43873 is complete except for damage to the proximal end (lateral one-third of the capitulum missing) and distal end (ectepicondyle missing). The following description relies primarily on features visible on SDSNH 43873.

The shaft is slender and similar in form to the humerus (USNM 23870) referred by Repenning and Tedford (1977) to *Imagotaria downsi*. The slenderness of the shaft and its large size (Table 5) suggest similarity to *Gomphotaria pugnax* (see Barnes and Raschke 1991). In posterior aspect, the lateral outline of the shaft is nearly straight and the medial outline is broadly concave. This contrasts with the more acutely concave medial profile of the humerus (UCMP 65318) questionably referred to *Dusignathus santacruzensis* by Repenning and Tedford (1977). Gross comparisons between UCMP 65318, USNM 23870, and SDSNH 43873 suggest that the latter two (*Imagotaria downsi* and *Dusignathus seftoni*) are more similar to each other than either is to UCMP 65318 (cf. *Dusignathus santacruzensis*). It should be noted that the holotype of *D. santacruzensis* does not include a humerus and that UCMP 65318 was only tentatively referred to this taxon. Thus, the actual morphology of the humerus of *D. santacruzensis* remains uncertain. However, this is not the case for *Gomphotaria*, another dusignathine walrus.

As in *Gomphotaria*, the proximal end of the humerus of *D. seftoni* has a rounded capitulum (head) positioned distinctly below the slender greater tuberosity. In *Valenictus*, *Pliopedia* (USNM 187328), and cf. *D. santacruzensis* (UCMP 65318) the greater tuberosity and humeral head are nearly at the same level. The lesser tuberosity of *D. seftoni* is knoblike and positioned distinctly below the capitulum, in contrast to the condition in *Imagotaria* (USNM 23870), in which the lesser tuberosity is nearly at the same level as the head. In medial aspect, the lesser tuberosity is broadened distally, while in anterior aspect the tuberosity is narrower than in *Valenictus*, *Pliopedia*, and cf. *D. santacruzensis*. The bicipital groove is broad and U-shaped.

The insertion for the deltoideus muscle is elongate and positioned on the pectoral crest as in *Imagotaria*, cf. *D. santacruzensis*, *Gomphotaria*, and *Aivukus* and differs from the posterolaterally displaced and isolated deltoid tubercles of *Odobenus*, *Valenictus*, and *Pliopedia* (USNM 187328). The pectoral crest itself is a slender and elongate keeled ridge that descends posteriorly, with some flexion, to join the distal surface of the shaft, as in *Imagotaria* (USNM 23870). This flexed posterior segment of the crest is intermediate in form between the gradually tapered crests of *Odobenus*, *Valenictus*, and *Pliopedia* (USNM 187328) and the abruptly flexed crests of *Aivukus* and *Gomphotaria*. As in all odobenids the distal portion of the pectoral crest is directed toward the medial lip of the trochlea, which is considerably broader than the radial capitulum. Distally, the trochlear surface makes an acute angle of about 76° with the shaft axis.

The entepicondyle is small relative to that of *Valenictus*. It is shaped much as in *Imagotaria* (USNM 23870) (i.e., a medially flattened knob in anterior aspect), not being triangular as in *Pliopedia* (USNM 187328) and cf. *D. santacruzensis* (UCMP 65318). Internally, the shaft of the humerus of *D. seftoni* is composed of cancellous bone, not osteosclerotic bone as in *Valenictus*. At 346 mm, SDSNH 43873 is longer (greater tuberosity to radial capitulum) than either *Pliopedia pacifica* (USNM 187328, 306 mm) or cf. *Dusignathus santacruzensis* (UCMP 65318, 271.6 mm) (Repenning and Tedford 1977).

Assignment of SDSNH 43873 and SDSNH 38256 to *Dusignathus seftoni* is based in part on the largeness of the former, which is compatible in size with the large mandible also referred to this species (SDSNH 20801). In addition, the elevated greater tuberosity of *D. seftoni* and the flexed pectoral crest are distinctive features shared with another dusignathine, *Gomphotaria*. And finally, the overall generalized morphology of the referred humeri clearly separates them from humeri of the only other odobenid known from the San Diego Formation, *Valenictus chulavistensis*.

Phylogenetic relationships.—*Dusignathus seftoni* is a dusignathine closely related to the late Miocene walruses *D. santacruzensis* and *Gomphotaria pugnax*. Synapomorphies supporting this relationship (Fig. 7) include (3) posteriorly directed V-shaped nasal/frontal suture, (32) upper and lower canines enlarged as tusks, and (45) dentary with sinuous ventral border (numbers refer to characters as discussed by Deméré 1994, this volume).

Referral of *D. seftoni* to *Dusignathus* is based largely on features of the lower jaw. These include the sharply divergent mandibular arch and presumed shortened rostrum, as well as the extremely deep horizontal ramus and unreduced closely appressed lower canines. In both species of *Dusignathus*, rostral shortening did not result in loss of cheek teeth. However, in *D. seftoni* the accommodation of the cheek teeth into a shortened tooth row involved rotation and close appression of the roots of individual teeth. In *D. santacruzensis* the lower postcanine teeth lack any indication of rotated roots. Although the possibility exists that root rotation is an ontogenetic feature, *D. seftoni* is distinguished by other characters, including C^1 with triangular cross-section, C_1 enlarged as a tusk, laterally convex upper and lower cheek-tooth rows, and larger size.

In *Dusignathus seftoni* as in *Gomphotaria pugnax*, plesiomorphic features such as a distinct sagittal crest, robust coronoid process, and large masseteric fossa imply a powerful jaw depressor musculature.

Discussion.—The genus *Dusignathus* is now known from two species, one from the late Miocene of central California and possibly Baja California and a second from the late Pliocene of southern California. *Dusignathus seftoni*, the geologically youngest known dusignathine walrus, clearly shows that members of this clade survived into late Pliocene time along the eastern North Pacific margin.

The holotype skull of *D. seftoni* is from a subadult individual, possibly a male, while the referred dentary and large humerus are from adult animals, almost certainly males. The dimensions of the dentary suggest that the new species was large, approaching modern *Odobenus*. Repenning and Tedford (1977) suggested that the type of *D. santacruzensis* was probably a female, so sexual dimorphism may account for some of the size discrepancy between the two species.

The shortened rostrum with steeply inclined tusks of *D. seftoni* is convergent with the condition in *Odobenus*. The size and cross-sectional shape of the upper and lower canines differ sufficiently from those of *D. santacruzensis* (the holotype and referred rostrum of Repenning and Tedford 1977:46, UCR 15244) to suggest that evolution of the San Diego species involved tusk development. The generalized morphology of the referred humeri suggests that this species, like *Imagotaria*, might have been more like otariids in its swimming habits than modern *Odobenus*. This is especially evident in the enlarged greater tuberosity, high and elongate pectoral crest, and relatively unenlarged entepicondyle. Repenning's (1976) suggestion that *Imagotaria* was a generalist neritic carnivore might apply equally to *Dusignathus seftoni*.

SUMMARY

The two new species of walruses described here increase our knowledge of odobenid evolution in many ways. *Valenictus chulavistensis* is possibly the most completely known fossil odobenine, represented by essentially every major skeletal element. This taxon preserves a reduced dentition previously unknown for marine carnivorans, emphasizing the morphological extremes possible in the marine realm. *Valenictus chulavistensis* clearly shows that possession of ever-growing tusklike upper canines is an inherited feature shared with the fossil *Alachtherium* and modern *Odobenus*. This realization, coupled with the observation that walruses do not use their tusks directly in benthic foraging, lends support to the hypothesis that walrus tusks evolved as social display structures, in a sense similar to the antlers of cervids. In addition, many other morphological features shared by *Odobenus*, *Alachtherium*, and *Valenictus* provide direct evidence for primitive character states near the base of the tusked odobenine clade.

Assignment of the new species to *Valenictus* clarifies the taxonomic and phylogenetic aspects of this formerly problematic taxon and provides a sense of the true taxonomic diversity of odobenine genera.

Dusignathus seftoni is the third described dusignathine species and illustrates the range of taxonomic diversity in this clade of double-tusked walruses. The shortened rostrum, with its condensed but complete dentition, parallels the condition in tusked odobenines but is associated with an unreduced temporal musculature.

Valenictus chulavistensis and *Dusignathus seftoni* were sympatric along the eastern North Pacific margin during the late Pliocene, approximately 2–3 Ma, illustrating the odobenids' past diversity. *V. chulavistensis* and *D. seftoni* may have avoided direct competition through resource partitioning, with the former specializing on benthic invertebrates and the latter remaining a generalist neritic fish and squid eater.

Extinction of the entire dusignathine clade must be viewed as a Pleistocene event, with only *Odobenus* of the odobenine clade surviving to the Recent. Recognition of *Valenictus chulavistensis* in Californian Tertiary deposits illustrates that tusked odobenines remained a part of the North Pacific pinniped fauna at least into the late Pliocene.

ACKNOWLEDGMENTS

Most of the fossils described in this report were salvaged from construction sites in the Rancho Del Rey housing development, city of Chula Vista. Fossils were collected by field crews from PaleoServices, Inc., of San Diego. Special thanks are extended to Richard A. Cerutti, Matthew W. Colbert, Bradford O. Riney, Donald R. Swanson, and Stephen L. Walsh of PaleoServices, Ed Elliott, Ken Screeton, and Mark Carpenter of McMillin Communities, and Doug Reid of the city of Chula Vista Planning Department. Children's Hospital of San Diego and especially Glenn Daleo of that institution generously provided technical expertise and use of their computerized axial tomography facility. For permission to study fossils under their care I thank also Lawrence G. Barnes (LACM) and Clayton E. Ray (USNM). Fritz Hertel assisted with measurements. Matthew W. Colbert, Blaire Van Valkenburgh, and Francis H. Fay provided critical review of the manuscript.

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The Family Odobenidae: A Phylogenetic Analysis of Fossil and Living Taxa

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ABSTRACT.—The modern walrus, *Odobenus rosmarus*, is a relict species, the lone survivor of a formerly diverse group of odobenid pinnipeds. Walruses had evolved in the North Pacific by at least the middle Miocene and were moderately diverse (five sympatric species) by the late Miocene. Even as recently as 3 million years ago there were at least three contemporaneous species of odobenids, two in the North Pacific and at least one in the North Atlantic. The Pleistocene record for walruses documents tusked odobenine walruses in both northern ocean basins as late as 500,000 years ago.

A phylogenetic (cladistic) analysis of all well-documented fossil and living walruses supports the monophyly of the Odobenidae. There are two major odobenid clades, the Dusignathinae (*Pontolis*, *Gomphotaria*, and *Dusignathus*) and the Odobeninae. The latter group contains the archaic odobenine *Aivukus* and a well-supported clade of tusked odobenines here named the Odobenini (*Pliopedia*, *Alachtherium*, *Prorosmarus*, *Valenictus*, and *Odobenus*). *Neotherium* and *Imagotaria* are generalized early odobenids at the base of the walrus radiation.

INTRODUCTION

Walruses (family Odobenidae) are represented today by a single living species, the holarctic *Odobenus rosmarus*. Perhaps the most characteristic anatomical feature of *Odobenus* is its pair of elongated ever-growing upper canine teeth (tusks) found in adults of both sexes. A rapidly improving fossil record reveals that these unique structures evolved in only a single lineage of walruses, the Odobenini, and that walruses enjoyed at least two major radiations. As noted by Repenning and Tedford (1977), the fossil record thus shows that "tusks do not a walrus make."

With the exception of an unconfirmed report of a walrus skull from the Mio–Pliocene Pisco Formation of coastal Peru, all fossil walruses are currently known only from Neogene deposits of the northern hemisphere. The oldest records are from the North Pacific, from middle Miocene deposits of central California correlative with the Barstovian North American Land Mammal Age (NALMA). Later Miocene (Clarendonian and Hemphillian NALMA correlative) records include fossils from the western United States (Oregon and California), Mexico (Baja California), and Japan. Pliocene fossils are known from the eastern and western United States (Virginia, North Carolina, South Carolina, Florida, Oregon, and California), Great Britain, Belgium, and Japan. Pleistocene walruses are known from the eastern and western United States (Maine, Massachusetts, New Jersey, Virginia, North Carolina, South Carolina, California, and Alaska), Canada, Great Britain, the Netherlands, France, and Japan. Thus the odobenids' fossil record includes specimens collected from Neogene deposits on both shores of the North Pacific and North Atlantic oceans. The ranges of fossil walruses extend into modern temperate and even subtropical latitudes (Ray 1960; Repenning 1976; Repenning et al. 1979), suggesting that the arctic lifestyle of modern *Odobenus rosmarus* is the result of rather recent dispersal and adaptation to boreal conditions.

Kellogg (1922:46–58) offered the first detailed discussion and review of walrus taxonomy and classification. He placed the fossil taxa *Alachtherium*, *Prorosmarus*, and *Trichecodon*, along with modern *Odobenus*, in the family Odobenidae and utilized a morphological series to present a phylogeny for the group. Because Kellogg did not recognize the odobenid affinities of such fossil pinnipeds as *Dusignathus*, *Pliopedia*, and *Pontolis* his concept of the Odobenidae corresponds to what modern workers recognize as the more exclusive subfamily Odobeninae, a clade containing primarily tusked walruses.

Repenning and Tedford (1977) summarized the state of odobenid paleontology and systematics as it was known at the time and recognized two subfamilies (Odobeninae and Dusignathinae) within an inclusive family Odobenidae (Table 1). In the Odobeninae they included the fossil taxa *Aivukus*, *Alachtherium*, and *Prorosmarus* as well as modern *Odobenus*; in the wholly extinct Dusignathinae they included the fossil taxa *Neotherium*, *Imagotaria*, *Dusignathus*, *Pliopedia*, *Valenictus*, and *Pontolis*.

Barnes (1989) proposed a classification (Table 1) without an inclusive family Odobenidae, instead recognizing the three subfamilies Odobeninae [= Odobeninae of Repenning and Tedford (1977)], Imagotariinae (*Neotherium*, *Pelagiarctos*, *Imagotaria*, *Pontolis*), and a restricted Dusignathinae (*Dusignathus*, *Pliopedia*, *Valenictus*). He grouped these three subfamilies with desmatophocids, otariids, and "enaliarctids" in an all-inclusive family Otariidae.

Barnes and Raschke (1991) followed the classification of Barnes (1989) and emphasized that only members of the Odobeninae were walruses, calling "imagotariine" and dusignathine taxa "walrus-like." Although this distinction may seem merely semantic, it suggests the authors' failure to recognize the common ancestry of "imagotariine," dusignathine, and odobenine taxa. I present evidence for this common ancestry below and so use the term "walrus" for all fossil and living odobenids.

The monophyly (*sensu* Hennig 1966) of the Odobenidae has not been explicitly demonstrated. Although previous workers (e.g., Kellogg 1922; Repenning and Tedford 1977; Barnes 1989) have presented characters useful for differentiating odobenids from other

TABLE 1. Previous classifications of fossil and living odobenids.

Repenning and Tedford (1977)	Barnes (1989)
Family Odobenidae	Family Otariidae
Subfamily Odobeninae	Subfamily Odobeninae
Aivukus	*Aivukus*
Alachtherium	*Alachtherium*
Prorosmarus	*Prorosmarus*
Odobenus	*Odobenus*
Subfamily Dusignathinae	Subfamily Dusignathinae
Neotherium	*Dusignathus*
Imagotaria	*Pliopedia*
Pontolis	*Valenictus*
Dusignathus	Subfamily Imagotariinae
Pliopedia	*Neotherium*
Valenictus	*Pelagiarctos*
	Imagotaria
	Pontolis

In A. Berta and T. A. Deméré (eds.)
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pinnipeds, these authors made no clear distinction between primitive and derived character states. Only shared derived character states (synapomorphies) serve as evidence of a group's monophyly.

In this report I provide the first phylogenetic (cladistic) analysis of odobenids and discuss highlights of walrus evolution as illuminated by the resulting phylogenetic framework. In doing so I also review the fossil record of odobenids (especially specimens and work published since 1977), emphasizing those features most relevant to phylogenetic reconstructions (i.e., synapomorphies).

SOURCES OF DATA

Fossil odobenids typically are represented by fragmentary material, most often isolated postcrania. Partial and complete skulls, as well as lower jaws, are also known. Unfortunately, many skeletal elements are not widely represented among named taxa, hampering comparisons. Important exceptions include the nearly complete holotype skeletons of *Gomphotaria pugnax* (see Barnes and Raschke 1991) and *Valenictus chulavistensis* (see Deméré 1994, this volume), as well as type and referred material of *Aivukus cedrosensis* and *Imagotaria downsii* (see Repenning and Tedford 1977).

Morphological data presented in this report are in many cases based on direct examination of fossil specimens in museum collections. I examined undescribed material of *Desmatophoca* and *Pinnarctidion* currently under study by A. Berta, undescribed material of *Neotherium* under study by L. G. Barnes, undescribed material of *Prorosmarus* under study by C. E. Ray, and new material of *Pontolis*.

Morphological data were also obtained from published reports, for *Aivukus* from Repenning and Tedford (1977); for *Alachtherium* from Hasse (1910), Rutten (1907), Berry and Gregory (1906), Kellogg (1922), and Erdbrink and van Bree (1990); for *Desmatophoca* from Barnes (1972, 1987) and Repenning and Tedford (1977); for *Dusignathus* from Kellogg (1927) and Repenning and Tedford (1977); for *Enaliarctos* from Mitchell and Tedford (1973), Berta and Ray (1990), and Berta (1991); for *Gomphotaria* from Barnes and Raschke (1991); for *Imagotaria* from Mitchell (1968), Repenning and Tedford (1977), and Barnes (1989); for *Neotherium* from Kellogg (1931) and Barnes (1988); for *Odobenus* from Ray (1960) and Fay (1982); for *Pliopedia* from Kellogg (1921) and Repenning and Tedford (1977); *for Pinnarctidion* from Barnes (1979); for *Pontolis* from True (1909) and Repenning and Tedford (1977); for *Prorosmarus* from Berry and Gregory (1906) and Repenning and Tedford (1977); *for Pteronarctos* from Barnes (1989, 1990); and for *Valenictus* from Mitchell (1961), Repenning and Tedford (1977), and Deméré (1994, this volume).

Recent workers (Rowe 1988; de Queiroz and Gauthier 1990) have called for rigorous use of the terms "definition" and "diagnosis" in systematic biology. In their usage, **definition** of a taxon is based upon ancestry and taxonomic membership, and **diagnosis** is a listing of shared derived homologous characters (synapomorphies) and the level of generality at which they occur. I use a third term, **characterization**, to refer to a listing of distinguishing characters, both shared derived and shared primitive homologous characters, and their taxonomic distribution.

Geologic ages and biostratigraphic correlations of fossil odobenids discussed here are modified from Ray (1976), Repenning and Tedford (1977), and Barnes (1989). Postcanine tooth is abbreviated Pc. Institutional acronyms for cited fossil specimens include BMNH, British Museum of Natural History, London, England; GMAU, Geological Museum of Amsterdam University, Amsterdam, Netherlands; IGCU, Instituto de Geología, Ciudad Universitaria, Universidad Nacional Autónoma de México, Mexico City, Mexico; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Antwerp, Belgium; LACM, Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NSM-PV, Vertebrate Paleontology, National Science Musuem, Tokyo, Japan; SBNHM, Department of Geology, Santa Barbara Natural History Museum, Santa Barbara, California; SDSNH, Department of Paleontology, San Diego Natural History Museum, San Diego, California; UCMP, Museum of Paleontology, University of California, Berkeley, California; UCR, Department of Geological Sciences, University of California, Riverside, California; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

PHYLOGENETIC ANALYSIS

Fifty-three skeletal characters (25 binary and 28 multistate) were scored for nine species/genera of fossil and extant odobenids. In addition, characters were scored for six outgroup taxa. The character–taxon matrix is presented in Table 2. As Rowe (1988) has suggested, I omitted incomplete and/or poorly known fossil taxa from the computer analysis but later added them to the phylogeny manually, using synapomorphies observed in the incomplete material. Taxa falling into this category include *Dusignathus santacruzensis*, *Pliopedia pacifica*, and *Prorosmarus alleni*. *Kamtschatarctos*, *Pelagiarctos*, and *Prototaria*, included by other workers in the Odobenidae, were excluded from this analysis because of their extreme incompleteness or their inaccessibility to me.

Character polarity within the Odobenidae is based on comparison with a series of successive outgroups (Maddison et al. 1984). These polarity decisions were used to construct a hypothetical ancestor. To test this procedure, I also had computer alogrithms decide global polarities for the ingroup (Swofford 1993). Both techniques yielded the same results. Outgroup taxa used were *Enaliarctos*, *Pteronarctos*, Otariidae (*sensu* Repenning and Tedford 1977), *Pinnarctidion*, Desmatophocidae (*sensu* Repenning and Tedford 1977), and Phocidae. Assumption of either of the competing hypotheses of pinniped relationships, monophyly (Wyss and Flynn 1993; Berta and Wyss 1994, this volume) or diphyly (Barnes 1989), did not affect assessment of polarities within the Odobenidae.

Enaliarctos, the earliest and least divergent pinniped, retains many primitive arctoid features (Barnes 1989; Berta 1991). *Pteronarctos*, believed to be the sister taxon to all other pinnipeds, shares the derived orbital-wall morphology (i.e., maxilla forming anterior margin of orbit) of this group (Berta 1991). *Pinnarctidion* is closely related to the desmatophocids (Barnes 1989; Berta and Wyss 1994, this volume), considered to be the sister taxon of odobenids (Repenning and Tedford 1977; Berta and Wyss 1994, this volume).

The data were analyzed on a Macintosh SE computer using PAUP (version 3.1.1; Swofford 1993) with all but characters 33 and 37 (see below under Dentition) treated as unordered. Unweighted and weighted treatments of the data were explored. In the latter case, all characters were assigned weights scaled to the number of possible state changes (12 for two states, 6 for three, 4 for four, and 3 for five). Computer runs were made with a hypothetical ancestor used to root the trees. In another series of computer runs, global polarity decisions made by the computer algorithm were used to root the trees. Global polarity decisions at the ingroup node were the same whether all outgroup taxa were used or whether only *Enaliarctos* and the Desmatophocidae were used. Use of only two outgroup taxa had the advantage of producing shorter trees with fewer homoplastic character arrangements.

TABLE 2. Character–taxon matrix showing the distribution of skull, dental, mandibular, and postcranial characters among fossil and modern odobenids. Characters scored 0 represent the ancestral state; characters scored 1–4 represent derived states. Missing data are scored as ?.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Enaliarctos spp.	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Pteronarctos sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Otariidae	0	0 & 1	2	2	1	2	2	0 & 1	0 & 1	0 & 2	0	0	0 & 1	0	0	0	0	0	0 & 2	0	0	0
4	Pinnarctidion spp.	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
5	Desmatophocidae	0	1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0 & 1	2	0	0
6	Phocidae	0	1	1	0	0 & 1	2 & 3	1	0 & 1	0	0	0	0	2	0	0	0	0	0	1	2	0	0
7	Neotherium mirum	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Imagotaria spp.	0	1	0	2	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
9	Pontolis magnus	0	1	1	2	1	1	1	0	1	0	0	0	1	1	1	0	2	0	2	0	0	0
10	Gomphotaria pugnax	0	0	1	2	1	1	1	1	1	0	0	0	?	?	0	0	?	0	2	0	0	0
11	Dusignathus spp	0	1	1	2	1	1	1	1	1	0	?	?	?	?	0	0	2	0	0	0	0	0
12	Aivukus cedrosensis	0	1	?	1	1	1	1	1	1	0	?	?	?	?	0	0	2	?	?	1	1	0
13	Alachtherium cretsii	1	1	?	1	1	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	?	1
14	Valenictus chulavistensis	1	1	0	1	1	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	1	1
15	Odobenus spp	2	2	0	1	1	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	1	1

		23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
1	Enaliarctos spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Pteronarctos sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	0	?	?
3	Otariidae	0	0 & 1	0	0	0	0	0	0	0	0	0 & 1	0 & 1	2	2	1 & 2	0	0	0	0	0	0	0
4	Pinnarctidion spp.	0	0	0	0	0	?	0	?	0	0	0	0	0	1	0	0	?	?	?	0	?	?
5	Desmatophocidae	0	0	0	0	0	0	0	0	0	0	0	0	1 & 2	2	1 & 2	0	0	0	0	0	0	0
6	Phocidae	0	0 & 1	0 & 1	0	0	0	0	0	0	0	1	0 & 1	5	2	1	0	0	0	0	0	0	0
7	Neotherium mirum	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
8	Imagotaria spp.	0	?	0 & 1	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0
9	Pontolis magnus	0	?	0	0	0	0	0	1	0	0	0	1	?	?	2	1	0	0	0	0	1	1
10	Gomphotaria pugnax	0	1	2	0	0	0	0	1	0	0	0	1	2	2	2	1	0	0	0	0	0	0
11	Dusignathus spp.	0	1	1	1	0	0	1	1	0	0	0	2	2	2	2	1	1	0	0	1	1	1
12	Aivukus cedrosensis	?	0	1	0	0	1	0	0	?	0	1	1	3	2	3	1	0	0	0	0	0	?
13	Alachtherium cretsii	1	?	1	1	1	2	0	0	1	1	2	2	3	2	3	2	0	0	1	1	0	1
14	Valenictus chulavistensis	1	2	3	3	1	3	0	0	2	2	3	3	4	3	4	3	1	0	1	1	0	1
15	Odobenus spp.	1	2	2	2	1	2	1	0	1	1	2	2	3	2	3	2	1	1	1	1	0	0

		45	46	47	48	49	50	51	52	53
1	Enaliarctos spp.	0	0	0	0	0	0	0	0	?
2	Pteronarctos sp.	?	?	?	?	?	?	?	?	?
3	Otariidae	0	0	0	1	0	0	0	0	0
4	Pinnarctidion spp.	0	0	0	?	?	?	?	?	?
5	Desmatophocidae	0	0	0	1	0	0	1	1	1
6	Phocidae	0	0	0	0	0	0	2	0	0
7	Neotherium mirum	0	0	1	2	1	1	1	1	?
8	Imagotaria spp.	0	0	1	2	1	1	1	1	?
9	Pontolis magnus	0	0	1	?	?	1	1	1	1
10	Gomphotaria pugnax	0	0	1	2	1	1	1	1	1
11	Dusignathus spp.	0	0	1	2	?	?	?	?	?
12	Aivukus cedrosensis	0	0	1	2	2	1	?	?	?
13	Alachtherium cretsii	1	0	1	2	2	1	?	?	?
14	Valenictus chulavistensis	2	1	1	2	2	1	1	1	1
15	Odobenus spp.	2	0	1	2	2	1	1	1	1

Employing the branch-and-bound option in PAUP and varying two factors (i.e., outgroup content and character weight) produced the following results:

Hypothetical ancestor/unweighted data—Nine most parsimonious trees of 101 steps and consistency index of 0.861.

Hypothetical ancestor/weighted data—Six most parsimonious trees of 746 steps and consistency index of 0.834.

Two outgroup taxa/unweighted data—Three most parsimonious trees of 108 steps and consistency index of 0.830.

Two outgroup taxa/weighted data—Two most parsimonious trees of 786 steps and consistency index of 0.830.

The same major groups were recognized in all trees, with differences in topology involving arrangement of terminal taxa within the Dusignathinae and Odobenini. A strict (Nelson) consensus tree summarizing these topologies is presented in Figure 1. Figure 2 is a composite cladogram combining the 50% majority-rule consensus trees with the manually plotted incomplete fossil taxa.

The results of the PAUP analysis were exported to MacClade version 3.0 (Maddison and Maddison 1992) and examined for patterns of character evolution within the most parsimonious topologies. Various alternate hypotheses were tested and compared with the PAUP-generated hypotheses. This allowed empirical evaluation of the robustness of the various phylogenetic hypothesis.

Odobenid Monophyly

The result of this computer-assisted phylogenetic analysis is a well-supported hypothesis of odobenid monophyly based on cranial, dental, and postcranial synapomorphies. Within the Odobenidae, a series of monophyletic groups can be recognized.

Odobenidae.—Diagnosis of this family is based upon five unequivocal synapomorphies (numbers refer to characters as discussed under Character Evidence below): (6) antorbital processes constructed from both frontal and maxilla, (47) distal trochlea of humerus with diameter of medial lip greater than diameter of capitulum, (48) distal portion of radius with enlarged radial process, (49) insertion for pollicle extensor muscle on first metacarpal developed as a pit or rugosity, and (50) scapholunar with distinct pit for the magnum.

The Odobenidae are defined as the monophyletic group containing the most recent common ancestor of *Neotherium* and *Odobenus* and all of its descendants. The family includes *Aivukus, Alachtherium, Dusignathus, Gomphotaria, Imagotaria, Neotherium, Odobenus, Pliopedia, Pontolis, Prorosmarus,* and *Valenictus* (Table 2).

So defined, the Odobenidae are the same as recognized by Repenning and Tedford (1977), who characterized this taxon by a number of features, many of which I have used also. Repenning and Tedford, however, used other characters that are not applicable at the level of the Odobenidae but are derived at a more general level within the Pinnipedia (e.g., skull without prominent supraorbital processes, also seen in desmatophocids), are synapomorphies of taxa within the Odobenidae (e.g., postcanine tooth roots simple and peglike, seen only in dusignathines and odobenines; I_3 medial to C_1, seen only in odobenines; femoral head distinctly higher than greater trochanter, seen only in *Odobenus*), or are characters whose distribution within the Pinnipedia is not well known (e.g., occipital condyles widely flaring, bony eustachian canal relatively large, and ratio of areas of tympanic membrane and oval window).

Barnes (1989) offered a phylogenetic hypothesis for "otarioids" that also included a listing of features characteristic of specific taxa. Although Barnes did not formally recognize an inclusive Odobenidae, his branching diagram depicts such a grouping (Barnes 1989: fig. 9, node 12). Some of Barnes' characters I have used as well, but Barnes also used characters symplesiomorphic at the level of the Odobenidae (e.g., large lesser trochanter of femur), characters homoplastic within the Pinnipedia [e.g., trochanteric fossa of femur lost (independently lost in several pinniped groups), optic foramen in posteroventral position (also seen in otariids)], and characters that are difficult to define (e.g., radius and ulna shortened).

I recognize three characters initially considered to represent odobenid synapomorphies but now seen to be more generally distributed and supportive of a sister-group relationship between odobenids and desmatophocids. These characters include (51) astragalus with calcaneal tuber, (52) calcaneal tuber of calcaneum with prominent tuberosity, and (53) entocuneiform strongly overriding the medial articular facet of the mesocuneiform. In all cases the derived state occurs also in *Allodesmus.*

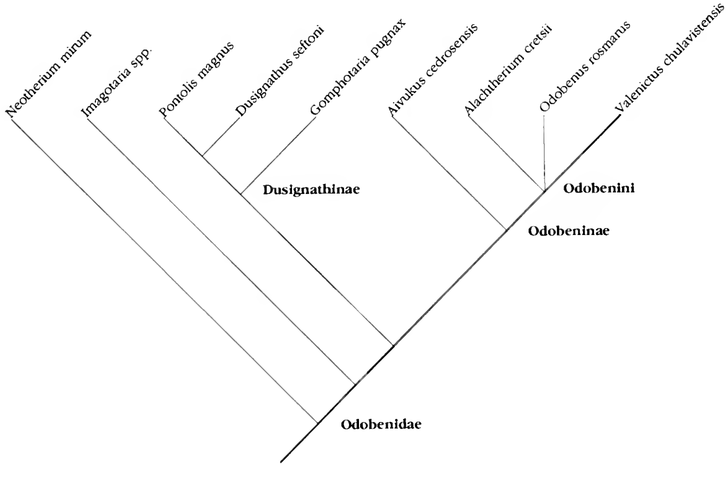

Figure 1. Strict-consensus tree of proposed relationships among fossil and living odobenids (characters discussed in text).

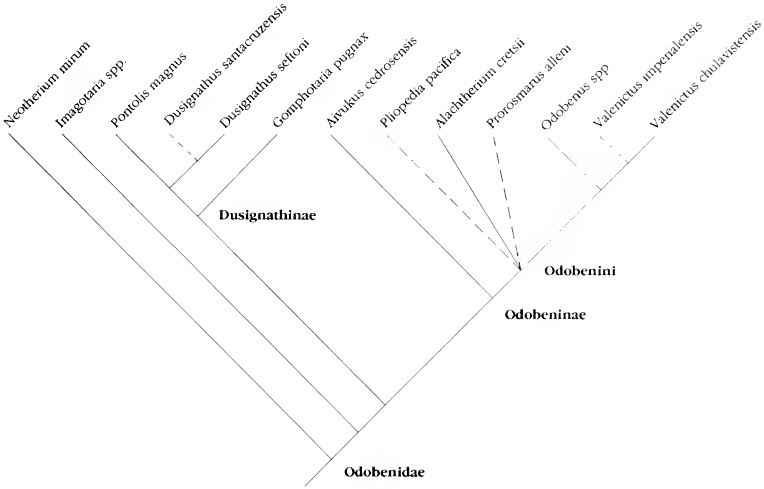

Figure 2. Fifty-percent majority-rule consensus tree with incomplete odobenid taxa added (dashed lines).

"Imagotariinae".—This taxon is paraphyletic, its members, *Neotherium* and *Imagotaria*, possessing the basal synapomorphies of the Odobenidae but lacking the synapomorphies of the dusignathine and odobenine walruses. Characterization of these "primitive" walruses is based primarily on characters they lack (i.e., the derived states of characters 38, 39, 40, and 46).

Imagotaria + *Dusignathinae* + *Odobenini*.—This group is supported by five unequivocal synapomorphies: (4) frontal/maxilla suture straight and divergent, (5) antorbital process large, (9) palate arched transversely, (13) pterygoid strut broad, and (14) basioccipital broad and pentagonal. Two equivocal synapomorphies also potentially diagnose this clade: (8) infraorbital foramen enlarged (reversed in *Pontolis*) and (37) P^4 with bilobed roots (reversed in *Pontolis*).

Dusignathinae + *Odobeninae*.—A monophyletic group containing odobenine and dusignathine walruses is supported by two unequivocal synapomorphies: (17) paramastoid process flattened and (38) postcanine tooth enamel thin or lost. Two equivocal synapomorphies are potentially diagnostic of this clade: (36) P^4 protocone shelf strongly reduced or lost (also seen in phocoids) and (37) postcanine teeth single-rooted (also seen in phocoids and some otariids).

Dusignathinae.—Diagnosis of this taxon is based upon one unequivocal synapomorphy: (30) upper and lower canines enlarged as tusks. In addition three equivocal synapomorphies may diagnose this taxon: (3) nasal/frontal suture V-shaped and posteriorly directed (a more acute "V" occurs in desmatophocids and phocids), (19) sagittal crest enlarged (reversed in *Dusignathus*; also seen in certain otariids), and (24) orbital vacuity anteriorly placed (also occurs in otariids).

The Dusignathinae are defined as the monophyletic group containing the most recent common ancestor of *Pontolis* and *Dusignathus* and all of its descendants and include *Gomphotaria* also.

The subfamily Dusignathinae so defined is more exclusive than that of Repenning and Tedford (1977) and except for the addition of *Pontolis* nearly the same as that of Barnes and Raschke (1991), who considered *Pontolis* an "imagotariine" walrus from the limited features preserved on the holotype braincase. Recognition and referral of additional cranial as well as postcranial material provides a more complete understanding of this taxon.

Odobeninae.—Diagnosis of this taxon is based upon seven unequivocal synapomorphies: (4) frontal/maxillary suture transversely directed, (21) postorbital process of jugal dorsoventrally expanded, (28) C_1 less than 75% the size of C^1, (33) postcanine teeth reduced to five, (35) P^3 and P^4 with simple peglike crowns, (37) P^4 with single circular root, and (49) first metacarpal with insertion for pollicle extensor muscle developed as a rugosity. In addition, one equivocal synapomorphy, (31) lower canine premolariform, potentially diagnoses this taxon. The crown of the lower canine of *Aivukus* is unknown and may or may not have been caniniform. Thus premolariform lower canines may have evolved at a lower level of universality and represent a synapomorphy of the Odobenini.

The Odobeninae are here defined as the monophyletic group containing the most recent common ancestor of *Aivukus* and *Odobenus* and all of its descendants. The subfamily thus includes *Aivukus*, *Alachtherium*, *Odobenus*, *Pliopedia*, *Prorosmarus*, and *Valenictus*.

Under this definition, the subfamily Odobeninae is nearly the same as that of Repenning and Tedford (1977) and Barnes (1989) except for the addition of *Valenictus* and *Pliopedia*.

Odobenini (new taxon).—Diagnosis of this new taxon is based upon 14 unequivocal synapomorphies: (1) external narial opening elevated above incisive margin, (9) palate arched transversely and longitudinally, (10) hard palate elongated (also occurs in the otariid *Otaria*), (16) mastoid processes as widest part of cranium, (20) zygomatic portion of squamosal blunt and robust, (22) temporal fossa shortened, (24) orbital vacuity posteriorly placed, (27) C^1 with well-developed globular dentine column, (28) C_1 less than 40% the size of C^1, (32) P^1 medial to C^1, (33) three or four upper postcanine teeth, (38) adult postcanine tooth crowns with cementum only (no enamel), (41) mandibular terminus vascular, and (45) deltoid tubercle of humerus on extreme lateral side of pectoral crest or separated from crest. Five equivocal synapomorphies also may diagnose this clade: (15) mastoid enlarged (also occurs in *Pontolis*), (26) I^3 medial to C^1 (also occurs in *Dusignathus*), (31) C_1 premolariform, (34) tooth row between P^1 and M^1 laterally convex (also in *Dusignathus*), and (42) mandibular arch sharply divergent (also occurs in *Dusignathus*).

In addition, six characters interpreted by the PAUP analysis as derived at the level of the Odobeninae appear *a posteriori* to represent synapomorphies of the Odobenini. These include (11) palatine telescoped beneath alisphenoid, (12) hamular process broad, (13) pterygoid strut lost, (18) lambdoidal crest with distinct flattened traction surface, (19) sagittal crest lost (also variably seen in phocoids), and (23) optic foramen funnel-shaped. Although the condition of these characters is yet unknown in *Aivukus* (i.e., they were coded as missing), because most of the six are correlated with cranial telescoping (exemplified by *Odobenus* and *Valenictus*), the absence of telescoping in *Aivukus* suggests that they are actually derived at the level of the Odobenini.

The Odobenini are defined as the monophyletic group containing the most recent common ancestor of *Alachtherium* and *Odobenus* and all of its descendants. Membership includes *Alachtherium*, *Odobenus*, *Pliopedia*, *Prorosmarus*, and *Valenictus*. *Prorosmarus* is assigned to this taxon because it possesses derived characters 28, 31, and 41. *Pliopedia* is considered a member of the Odobenini on the basis of derived characters 18, 19, and 45. Previously, *Pliopedia* and *Valenictus* were considered members of either the Dusignathinae (Repenning and Tedford 1977) or the "Imagotariinae" (Barnes 1989). The type genus of this new tribe is *Odobenus*.

As defined here, the Odobenini contain all of the odobenine walruses with enlarged upper canines of tripartite construction and telescoped crania. In this light, the basal odobenine *Aivukus* is a metaspecies (Donaghue 1985) and possible ancestor of the Odobenini (i.e., it possesses the odobenine synapomorphies but lacks the many synapomorphies of the tusked odobenines).

Character Evolution

Dentition.—Odobenids underwent a general evolutionary trend toward homodonty that entailed a reduction in the number of roots from three to two to one, simplification of postcanine tooth crowns from three to two to one cusps, and loss of enamel. A similar (except for loss of enamel), convergent pattern of tooth simplification also occurred in otariids (Berta and Deméré 1986), desmatophocids (Barnes 1987), and phocids (C. A. Repenning, pers. comm.).

Tusks evolved independently in the Dusignathinae and the Odobenini. In the former, enlargement of the upper canines was accompanied by enlargement of the lower canines (Repenning and Tedford 1977). In the Odobenini, only the upper canines were enlarged. This enlargement, and the associated development of a central globular dentine column, first evolved in the most recent common ancestor of *Alachtherium*, *Valenictus*, and *Odobenus* and is strong evidence that modern *Odobenus* inherited its tusks. In this historical light these unique dental structures clearly do not represent adaptations to the present arctic range of *Odobenus* but rather are structures transported into this boreal habitat by the temperate and/or subtropical ancestor of *Odobenus*. As discussed by Deméré (1994, this volume) the tusks most likely evolved as structures for social display under the pressures of sexual selection.

Other dental evolutionary trends in the Odobenini include reduction in number of postcanine teeth with successive loss of M^1 and M^2, reduction in number of upper incisors from three to two to one (I^{1-2} are lost), displacement of I^3 posteriad to a position medial to C^1 and in line with the postcanine teeth, and migration of Pc^1 (probably P^2) to a position medial to C^1. *Valenictus chulavistensis* exhibits the most derived complex of dental characters with loss of all teeth, save the upper tusks.

Cranium.—The most recent common ancestor of *Alachtherium*, *Valenictus*, and *Odobenus* had a skull different from that of other odobenids. The external nares had moved from a ventral position almost level with the tooth row to an elevated position well above the tooth row, a modification associated with palatal vaulting and the evolution of suction feeding. Elongation of the palate was also part of this adaptation to oral suction and involved telescoping of the rostrum back and under the anterior portion of the braincase, with the posterior border of the palatine reaching a position in line with the postglenoid fossa and the orbitosphenoid becoming compressed in the orbital wall and changing from a horizontally elongated bone to one that is steeply inclined and marked by a funnel-shaped optic foramen. The pterygoid strut was lost with the concomitant shift in the origin for the internal pterygoid muscle to the orbital wall of the palatine bone. The hamular process of the pterygoid moved to a more medial position and attained a broad, horizontally directed form. The temporal fossa was shortened and the sagittal crest was lost as the temporalis musculature became reduced. The mastoid bone was greatly enlarged both horizontally and ventrally as the neck musculature developed to buttress the massive head with its enormous canines.

Skulls of dusignathine walruses are less specialized than those of the Odobenini, but nonetheless have diverged from those of *Imagotaria* and *Neotherium*. Greatly enlarged sagittal crests in *Gomphotaria* and *Pontolis* imply a well-developed temporalis musculature, which together with retention of six postcanine teeth and a relatively flat palate suggests a more generalist marine predator than the Odobenini, which feed by benthic suction. *Dusignathus* evolved several features convergent with the Odobenini (shortened rostrum, convex postcanine tooth row, and fused mandibular symphysis) but also retained enlarged lower canines (to go with the large uppers) and a strong temporalis musculature.

Lower jaw.—The lower jaws of odobenids reveal a variety of modifications, undoubtedly strongly correlated with the changes seen in the skulls. In odobenines the lower jaw evolved a strongly upturned symphyseal region that curves medially around the enlarged upper canines in the Odobenini. The anterior border of the mandible developed into an expanded roughened and pitted surface for the mobile lips. This character complex evolved in the common ancestor of *Alachtherium* and *Odobenus*. *Alachtherium* and *Prorosmarus* retain two lower incisors and four postcanines. In *Odobenus* the incisors are lost and the postcanine series is reduced to only three teeth. As with its upper dentition, *Valenictus* is the most dentally derived of the Odobenini, with loss of all lower teeth. Fusion of the mandibular symphysis evolved in the common ancestor of *Valenictus* and *Odobenus*. In *Valenictus* the symphyseal region is delicate and widest dorsally. In *Odobenus mandanoensis* from the Pleistocene of Japan (as in *O. rosmarus*), the symphysis is buttressed by the addition of bone so that it is widest ventrally. Evidently this strongly buttressed symphysis evolved in the common ancestor of *O. mandanoensis* and *O. rosmarus*.

CHARACTER EVIDENCE

The following section presents the cranial, dental, and postcranial characters employed in the cladistic analysis. For each character, alternate character states, taxonomic distribution of states, and polarity assessment are discussed. Outgroup taxa include species of *Enaliarctos*, *Pteronarctos*, Otariidae, *Pinnarctidion*, Desmatophocidae (*Desmatophoca* and *Allodesmus*), and Phocidae. Some discussions also include *a posteriori* assessments of character evolution based upon the distribution of character states in the proposed phylogenetic hypothesis (Fig. 1).

Cranium

1. *External narial opening*. 0 = low, 1 = intermediate, 2 = high. The external narial opening is low and almost level with the tooth row in most pinnipeds (primitive condition). In *Odobenus rosmarus* the external nares are elevated well above the tooth row (Repenning and Tedford 1977) (derived condition 2). The nares' position in *Alachtherium* (see Erdbrink and van Bree 1990:pl. 1B) and *Valenictus* is intermediate (derived condition 1). Elevation of the narial opening may be related to the extreme palatal vaulting characteristic of the suction-feeding Odobenini. Enlargement of the upper canines and broadening of the muzzle may also be correlated with this elevated position of the external narial opening.

2. *Ascending process of premaxilla, overlap with nasal*. 0 = long, 1 = short, 2 = none. In *Allodesmus* (Barnes 1972), *Desmatophoca* (Barnes 1987), and phocids (Wyss 1987) the ascending process of the premaxilla has a very short overlapping contact externally with the nasal. In *Odobenus rosmarus* the two bones overlap only within the nasal opening, with the maxilla contacting the nasal along its entire external lateral border. In many neonates of *O. rosmarus* an irregular band of premaxilla (ascending process) is visible externally, sandwiched between the maxilla and nasal. This is roofed over in adults. In fossil odobenids an ascending process is always visible externally, where preserved. The length of overlap, however, is variable; it is relatively long (premaxilla overlaps more than 50% of nasal) in *Gomphotaria* and *Neotherium*, short (overlap <50%) in *Imagotaria*, *Dusignathus*, *Aivukus*, and *Valenictus*. Wyss' (1987) and Barnes' (1992) suggestion that a long overlap is the primitive condition is supported by a long overlap in *Enaliarctos emlongi* (see Berta 1991), *Pteronarctos goedertae* (see Barnes 1989), and *Pinnarctidion* (A. Berta, pers. comm.). I postulate that the short overlap evolved independently at least twice, once in the desmatophocids and again in the odobenids. The condition in *Gomphotaria* represents a reversal.

3. *Nasal/frontal suture*. 0 = transverse, 1 = V-shaped, 2 = W-shaped. The posterior border of the nasal is blunt and nearly transverse in most outgroup taxa and in *Neotherium*, *Imagotaria*, and *Odobenus* (Figs. 3A, E) (primitive condition). The condition in *Aivukus* and *Alachtherium* is unclear. Although two derived states are recognized, the homology of the first, a V-shaped nasal/frontal suture (point of V directed posteriorly between frontals, Figs. 3B–D), is questionable. Two variations of this condition are seen with *Pontolis* (USNM 314300), *Gomphotaria*, and *Dusignathus* having a broad V-shaped suture (Fig. 3D) and *Desmatophoca*, *Allodesmus* (Fig. 3B), and phocids (Fig. 3C) having an acute V-shaped nasal/frontal suture. This distribution suggests the independent evolution of character state 1 in phocoids and in dusignathine walruses. A second derived condition occurs in living and fossil otariids (e.g., *Zalophus*, *Eumetopias*, *Otaria*, and *Thalassoleon*), in which the suture (Fig. 3F) is W-shaped (i.e., the frontals extend anteriorly between the nasals; King 1983).

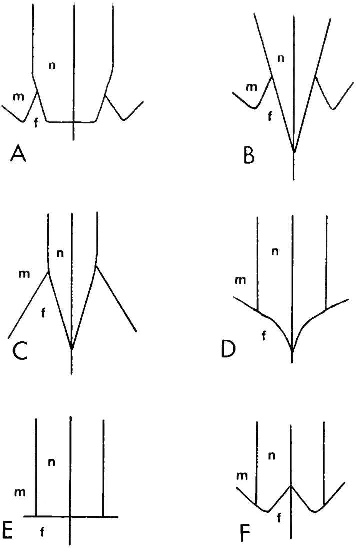

Figure 3. Rostral suture patterns of selected fossil and living pinnipeds. A, *Enaliarctos*, *Pteronarctos*, and *Neotherium*; B, *Desmatophoca* and *Allodesmus*; C, *Phoca*, *Leptonychotes*, and *Halichoerus*; D, *Pontolis*, *Gomphotoria*, and *Dusignathus*; E, *Imagotaria* and *Odobenus*; F, *Eumetopias*, *Otaria*, and *Zalophus*. Skeletal elements: f, frontal; m, maxilla; n, nasal. Not to scale.

4. *Frontal/maxilla suture*. 0 = V-shaped, 1 = straight, transverse, 2 = straight, divergent. In all of the fossil outgroup taxa, as well as in *Neotherium* (LACM 131950), the frontal/maxilla suture is characterized by a narrow anteriorly directed V-shaped segment of the frontal that invades the maxilla immediately adjacent to the nasals (Fig. 3A) (primitive condition). Loss of this V-shaped frontal segment is derived, and two states can be recognized. Lateral to the nasals the suture is either transverse (state 1, Fig. 3E) or anterolaterally divergent (state 2, Fig. 3D) relative to the sagittal plane. In *Imagotaria* and the dusignathines *Pontolis*, *Gomphotaria*, and *Dusignathus*, the suture, as it leaves the nasals, is straight and sharply divergent relative to the sagittal plane (approximately 62°, 55°, and 58°, respectively). In the odobenines *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus*, the suture is straight and nearly transverse (approximately 85°, 80°, 74°, and 85°, respectively).

5. *Antorbital process*. 0 = small/absent, 1 = large. The primitive condition is either a small, weakly developed antorbital process, as in *Enaliarctos*, *Pteronarctos*, *Pinnarctidion*, and *Neotherium*, or no process, as in *Allodesmus* and *Desmatophoca*. The derived condition of a large process occurs in otariids, certain lobodontine phocids, and the later-diverging odobenids *Imagotaria*, *Pontolis* (seen on USNM 335554), *Gomphotaria*, *Dusignathus* (seen on

SDSNH 38342), *Alachtherium* (seen on GMAU K-8052), *Valenictus* (seen on SDSNH 38228), and *Odobenus*. The distribution of this character suggests that the large antorbital process evolved independently in lobodontine phocids, otariids, and odobenids (except *Neotherium*).

6. *Antorbital process.* 0 = constructed from frontal, 1 = constructed from frontal and maxilla, 2 = constructed from maxilla only, 3 = absent. The small antorbital process of *Pteronarctos* appears to lie entirely within the frontal bone (Barnes 1990) (primitive condition). In all fossil and modern odobenids the frontal/maxilla suture splits the antorbital process, which is thus formed from both bones. A second, derived condition evolved independently in otariids and lobodontine phocids, in which the antorbital process is anterior to the frontal/maxilla suture and entirely within the maxilla. The absence of the process in desmatophocids and most phocids is assigned state 3.

7. *Supraorbital processes of frontals.* 0 = weak, 1 = absent, 2 = strong. In all of the fossil outgroup taxa the supraorbital process is present but weakly developed (primitive condition). Two derived character states are recognized. The supraorbital process is absent in fossil and living odobenids and in phocids (derived state 1). A strongly developed process (derived state 2) does not occur among the ingroup but is present in living and fossil otariids (see Repenning and Tedford 1977; King 1983).

8. *Infraorbital foramen.* 0 = small, 1 = large. The infraorbital foramen in outgroup taxa and in *Neotherium* (LACM 131950) is small (primitive condition) relative to that seen in *Odobenus*. Enlarged foramina are found in all other fossil odobenids. In *Dusignathus*, *Alachtherium*, *Valenictus*, and *Odobenus* the enlargement is associated with a shortened rostrum. The shortened rostrum of *Dusignathus* is convergent on the condition seen in the Odobenini. In *Imagotaria*, *Gomphotaria*, and *Aivukus*, however, no rostral shortening is associated with the large infraorbital foramen. The enlarged foramen in *Odobenus rosmarus* is correlated with increased innervation and blood flow to the muzzle with its mustache. The phocid *Erignathus* has a well-developed rostral mustache and a correspondingly large infraorbital foramen. Reversal to the primitive condition is hypothesized for *Pontolis*, with its elongated rostrum and relatively small infraorbital foramen.

9. *Palate.* 0 = flat, 1 = arched transversely, 2 = arched longitudinally and transversely. The primitive condition of a relatively flat palate is invariant in the outgroup taxa and also occurs in *Neotherium*. The palate of *Imagotaria* is transversely but not longitudinally arched (derived condition 1). The Odobenini have highly vaulted/arched palates (derived condition 2). This vaulting occurs in both the transverse and longitudinal planes, with the degree of vaulting greatest between the anterior incisors and the end of the postcanine tooth row. The vaulted palate is associated with strong oral suction, the mode of feeding of the living walrus (Fay 1982). The suction-feeding otariid *Otaria byronia* also has a vaulted/arched palate but the greatest degree of its arching is more posteriorly positioned, between the last postcanine tooth and the internal narial opening, suggesting that the tusked odobenines and *Otaria* independently acquired functionally similar but nonhomologous arched palates. The distribution of this character suggests that a transversely arched palate evolved early in odobenid history and that the vaulted palate of the Odobenini is a synapomorphy of this group of specialized walruses.

10. *Palate.* 0 = short, 1 = long, with long maxilla and short palatine, 2 = long, with long maxilla and long palatine. The primitive condition of a relatively short palate (Figs. 4A, B) occurs in outgroup taxa and in *Neotherium*, *Imagotaria*, *Gomphotaria*, and *Aivukus*. The derived condition of an elongated palate evolved independently in two groups of pinnipeds. In the Odobenini (Figs. 4E–G) only the maxilla is elongated and the rostrum is telescoped against and beneath the braincase (derived condition 1). In *Otaria* the palate is formed from both elongated palatines and maxillae and is not telescoped beneath the braincase (derived condition 2).

The length of the palate is evaluated by determining the position of the anterior border of the internal narial opening relative to the position of the postglenoid fossa. The narial border of elongated palates reaches the level of the postglenoid fossa. Elongation of the palate is correlated with an increased efficiency of oral suction (Fay 1982).

11. *Palatine.* 0 = abutting alisphenoid, 1 = underlying alisphenoid. In pinnipeds, the palatine bone generally forms a squamous suture with the pterygoid bone (which it overlies) and a plane suture with the alisphenoid (primitive condition). This condition (Fig. 5A) occurs in all outgroup taxa and most odobenids (e.g., *Neotherium*, *Imagotaria*, *Pontolis*). The derived condition occurs in the tusked odobenines, whose palatine and pterygoid share a plane suture and palatine and alisphenoid share a squamous suture. In this configuration (Fig. 5B) the alisphenoid almost entirely overlies the palatine, with the result that the pterygoid lies entirely posterior to the palatine (externally). The condition in *Aivukus* is unknown, but other aspects of the skull (e.g., short palate) suggest that it had the primitive condition.

12. *Hamular process of pterygoid.* 0 = narrow, 1 = broad. Most pinnipeds have a hamular process that is transversely compressed, anteroposteriorly elongated, and hooked posteroventrally (primitive condition). In contrast, the enlarged hamular process of the Odobenini is transversely broadened, dorsoventrally compressed, and flared and hooked posterolaterally. A special condition occurs in *Otaria*, in which the hamular process is transversely compressed and projects ventrally. The condition in *Aivukus* is unknown, but other aspects of its skull (e.g., short palate) suggest that it had the primitive condition. Character state 1 represents a synapomorphy of the Odobenini.

13. *Pterygoid strut.* 0 = narrow, 1 = broad, 2 = absent. The pterygoid strut (Barnes 1990), defined as the horizontally positioned expanse of palatine, alisphenoid, and pterygoid lateral to the internal narial opening and hamular process, is the site of origin for the internal pterygoid muscle. The primitive condition as seen in *Enaliarctos*, *Pteronarctos*, and *Neotherium* is a distinct but narrow pterygoid strut. Two derived conditions can be recognized. A broad pterygoid strut with a large ventral exposure of the alisphenoid and pterygoid occurs in *Imagotaria* (Fig. 4B) and *Pontolis* (USNM 314300, Fig. 4C) (derived condition 1). The pterygoid strut is absent in the Odobenini (Figs. 4E–G) (derived condition 2). In the latter group, the palatine underlies the alisphenoid (character 11) and the muscle attachment is confined to the orbital wall. Loss of the pterygoid strut is also seen in phocids and the otariid *Otaria*. In the latter case, the alisphenoid lies posterior to the palatine and the hamular process forms a vertical surface continuous with the orbital wall. In both cases the palate is extended posteriorly, an apparent adaptation for strong oral suction.

14. *Basioccipital.* 0 = narrow and parallel-sided, 1 = broad and pentagonal. The primitive condition occurs in the outgroup taxa as well as in *Neotherium* (LACM 131950). A basioccipital that is relatively short, broad, and pentagonal represents the derived condition and occurs in many odobenids, e.g., *Imagotaria* (USNM 335594), *Pontolis* (USNM 3792), *Valenictus* (SDSNH 38227), and *Odobenus*. Expressing the width of the basioccipital as a percentage of its length provides a means for evaluating this character. In *Odobenus* the width of the basioccipital is about 125% of its length, in *Pontolis* 100%, in *Neotherium* about 80%, and in *Enaliarctos mealsi* about 83%. The derived condition is defined as a ratio greater than 90%.

15. *Mastoid process.* 0 = small, 1 = large. The mastoid process is primitively small in the outgroup taxa and in *Neotherium*, *Imagotaria*, *Gomphotaria*, and *Aivukus*. The derived condition of a greatly enlarged mastoid process constructed internally of cancel-

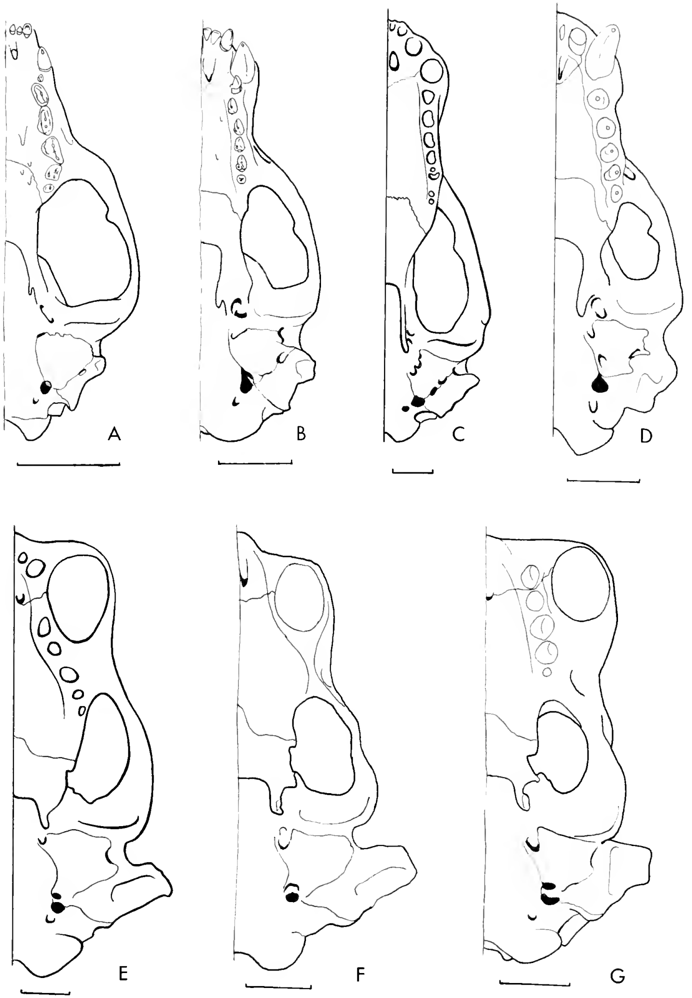

Figure 4. Ventral aspect of skulls of selected fossil and living pinnipeds. A, *Enaliarctos mealsi* (Jewett Sand, early Miocene, after Tedford 1976); B, *Imagotaria downsi* (Santa Margarita Formation, late middle Miocene, after Repenning and Tedford 1977); C, *Pontolis magnus* (Empire Formation, late late Miocene); D, *Aivukus cedrosensis* (Almejas Formation, late late Miocene, after Repenning and Tedford 1977); E, *Alachtherium cretsii* (Scaldisian sands, early Pliocene, after Hasse 1910); F, *Valenictus chulavistensis* (San Diego Formation, late Pliocene); G, *Odobenus rosmarus* (Recent). Scale bar, 5 cm.

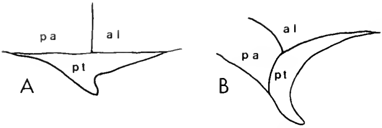

Figure 5. Pterygoid/alisphenoid suture patterns in odobenids. A, taxa outside the Odobenini; B, Odobenini. Skeletal elements: al, alisphenoid; pt, pterygoid; pa, palatine. Not to scale.

lous bone occurs in the tusked odobenines *Odobenus*, *Valenictus*, and *Alachtherium*. In *Pontolis* (USNM 314300) the mastoid process is enlarged also but does not descend to the same level as that of the Odobenini and presumably enlarged independently.

Enlargement of the mastoid process is related to an increase in mass of the neck musculature of *Odobenus* and other tusked odobenines.

16. *Widest part of skull*. 0 = zygomatic arch, 1 = mastoid processes. In *Enaliarctos*, *Pinnarctidion*, *Desmatophoca*, and early odobenids (e.g., *Neotherium* and *Imagotaria*) the skull is widest at the level of the zygomatic arch (primitive condition). In the Odobenini the mastoid region is the widest part of the skull (Figs. 4E–G). This synapomorphy is probably correlated with enlargement of the mastoid process and shortening of the skull. As mentioned, *Pontolis* has an enlarged mastoid, but its skull is not shortened and consequently the widest part of the cranium is at the zygomatic arch.

17. *Paramastoid process*. 0 = small, knoblike, 1 = elongated, posteriorly directed, 2 = flattened. The paramastoid process of *Enaliarctos*, *Pteronarctos*, otariids, and phocids as well as *Neotherium* and *Imagotaria* is primitively small and knoblike (Berta 1991). In *Pinnarctidion*, *Desmatophoca*, and *Allodesmus* (see Barnes 1987: fig. 9), the process is elongated and posteriorly directed (derived condition 1). In the dusignathine and odobenine walruses the process is flattened and platelike (derived condition 2).

18. *Lambdoidal crest*. 0 = crestlike, 1 = flattened. The lambdoidal crest (occipital crest of Repenning and Tedford 1977:52) in most pinnipeds is a sharp, narrow ridge following the parietal/occipital suture from the cranial vertex to the mastoid process. Primitively, this crest is narrow and overhangs the occipital shield as a posterodorsally directed projection (e.g., in outgroup taxa and *Neotherium* and *Pontolis*). In *Alachtherium* (see Erdbrink and van Bree 1990: pl. 1), *Pliopedia* (see Repenning and Tedford 1977:pl. 24, fig. 6), *Valenictus* (see Deméré 1994, this volume:figs. 1A, 2A,B), and *Odobenus* the vertex of the lambdoidal crest is marked by a large flattened crescentic traction surface presumably for insertion of the splenius musculature (an important neck extensor). In their reconstruction of the cranium of *Aivukus*, Repenning and Tedford (1977: fig.1) included an incipient flattened traction surface on the cranial vertex. However, this region is not well preserved on the holotype cranium, and its presence in *Aivukus* cannot be accurately determined. Other aspects of the skull (e.g., relatively small mastoid process) suggest that *Aivukus* had the primitive condition.

19. *Sagittal crest*. 0 = small, 1 = absent, 2 = large. Outgroup taxa as well as most early odobenids (e.g., *Neotherium* and *Imagotaria*) have a distinct but low sagittal crest (primitive condition). Two derived character states are recognized. In the Odobenini the sagittal crest is completely lost (derived condition 1). In the dusignathines *Pontolis* (USNM 395567) and *Gomphotaria*, the sagittal crest is greatly enlarged (derived condition 2). The small sagittal crest on the holotype of *Dusignathus seftoni* (SDSNH 38342) may be related to the specimen's not being mature, and it is possible that adult males had the enlarged crests seen in *Pontolis* and *Gomphotaria*. Repenning and Tedford (1977) reported that *Aivukus* lacks a sagittal crest. However, the holotype cranium is damaged in this area and thus cannot be accurately evaluated. The unreduced temporal fossa (character 22) of *Aivukus*, suggesting well-developed temporalis musculature, indicates that this taxon may have possessed a sagittal crest. The sagittal crest is variable in several species of extant pinnipeds (King 1983), in most cases because of sexual dimorphism, males typically having stronger crests than females (e.g., *Zalophus*). The crest in undescribed specimens of *Desmatophoca* varies between small and absent (A. Berta, pers. comm.).

20. *Zygomatic process of squamosal*. 0 = long/slender, 1 = short and robust, 2 = expanded. The zygomatic portion of the squamosal is primitively long and slender in outgroup taxa and *Neotherium*, *Imagotaria*, *Gomphotaria*, *Dusignathus*, and *Aivukus*. Two derived states are recognized. The Odobenini possess a shortened and robust process that has a plane suture with the jugal (derived state 1). *Desmatophoca*, *Allodesmus* (see Barnes 1972), and phocids (see King 1983) have an expanded process with a mortised jugal/squamosal suture (derived state 2).

21. *Postorbital process of jugal*. 0 = small, 1 = dorsoventrally expanded. The postorbital process of the jugal is relatively small in the outgroup taxa and *Neotherium* (primitive condition). The dorsoventrally expanded and robust process of *Aivukus*, *Valenictus*, and *Odobenus* is a synapomorphy of the Odobeninae. Although the zygomatic arch is not preserved in *Alachtherium* the shortening of its temporal fossa suggests that this taxon also had the derived postorbital process.

22. *Temporal fossa*. 0 = elongate, 1 = shortened. The primitive condition of a relatively long temporal fossa occurs in the outgroup taxa and many early odobenids. The Odobenini possess the derived condition of an anteroposteriorly shortened temporal fossa. Reduction in the size of the temporal fossa probably correlates with telescoping of the cranium and a decrease in the strength of the temporalis muscle. Functionally, this change is associated with emphasis in the Odobenini on suction feeding rather than biting.

23. *Optic foramen and orbitosphenoid*. 0 = platelike, 1 = funnel-shaped. In *Enaliarctos* (Mitchell and Tedford 1973) and *Pteronarctos* (Barnes 1990) the optic foramen is situated anteriorly in the orbitosphenoid, which continues as a plate well anterior to the foramen. The primitive condition is also seen in *Pinnarctidion*, *Neotherium* (LACM 131950), and *Imagotaria* (USNM 335594), as well as in otariids. In the Odobenini, the optic foramen is funnel-shaped and lies almost directly above the orbital fissure. In addition, the orbitosphenoid is not produced as a plate anterior to the foramen. The condition in *Aivukus* is unknown, but other aspects of the skull (e.g., lack of cranial telescoping) suggest that it had the primitive condition.

24. *Orbital vacuity*. 0 = absent, 1 = present/anteriorly positioned, 2 = present/posteriorly positioned. The orbital wall of the outgroup taxa, as well as of *Neotherium*, *Imagotaria*, and *Aivukus* is a continuous, unbroken surface (primitive condition). Extant pinnipeds (i.e., otariids, phocids, and *Odobenus*), however, as well as some fossil taxa (e.g., *Gomphotaria*, *Dusignathus*, and *Valenictus*) possess unossified areas or vacuities in the orbital wall. The occurrence of vacuities is considered derived (Wyss 1987), and two states are recognized. In otariids, phocids, and dusignathine walruses the vacuities are anteriorly placed, with the maxilla forming the anterior border of the vacuity (derived state 1). In contrast, the orbital vacuity in *Odobenus* and *Valenictus* is posteriorly placed relative to derived state 1 and is bordered anteriorly by a thin plate of the palatine (derived state 2). *Valenictus* possesses the same condition seen in *Odobenus*. The nature of the anterior border of the orbital vacuity in *Alachtherium* is unknown, but is most likely condition 2.

The distribution of character state 1 suggests that anteriorly placed vacuities evolved independently in phocids, otariids, and dusignathines.

Dentition

25. *Upper incisors.* 0 = I^{1-3}, 1 = I^{2-3} only, 2 = I^3 only, 3 = incisors lost. Outgroup taxa, as well as early odobenids (e.g., *Neotherium*), have the primitive condition of three upper incisors per side (Figs. 4A–C). Three derived character states are identified. Reduction to two upper incisors (i.e., loss of I^1) occurs in *Dusignathus*, *Aivukus*, and *Alachtherium* (derived condition 1). *Imagotaria* displays a polymorphism with three incisors (Fig. 4B) in the holotype (SBNHM 342) and a referred female (USNM 23858; Repenning and Tedford 1977) but only two incisors (I^1 lost) in a juvenile male (Repenning and Tedford 1977:pl. 8, fig. 1) and an undescribed cranium from the Empire Formation (USNM 335599).

Reduction to only one incisor ($I^{1, 2}$ lost) in *Gomphotaria* and adult *Odobenus* represents a second derived state (Fig. 4G). A polymorphism also crops up in *Odobenus*, in which I^2 is sometimes present (Fay 1982). Loss of all incisors in *Valenictus* (Fig. 4F) is an autapomorphy of this taxon (derived condition 3).

The distribution of this character indicates independent loss of I^1 in "monachine" seals and later-diverging odobenids (e.g., *Imagotaria* + dusignathines + odobenines) and independent loss of I^2 in *Odobenus* and *Gomphotaria*. The condition in *Pontolis* is viewed as a reversal. In the Odobenini loss of incisors is correlated with an emphasis on suction feeding.

26. *Position of I^c.* 0 = anterior to C^1, 1 = medial to C^1 (anterior to incisive foramen), 2 = medial to C^1 (lateral to incisive foramen), 3 = I^c absent. In the outgroup taxa and early odobenids (e.g., *Neotherium* and *Imagotaria*) the upper incisors, especially $I^{1, 2}$, are positioned at the anterior border of the premaxilla (Figs. 4A, B) anterior to the canine (primitive condition). In *Dusignathus* (SDSNH 38342) and *Alachtherium* (GMAU K-8052) the incisors are medial to the anterior half of the canine (Fig. 4E) but anterior to the incisive foramen (derived condition 1). In adult *Odobenus*, $I^{1, 2}$ are typically lost and I^3 is more posteriorly located on the medial side of the enlarged canine (Fig. 4G), lateral to the incisive foramen (derived condition 2). Loss of all upper incisors (Fig. 4F) is an autapomorphy of *Valenictus*.

The distribution of these character states suggests that derived condition 1 evolved independently in *Dusignathus* and the Odobenini.

27. *Globular dentine in C^1.* 0 = absent, 1 = present. Ray (1960) described the unique structure of the ever-growing tusks of *Odobenus* (*O. rosmarus* and *O. huxleyi*), noting the central column of globular dentine surrounded first by a thick ring of orthodentine and then by a thin outer layer of cementum. Enamel is lacking in adult *Odobenus* tusks (Fay 1982). This unique dental structure is also seen in *Valenictus* (see Deméré 1994, this volume) and is inferred for *Alachtherium* on the basis of isolated tusks from the Antwerp Pliocene and for *Prorosmarus* on the basis of isolated tusks from the Yorktown Formation (C. E. Ray, pers. comm.). Although *Gomphotaria* also has enlarged upper canines, computed tomography images reveal a thin outer layer of cementum overlying a thick core of orthodentine, with no evidence of a central globular dentine column. Barnes and Raschke (1991) also noted patches of enamel on the tusks of *Gomphotaria*. The canines of *Aivukus* lack globular dentine (Repenning and Tedford 1977). Possession of a central column of globular dentine is a synapomorphy of the Odobenini.

28. *Size of C_1 relative to C^1.* 0 = nearly equal (100–80%), 1 = reduced (75–45%), 2 = very reduced (40–20%), 3 = C_1 absent. The anteroposterior diameter of the lower canines can be expressed as a percentage of the anteroposterior diameter of the upper canines. In *Enaliarctos emlongi* this measure is 104%, in *Imagotaria downsi* 84–86%, in *Dusignathus santacruzensis* 85%, in *Gomphotaria pugnax* 86%, in *Pontolis magnus* 89%, in *Aivukus cedrosensis* 65%, and in *Odobenus rosmarus* 29–31%. Nearly equal (100–80%) upper and lower canines represent the primitive condition. Two derived states may be recognized. Lower canines reduced to between 75% and 45% of the upper canines (e.g., *Aivukus*) represent derived condition 1; further reduction (40–20%) (e.g., *Odobenus*) represents derived condition 2. Although no associated upper and lower dentitions are known for *Alachtherium*, it is clear that the lower canines of the holotype dentary of *A. cretsii* are considerably smaller than the greatly enlarged upper canines inferred from empty alveoli in the known crania. The same is almost certainly true for *Prorosmarus*, in which the lower canine is small and the lateral concavity of the dentary (in occlusal aspect) suggests enlarged upper canines. Character state 1 is an odobenine synapomorphy; character state 2 is a synapomorphy of the Odobenini. Loss of C_1 is an autapomorphy of *Valenictus*.

29. *Upper canine.* 0 = procumbent, 1 = steeply inclined. In the outgroup taxa and *Neotherium*, *Imagotaria*, *Gomphotaria*, *Alachtherium*, and *Valenictus* the upper canine is strongly to moderately procumbent (primitive condition). In *Odobenus* and *Dusignathus seftoni* (see Deméré 1994, this volume) the canines are more vertically oriented (derived condition). This derived state evidently evolved independently in the two taxa. Such convergence between *Dusignathus seftoni* and *Odobenus rosmarus* is also seen in characters 34, 39, and 42.

30. *C^1 and C_1 enlarged as tusks.* 0 = no, 1 = yes. In the outgroup taxa and *Neotherium* and *Imagotaria* the upper and lower canines are not enlarged relative to the adjacent postcanine teeth (primitive condition). Enlargement of both upper and lower canines is a synapomorphy of the dusignathines. As mentioned (character 27), the upper canines of these taxa are constructed differently from those of the tusked odobenines. Although *Dusignathus santacruzensis* has relatively elongated upper and lower canines of equal size (Repenning and Tedford 1977), they are not enlarged as tusks. In *D. seftoni*, however, upper and lower tusks are developed. Evaluation of this character is based on the size difference between the diameters of the canines and those of adjacent postcanine alveoli.

31. *Lower canine.* 0 = caniniform, 1 = premolariform, 2 = absent. Outgroup taxa and *Neotherium*, *Imagotaria*, and *Dusignathus* primitively possess caniniform lower canines. Premolarization, in *Odobenus*, *Alachtherium*, and *Prorosmarus* (see Berry and Gregory 1906), involves loss of the enamel crown and carina, transverse expansion of the root, and shortening and simplification of the crown. Because the condition in *Aivukus* is currently unknown, premolarization of the canine may represent a synapomorphy of the Odobeninae or more exclusively of the Odobenini. Loss of the lower canines is an autapomorphy of *Valenictus*.

32. *Position of Pc^1.* 0 = posterior to C^1, 1 = medial to C^1, 2 = absent. Primitively, the position of the first upper postcanine tooth (Pc^1) in carnivorans is posterior to the upper canine (Figs. 4A–C). In *Alachtherium* (GMAU K-8052 and the Hasse 1910 specimen) and *Odobenus*, Pc^1 has moved to a position medial to the canine (Figs. 4E, G). The distribution of this character suggests that condition 1 is a Odobenini synapomorphy, with the loss of all lower postcanine teeth being an autapomorphy of *Valenictus* (Fig. 4F).

33. *Upper postcanine teeth.* 0 = six, 1 = five, 2 = three or four, 3 = zero. Outgroup taxa and *Neotherium*, *Pontolis*, and *Dusignathus* have the primitive pinniped dental formula of six postcanine teeth (Barnes 1989; Berta 1991). Reduction to five teeth (i.e., loss of M^2) as in *Aivukus* (derived condition 1), to three or four teeth as in *Alachtherium* and *Odobenus* (derived condition 2), or zero as in *Valenictus* (condition 3) represents three derived states. Although the type of *Gomphotaria pugnax* has only five postcanine teeth, a

referred rostrum (JMTC 907-170) has alveoli for six teeth, suggesting that the condition in this species is variable.

34. *P^1–M^1, postcanine tooth row.* 0 = laterally concave, 1 = straight, 2 = laterally convex, 3 = postcanine teeth absent. In the outgroup taxa, the upper postcanine tooth row forms a sigmoidal curve with the P^1–M^1 portion laterally concave in occlusal view (Barnes 1989). In *Neotherium*, *Imagotaria* (Fig. 4B), *Aivukus*, *Gomphotaria*, and *Pontolis* (Fig. 4C, D) the tooth row is nearly straight. The tooth row is also variably straight in phocids and otariids. In *Alachtherium* (Fig. 4E), *Odobenus* (Fig. 4G), and *Dusignathus* (see Deméré 1994, this volume) the tooth row is laterally convex. Loss of all postcanine teeth is an autapomorphy of *Valenictus*.

This distribution suggests that a straight tooth row evolved several times, once in the common ancestor of *Neotherium* and all other odobenids, and again in certain otariids. A convex tooth row evolved twice, once in the Odobenini and once in *Dusignathus*. This convergence towards a laterally convex tooth row is probably a function of the rostral shortening seen in both *Dusignathus* and the tusked odobenines.

35. *P^3 and P^4, crowns.* 0 = three cusps, 1 = two cusps, paracone emphasized, 2 = one cusp only, 3 = simple peglike crown, 4 = teeth absent, 5 = complex labial cusps. The crowns of P^3 and P^4 of *Enaliarctos mealsi*, *E. emlongi*, and *E. barnesi* are characterized by a well-developed paracone, a distinct metacone, and a strong protocone shelf that is anteromedially placed (Barnes 1989; Berta 1991). In *Pinnarctidion* (USNM 314325), P^4 has a well-developed paracone, a strong metacone, and a well-developed posteromedial protocone shelf (A. Berta, pers. comm.). In *Desmatophoca*, P^4 has a well-developed central cusp (= paracone), a small posterolateral cuspule (metacone?), and a narrow cingulum rimmed by tiny lingual cuspules. In *Neotherium*, P^3 has a well-developed paracone, a distinct but reduced metacone, and a posteromedial shelf with a well-developed lingual cuspule (L. G. Barnes, pers. comm.). In *Imagotaria downsi* the crowns of P^3 and P^4 possess a strong anterolateral cusp (= paracone) but a very weakly developed posterolateral cuspule (metacone?). The strong protocone shelf is posteromedially placed and has a well-developed lingual cuspule (Repenning and Tedford 1977). In a referred rostrum of *Gomphotaria pugnax* (JMTC 907-170), the crown of P^4 has a single lateral cusp (= paracone) with a distinct lingual cingulum expanded slightly at its posteromedial corner. The posterior premolars in *Dusignathus santacruzensis* are unknown. The simple single-cusped conical crown of P^2 in the type, however, suggests that the condition of the crown of P^4 was like that described for *Gomphotaria*. In the Odobeninae, P^3 and P^4 have simple peglike crowns (Repenning and Tedford 1977; Fay 1982; Erdbrink and van Bree 1990), an odobenine synapomorphy. Loss of all postcanine teeth is an autapomorphy of *Valenictus*. The condition in *Pontolis* is unknown.

36. *P^4, protocone shelf.* 0 = strong and anteromedially placed, 1 = strong and posteromedially placed with small cuspules, 2 = reduced or absent, 3 = P^4 absent. *Enaliarctos* has a functional carnassial (Berta 1991) with a strong protocone shelf that is anteromedially placed. *Pinnarctidion* and *Neotherium* have a P^4 with a posteromedially placed protocone shelf. This modification is associated with loss of the embrasure pit between P^4 and M^1 and is correlated with reduction in occlusal shear (i.e., P^4 is no longer a functional carnassial). In *Neotherium*, the protocone shelf bears two small cuspules. In *Imagotaria downsi* the protocone shelf is reduced (relative to *Neotherium*) and is variable in the number and size of cuspules. In other odobenids the shelf is greatly reduced or absent. Loss of P^4 is an autapomorphy of *Valenictus*.

The distribution of this character suggests that a reduced protocone shelf evolved at least twice, once in the common ancestor of the dusignathines and odobenines and once in the desmatophocids.

37. *P^4, number of roots.* 0 = three; 1 = two; 2 = one bilobed root; 3 = one root, 4 = P^4 absent. As noted by Barnes (1989) and Berta (1991), the P^4 of *Enaliarctos* and *Pinnarctidion* has three separate roots, one above each of the principal cusps. Three derived character states are recognized. Derived state 1 is characterized by a reduction in the number of roots to two as in *Pteronarctos* (Barnes 1990), *Desmatophoca* (A. Berta, pers. comm.), and *Neotherium* (L. G. Barnes, pers. comm.), with the single anterior root well separated from the posterior bilobed root and formed from coalesced metacone and protocone roots. Derived state 2 is represented by a further reduction to only a single vestigially bilobed root through fusion of the anterior root to the posterior root as seen in *Imagotaria*, *Pontolis* (USNM 314300), *Dusignathus* (SDSNH 38342), and *Gomphotaria*. In the latter two taxa the roots are relatively swollen and have a diameter greater than the tooth crowns'. Derived state 3 consists of reduction to a single nearly circular root and is an odobenine synapomorphy. This reduction in number of postcanine tooth roots is correlated with development of homodonty (Barnes 1989). Loss of all postcanine teeth is an autapomorphy of *Valenictus*.

The distribution of this character indicates that reduction to two roots evolved independently in the outgroup taxa *Pteronarctos* and *Desmatophoca* and in the odobenids. Similar trends towards root reduction and homodonty evolved independently in otariids (Repenning and Tedford 1977; Berta and Deméré 1986; Barnes 1989).

38. *Postcanine tooth enamel.* 0 = well-developed enamel layer; 1 = thin and/or patchy enamel layer; 2 = cementum only (no enamel on adult teeth), 3 = postcanine teeth lost. Well-developed enamel is primitive for carnivorans. Two derived characters are recognized. The thin enamel crowns of *Dusignathus* (see Repenning and Tedford 1977) and the patchy remnants of enamel on adult teeth of *Gomphotaria* (see Barnes and Raschke 1990) and *Aivukus* (see Repenning and Tedford 1977) represent derived state 1. Loss of an enamel layer is seen in adult Odobenini and represents derived state 2. Loss of all postcanine teeth is an autapomorphy of *Valenictus*.

Mandible

39. *Mandibular symphysis.* 0 = unfused, 1 = fused. Pinnipeds primitively have an unfused mandibular symphysis. The derived condition of a fused symphysis occurs in *Valenictus* and *Odobenus*. There is some sexual dimorphism in *Odobenus rosmarus*, whose adult females may have unfused symphyses (C. E. Ray, pers. comm.). The mandibular symphysis is also fused in *Dusignathus seftoni*.

The distribution of this character suggests that a fused symphysis evolved twice, once in the common ancestor of *Valenictus* and *Odobenus* and again in *Dusignathus*. A less parsimonious hypothesis is that fusion evolved several times within the Odobenini.

40. *Mandibular symphysis with extra bone.* 0 = no, 1 = yes. *Odobenus rosmarus* is characterized by a very heavy and swollen mandibular symphysis that is widest ventrally. *Odobenus mandanoensis* also has a very heavy symphyseal region, but in it the widest part is dorsally placed (Tomida 1989: figs. 4A–C). In other odobenine walruses, as well as pinnipeds in general, there is no increase in the mass of the symphysis (primitive condition). The derived condition is a synapomorphy uniting the species of *Odobenus*. Increased mass of the symphysis reduces kinesis between the left and right dentaries and may be an adaptation to strong oral suction.

41. *Mandibular terminus.* 0 = smooth, compact, 1 = vascular. The distal terminus of the lower jaw in tusked odobenines is roughened and pitted, in contrast with the smooth surfaces seen in other pinnipeds (primitive condition). Fay (1982) discussed the oral opening in *Odobenus*, noting that the terminus of the lower jaw is covered by a tough, cornified surface that he suspected functioned

to hold prey securely. The roughened surface of the odobenine mandibles may be related to increased vascularization for this cornified lower lip. Although the condition in *Aivukus* is unknown, that taxon's lack of a laterally convex tooth row (character 34) suggests that *Aivukus* retained the primitive condition.

42. *Mandibular arch.* 0 = nearly parallel, 1 = sharply divergent. The mandible of *Enaliarctos emlongi* (Berta 1991) forms an elongated arch in occlusal aspect, with the right and left rami meeting at a sharply acute angle of about 33° (primitive condition). As deduced from the structure of the upper jaw, other species of *Enaliarctos*, *Pteronarctos*, and *Pinnarctidion* had a similar mandibular architecture. In *Neotherium* this angle is about 20°, in *Imagotaria* about 36°, and in *Gomphotaria* about 42°. The derived condition of a sharply divergent mandibular arch occurs in *Dusignathus* (angle of 58°–60°), and the Odobenini (angle of 58°-60°). A sharply divergent mandibular arch is correlated with rostral shortening.

The distribution of the derived condition in these taxa suggests convergent evolution of a shortened rostrum in *Dusignathus* and the Odobenini.

43. *Dentary, ventral border.* 0 = straight, 1 = sinuous. In lateral view, the ventral border of the horizontal ramus (between the symphysis and pterygoid process) is nearly straight in the outgroup taxa, *Neotherium* (Fig. 6A), and *Imagotaria* (Fig. 6B) (primitive condition). The condition in the Odobenini is complicated by the upturning of the symphysis, but in general the ventral margin preserves the primitive condition (Figs. 6D–F). As noted by Repenning and Tedford (1977), the type dentary of *Dusignathus santacruzensis* has a markedly sinuous ventral margin (Fig. 6C). This condition also occurs in *Dusignathus seftoni* (SDSNH 20801) and *Pontolis* (USNM 335563).

The distribution of this character suggests that a sinuous ventral border may have evolved only once in the common ancestor of *Pontolis* and *Dusignathus*. The condition in *Gomphotaria* would thus represent a reversal. An alternate hypothesis is parallel evolution of a sinuous ventral border in *Dusignathus* and *Pontolis*.

44. *Dentary, marginal process.* 0 = weakly developed, 1 = strongly developed. The marginal process (Davis 1964:61) is variably developed in pinnipeds. This process is the main area for

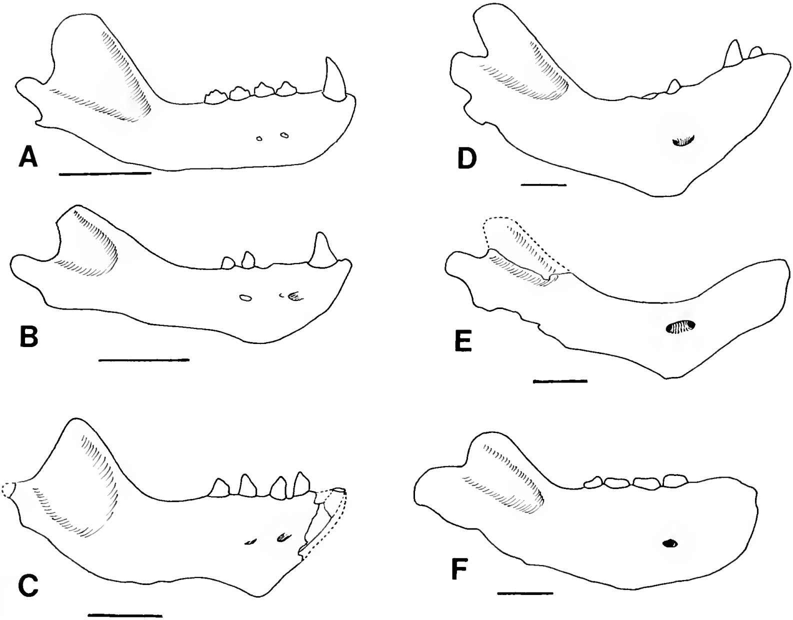

Figure 6. Lateral aspect of right dentaries of selected fossil and living odobenids. A, *Neotherium mirum* (Round Mountain Silt, middle Miocene); B, *Imagotaria downsi* (Santa Margarita Formation, late middle Miocene, after Repenning and Tedford 1977); C, *Dusignathus santacruzensis* (Purisima Formation, late late Miocene); D, *Alachtherium cretsii* (Saldisian sands, early Pliocene); E, *Valenictus chulavistensis* (San Diego Formation, late Pliocene); F, *Odobenus rosmarus* (Recent). Scale bar, 5 cm.

insertion of the digastric muscle, the principal jaw depressor. The primitive condition of a weakly developed process (or no process at all) occurs in *Neotherium* and *Imagotaria*. The derived condition of an enlarged marginal process occurs in *Pontolis*, *Dusignathus*, *Valenictus*, *Alachtherium*, and *Prorosmarus*. In *Odobenus rosmarus* the marginal process is secondarily reduced, possibly in relation to the increased mass of the horizontal ramus. The reduced marginal process of *Gomphotaria* is also viewed as a reversal.

Postcrania

45. *Humerus, deltoid tubercle.* 0 = on pectoral crest, 1 = on lateral edge of crest, 2 = off crest. The scar for insertion of the deltoideus muscle is primitively located on the pectoral crest (Fig. 7B) of the humerus (Repenning and Tedford 1977). This condition is seen in the outgroup taxa and in many odobenids (*Neotherium*, *Imagotaria*, *Pontolis*, and *Aivukus*). In *Odobenus*, *Valenictus* (see Deméré 1994: fig. 6, this volume), and *Pliopedia* (see Repenning and Tedford 1977:pl. 17, fig. 3) the scar is separate from and posterior to the crest (Fig. 7A). In *Alachtherium* (IRSNB M.170) the tuberosity occupies an intermediate position (i.e., posterior to the crest but still joined to it). A left humerus (MCZ 7713) referred to *Prorosmarus alleni* by Repenning and Tedford (1977; citing C. E. Ray) also preserves the intermediate condition.

The distribution of the derived character states suggests a transformation series from a laterally placed deltoid insertion to eventual separation of the insertion from the crest. Character state 1 appears to represent a synapomorphy of the Odobenini, while state 2 represents a synapomorphy uniting *Pliopedia*, *Valenictus*, and *Odobenus*.

46. *Humerus, medial entepicondyle.* 0 = small, 1 = enlarged. Primitively, the entepicondyle of the pinniped humerus is small (Fig. 7) relative to the greatly enlarged entepicondyle observed in *Valenictus* (see Repenning and Tedford 1977; Deméré 1994, this volume). Enlargement of the entepicondyle is probably related to an increased mass of the intrinsic flexor musculature of the forelimb (Howell 1929) and is an autapomorphy of *Valenictus*.

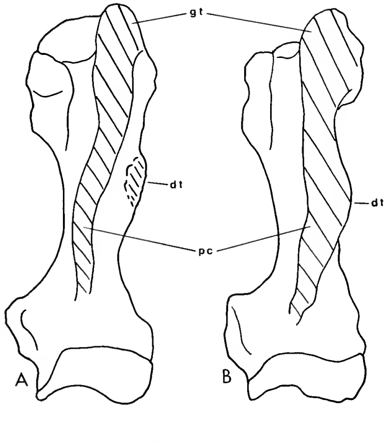

Figure 7. Anterior aspect of left odobenid humeri. A, *Odobenus rosmarus*; B, *Aivukus cedrosensis* (after Repenning and Tedford 1977). Skeletal elements: dt, deltoid tubercle; gt, greater tuberosity; pc, pectoral crest.

47. *Humerus, diameter of distal trochlea.* 0 = medial lip same (or smaller) diameter as distal capitulum, 1 = medial lip diameter greater than distal capitulum. Among pinnipeds, the anteroposterior diameter of the medial lip of the distal humeral trochlea is smaller than or equal to the diameter of the distal capitulum (primitive condition). The derived condition of a distinctly larger medial lip is a synapomorphy for odobenids (Repenning and Tedford 1977:8).

48. *Radius, distal end.* 0 = unexpanded, 1 = expanded, with small radial process, 2 = expanded, with large radial process. As noted by Berta and Ray (1990), the distal end of the radius of *Enaliarctos mealsi* is unexpanded (primitive condition). Two derived conditions are recognized, with only one applying to the ingroup. An expanded distal end with a relatively small radial process (Repenning and Tedford 1977:pl. 2) occurs in otariids and *Allodesmus* (derived condition 1). An expanded distal end with a relatively large and distally projecting radial process is found in odobenids and represents a synapomorphy for the entire group.

49. *Metacarpal I, insertion of pollicle extensor.* 0 = smooth, 1 = pit, 2 = rugosity. The insertion for the pollicle extensor muscle on the dorsoproximal surface of metacarpal I is variably expressed. Primitively, the dorsoproximal surface is smooth. In *Imagotaria*, *Pliopedia*, and *Gomphotaria* there is a conspicuous pit (Barnes 1989) (derived condition 1), while in *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus* a rugosity marks the insertion (Repenning and Tedford 1977:21) (derived condition 2). Presence of a pit or rugosity is an odobenid synapomorphy.

50. *Scapholunar.* 0 = no pit for magnum, 1 = well-formed pit. In odobenids, the magnum articulates with the scapholunar in a conspicuous and often deep pocket or pit (Repenning and Tedford 1977:36). Although the derived condition is invariant in the ingroup, it provides support for the monophyly of the group. The primitive condition is a flat articular surface for the magnum as preserved in *Allodesmus*, phocids, and otariids.

51. *Astragalus, calcaneal process.* 0 = absent, 1 = present, 2 = elongated. As discussed by Berta and Ray (1990:151), the astragalus of *Enaliarctos mealsi* lacks a posteromedial calcaneal process. This represents the primitive condition for pinnipeds. Two derived character states are recognized, with only one found in the ingroup. In *Allodesmus* (see Kellogg 1931: fig. 53) and odobenids the calcaneal process is distinct but variably developed (derived condition 1), either strong and posteroventrally directed as in *Imagotaria* (Repenning and Tedford 1977:pl. 14, figs. 25, 26) or more weakly developed as in the Odobenini. The second derived state occurs in the phocids, whose astragalus has a strong caudally directed calcaneal process that is nearly as long as the calcaneal tuber (King 1983; Berta and Ray 1990).

The distribution of character state 1 suggests that a distinct but unelongated process evolved in the common ancestor of odobenids and the Desmatophocidae.

52. *Calcaneum, calcaneal tuber.* 0 = straight, 1 = prominent medial tuberosity. The calcaneal tuber is primitively straight-sided in pinnipeds (Repenning and Tedford 1977; Berta and Wyss 1994, this volume). The derived condition of a prominent medial tuberosity on the proximal end of the calcaneal tuber occurs in *Allodesmus* and odobenids, especially *Imagotaria* (Repenning and Tedford 1977: pl.15, figs. 3–6). Although this character does not vary within the ingroup it does provide evidence for the sister-group relationship of odobenids and desmatophocids.

53. *Entocuneiform, mesocuneiform articulation.* 0 = abutting, 1 = overlapping. Primitively, the entocuneiform of pinnipeds articulates with the mesocuneiform along a straight butt joint. In addition, the distal articular facet for articulation with the first metatarsal is

short and quadrate. The primitive condition is preserved in extant otariids. The derived condition is an entocuneiform that strongly overlaps the mesocuneiform such that the concave articular facet for the mesocuneiform is positioned subparallel to the facet for the navicular articulation, not at right angles to it. In addition, the distal condyle of the entocuneiform is relatively elongated and rounded. This derived character complex occurs in all the studied odobenids in which the tarsals were preserved (*Pontolis*, *Gomphotaria*, *Valenictus*, and *Odobenus*). Kellogg (1925:107–108; fig. 14) briefly discussed this character complex in his description of a fossil odobenid ankle from the Towsley Formation (UCMP 24070-24082) that he tentatively referred to *Pontolis magnus*. Repenning and Tedford (1977:24) transferred this specimen to *Imagotaria downsi*. In a later report Kellogg (1931:292–294; figs. 60–63) described the entocuneiform of *Allodesmus*, noting similarities with the same bone in *Odobenus*. The condition in *Enaliarctos* is unknown.

The distribution of this character in the outgroup taxa supports two alternative hypotheses, that the derived state evolved independently in desmatophocids and odobenids or, more parsimoniously, that the derived state evolved only once in the common ancestor of these two taxa.

SYSTEMATICS

This review is not meant to serve as a formal and exhaustive systematic treatment but rather as a summary of recent literature and new specimens collected since the monograph of Repenning and Tedford (1977). For certain taxa, the discussions are more extensive than for others. This difference in treatment is due either to recovery of new and previously undescribed material referable to nominal taxa or to taxonomic and/or nomenclatural complexity that requires elaboration.

Because the primary emphasis of this report is to explore phylogenetic relationships within the Odobenidae, the taxon discussions focus on synapomorphies rather than on symplesiomorphies. Symplesiomorphies are important in characterizing taxa, but because they do not provide evidence of recent common ancestry they are not as useful for unraveling phylogeny.

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Infraorder Pinnipedia Illiger, 1811

Family Odobenidae Allen, 1880

Definition.—The monophyletic group containing the most recent common ancestor of *Neotherium* and *Odobenus* and all of its descendants.

Diagnosis.—Pinnipeds with antorbital process constructed from both frontal and maxilla, supraorbital process of frontal absent; diameter of medial lip of distal trochlea of humerus greater than diameter of capitulum, distal portion of radius with enlarged radial process, insertion for pollicle extensor muscle on first metacarpal developed as a pit or rugosity, and scapholunar with distinct pit for magnum (odobenid synapomorphies).

Neotherium Kellogg, 1931

Type species.—*Neotherium mirum* Kellogg, 1931.
Distribution.—Middle Miocene of the eastern North Pacific.
Included species.—Type species only.
Emended diagnosis.—A small odobenid with adventitious root on P^2 (possible autapomorphy, Barnes 1989:14), antorbital process bifurcated by maxilla/frontal suture, supraorbital process of the frontal lost, medial distal trochlea of humerus broader than radial capitulum (odobenid synapomorphies); embrasure pit on palate between P^4 and M^1 lost, medial tuberosity of calcaneum prominent, and calcaneal process of astragalus distinct (synapomorphies at level of desmatophocid and odobenid common ancestry).

Neotherium mirum Kellogg, 1931

Neotherium mirum Kellogg 1931; Mitchell and Tedford 1973; Mitchell 1961; Barnes 1988, 1989.

Lectotype.—USNM 11542, a right calcaneum (Mitchell and Tedford 1973:266).
Type locality.—Sharktooth Hill, Kern County, California.
Horizon and age.—Sharktooth Hill Bonebed, Round Mountain Silt, middle Miocene (Barstovian NALMA correlative, ca. 13–14 Ma).
Diagnosis.—As for the genus.
Referred material.—Kellogg (1931) included an astragalus (USNM 11543), cuboid (USNM 11552), and navicular (USNM 11548) in the original hypodigm and referred several additional postcranial elements to this taxon. Mitchell and Tedford (1973) referred additional material, including a humerus (LACM 4319), to it. Barnes (1988) referred a partial dentary (LACM 12300) to *N. mirum* and mentioned a large collection of topotypic material under study.
Discussion.—Repenning and Tedford (1977) recognized the odobenid affinities of the type material of *Neotherium mirum*, noting the prominent medial tuberosity of the calcaneum and the distinct calcaneal process of the astragalus. Humeri referred to this taxon preserve the distal articular synapomorphies of the Odobenidae. Barnes (1988:fig. 4) referred a partial left dentary to *N. mirum* and described the anterior lower dentition. P_2–M_1 are double-rooted and have transversely compressed crowns with a prominent central cusp flanked by reduced anterior and posterior cuspules. In most aspects, *Neotherium* is a generalized odobenid, possessing the basal synapomorphies of the family but lacking the derived features of later-diverging members.

Repenning and Tedford (1977) and Barnes (1988) noted a distinct bimodality in the size of skeletal elements and suggested that *N. mirum* was sexually dimorphic.

A large collection of topotypic cranial (including a complete skull), dental, and postcranial material is currently under study by L. G. Barnes, who generously allowed me to examine critical specimens. I discuss this material only in the context of the phylogenetic analysis (Table 2).

Imagotaria Mitchell, 1968

Type species.—*Imagotaria downsi* Mitchell, 1968.
Distribution.—Late middle to late late Miocene of the eastern North Pacific.
Included species.—*Imagotaria downsi* Mitchell, 1968 and *Imagotaria* sp. cf. *I. downsi*.
Emended diagnosis.—Medium-sized odobenids with strongly developed and posteroventrally directed calcaneal process of the astragalus (possible autapomorphy of *Imagotaria*), upper postcanine teeth with single, vestigially bilobed roots (also seen in certain dusignathines), palate transversely arched, frontal/maxilla suture straight and transverse, premaxilla with overlap of nasal short, antorbital process enlarged, infraorbital foramen large, pterygoid strut broad, and basioccipital broad and pentagonal (synapomorphies at level of dusignathine and odobenine common ancestry).

Imagotaria downsi Mitchell, 1968

Imagotaria downsi Mitchell, 1968; Repenning and Tedford 1977.
Imagotaria sp. Barnes 1971.

Holotype.—SBNHM 342, parts of the skull, partial right and left dentaries, isolated upper and lower postcanine teeth, partial hyoid, partial atlas, partial thoracic vertebra, glenoid regions of both scapulae, and partial right and left humeri.

Type locality.—Great Lakes Carbon Company quarry, Lompoc, Santa Barbara County, California.

Horizon and age.—Sisquoc Formation (diatomite); late middle to early late Miocene (Clarendonian NALMA correlative, ca. 9–12 Ma).

Diagnosis.—As for the genus.

Referred material.—Mitchell (1968:1865–1866) referred a horizontally split and crushed skull (USNM 13487) from the Sisquoc Formation to *I. downsi*. Repenning and Tedford (1977:22–24) referred cranial and postcranial material collected from the Santa Margarita Formation (early late Miocene, Clarendonian NALMA correlative) as exposed in Santa Cruz County, California, to *I. downsi*. Most of this referred material came from a single fossil accumulation, perhaps a rookery.

Discussion.—*Imagotaria downsi* exhibits several symplesiomorphies useful in distinguishing it from other members of the clade *Imagotaria* + Dusignathinae + Odobeninae, including low sagittal crest, inflated tympanic bulla, and $P^{3,4}$ with strong anterolateral cusp (= paracone), weakly developed posterolateral cuspule (metacone?), and strong posteromedially placed protocone shelf with well-developed lingual cuspule. Thus, *Imagotaria downsi* is more readily distinguished by characters that it lacks than by autapomorphies, i.e., it possesses the synapomorphies of the clade *Imagotaria* + Dusignathinae + Odobeninae but lacks the features derived in the odobenines and dusignathines). Its only probable autapomorphy is the strongly developed calcaneal process of the astragalus (Repenning and Tedford 1977:39–40). The humerus of *Imagotaria downsi* is generalized, with an elongated and keeled pectoral crest that descends with a marked flexion to the distal surface of the relatively slender shaft.

With the additional specimens referred to *Imagotaria downsi* by Repenning and Tedford (1977), this taxon is one of the most completely known fossil odobenids. The sample size is large enough to reveal both sexual dimorphism and polymorphism in certain dental features (e.g., either two or three upper incisors).

$$\text{Dentition: } \frac{3\text{I}, 1\text{C}, 4\text{P}, 2\text{M}}{2\text{I}, 1\text{C}, 4\text{P}, 1(2)\text{M}} \times 2 = 36(38)$$

Imagotaria sp. cf. *I. downsi*

Material.—In the Emlong Collection at the USNM (Ray 1976) are several complete skulls, including USNM 335599 and 335594, isolated jaws, and postcrania referable to *Imagotaria*. This material may represent more than one taxa and will be described in a subsequent report.

Locality.—Coos Bay, Coos County, Oregon.

Horizon and age.—Empire Formation; late late Miocene (Hemphillian NALMA correlative, ca. 5–8.5 Ma).

Discussion.—Referral of these fossils to *Imagotaria* is based on their possession of derived characters not seen in *Neotherium* but reported for *I. downsi* and on their lack of dusignathine and odobenine synapomorphies. The Oregon specimens differ from the type material in their mastoid–paramastoid crest being aligned subparallel to the sagittal plane (not divergent as in the holotype) and consistent loss of I^1. The palate is arched transversely and bordered by straight postcanine tooth rows possessing four premolars and two molars. I^1 is lost, and $I^{2,3}$ are positioned anterior to the unenlarged canine. The pterygoid strut is extremely broad. The sagittal crest is low and extends posteriorly to a sharply edged and overhanging lambdoidal crest. The frontal lacks a supraorbital process, but the antorbital process is large and split by the frontal/maxilla suture.

This material was included in this report because it allows determination of character states not preserved in the type and referred material of *I. downsi* (e.g., maxilla/frontal suture and antorbital processes).

Subfamily Dusignathinae (*sensu* Repenning and Tedford, 1977)

Definition.—The monophyletic group containing the most recent common ancestor of *Pontolis* and *Dusignathus* and all of its descendants.

Diagnosis.—Odobenids with upper and lower canines enlarged as tusks; nasal/frontal suture V-shaped and posteriorly directed (a more acute "V" occurs in desmatophocids and phocids); sagittal crest enlarged (reversed in *Dusignathus*; also seen in certain otariids); and orbital vacuity anteriorly placed (also occurs in otariids).

Dusignathus Kellogg, 1927

Type species.—*Dusignathus santacruzensis* Kellogg, 1927

Distribution.—Late late Miocene to late Pliocene of the eastern North Pacific.

Included species.—*Dusignathus santacruzensis* Kellogg, 1927, and *Dusignathus seftoni* Deméré, 1994 (this volume).

Definition.—The monophyletic group containing the most resent common ancestor of *D. santacruzensis* and *D. seftoni* and all of its descendants.

Emended diagnosis.—Medium-sized dusignathine walruses with mandibular rami deep, left and right dentaries meeting at acute angle of 60° at symphysis to form a narrow V-shaped "chin," lower canines closely appressed to each other, and rostrum relatively shortened (autapomorphies of *Dusignathus*). Equivocal dusignathine synapomorphies that support alternative arrangements of members of this clade include upper and lower canines slightly to greatly enlarged, squamosal fossa relatively large above the external auditory meatus (apomorphies shared with *Gomphotaria*), and ventral border of dentary sinuous (apomorphy shared with *Pontolis*).

Dusignathus santacruzensis Kellogg, 1927

Dusignathus santacruzensis Kellogg, 1927; Mitchell 1968; Repenning and Tedford 1977; Barnes and Raschke 1991.

Holotype.—UCMP 27121, associated left and right dentaries, part of right maxilla with C^1 and $P^{1,2}$, isolated teeth (including two upper incisors), cranial fragment with lambdoidal crest and portion of occiput, and partial right temporal bone (mastoid, petrosal, and base of zygomatic process of squamosal).

Type locality.—UCMP V-2701, Santa Cruz County, California.

Horizon and age.—Purisima Formation, late late Miocene (Hemphillian NALMA correlative, ca. 5–8.5 Ma).

Emended diagnosis.—A species of *Dusignathus* with tooth wear in-line on anterior and posterior margins of postcanine tooth crowns (possible autapomorphy), auditory bulla slightly inflated, sagittal crest low, occipital crest low, canines not ever-growing, and zygomatic arch slender (plesiomorphies shared with *Enaliarctos*, *Neotherium*, and *Imagotaria*).

Referred material.—Repenning and Tedford (1977:43–44) referred fore- and hindlimb elements collected from the Purisima Formation to *D. santacruzensis*. These authors also referred a rostral fragment (UCR 15244) with I^3, C^1, and P^{1-3} collected from the Almejas Formation (late late Miocene, Hemphillian NALMA correlative of Isla Cedros, Baja California, Mexico) to this taxon. A complete right humerus (UCMP 65318) collected from the Purisima Formation was questionably referred to *D. santacruzensis* by Repenning and Tedford (1977).

Discussion.—The maxillary fragment of the holotype contains

C^1 and $P^{1,2}$, with the premolars single-rooted with smooth, thin enamel crowns and slight lingual cingula. In occlusal aspect, the canine and premolars are in line (i.e., C^1 is not set outside the tooth row as in odobenines). The maxilla is not swollen around the base of the procumbent and deeply rooted C^1 (root extending to a position above P^2). The crown of C^1 is caniniform and only slightly worn [in marked contrast to the extreme wear shown by the lower canine that suggests occlusion with a large I^3, as noted by Repenning and Tedford (1977)]. C^1 is not greatly enlarged relative to the postcanine teeth but apparently is positioned lateral to the lower dentition when the jaws occlude.

The lower jaw has an unfused and elongated bony symphysis with a slender but distinct genial tuberosity (Fig. 6C). The horizontal rami are deep and narrow with sinuous ventral borders. C_1 is unreduced relative to C^1 and has a closed root. The roots of all the postcanine teeth are short, swollen, oval, single-rooted pegs, in which the greatest diameter exceeds that of the crown. *Gomphotaria* has similar lower postcanine teeth except that the roots are more circular in cross-section (Barnes and Raschke 1991). In *Dusignathus*, wear on the upper and lower postcanine teeth is concentrated on the anterior and posterior edges of the thin enamel crowns.

Cranial fragments preserve portions of a low sagittal crest, a distinct lambdoidal crest, and an occipital crest. The type's right squamosal fragment preserves a slender zygomatic process and large open external auditory meatus. The mastoid process makes an acute angle with the long axis of the skull.

Except for the wear pattern, dental features alone do not distinguish *Dusignathus santacruzensis* from *Gomphotaria pugnax*. *Dusignathus* differs however, in being much smaller and having widely divergent, relatively shortened, deep mandibular rami. This distinctive mandible suggests that *Dusignathus* had a shorter rostrum than did *Gomphotaria*. In addition, *Gomphotaria* had enlarged and fluted upper canines, *Dusignathus* much smaller and smooth-surfaced canines.

The humerus (UCMP 65318) questionably referred to this taxon by Repenning and Tedford (1977) is quite generalized and preserves the elongated and sharply keeled pectoral crest (with conjoined deltoid insertion) seen in *Neotherium*, *Imagotaria*, and *Gomphotaria*.

Repenning and Tedford (1977) discussed the holotype and referred material of *D. santacruzensis* thoroughly. Unfortunately, no new material has been collected since.

$$\text{Dentition: } \frac{1(2)I,\ 1C,\ 4P,\ 1(?)M}{0I,\ 1C,\ 4P,\ 1M} \times 2 = 26(28)$$

Dusignathus seftoni Deméré, 1994

Dusignathus seftoni Deméré, 1994 (this volume).

Holotype.—SDSNH 38342, skull lacking the basicranium.

Type locality.—SDSNH locality 3468, Chula Vista, San Diego County, California.

Horizon and age.—San Diego Formation, late Pliocene (Blancan NALMA correlative, ca. 2-3 Ma).

Diagnosis.—A species of *Dusignathus* with upper and lower postcanine teeth forming a laterally convex arch (in occlusal aspect), postcanine teeth in upper and lower jaws with transverse axes of roots medially rotated, roots of all postcanine teeth closely appressed, dentary with masseteric fossa deeply excavated and symphysis fused (autapomorphies of *D. seftoni*), upper and lower canines enlarged, nasal/frontal suture V-shaped posteriorly (dusignathine synapomorphies), sagittal crest low, six postcanine teeth, and I^1 lost (symplesiomorphies at level of the Odobenidae).

Referred material.—SDSNH 20801, right dentary with portions of the symphyseal region of the left dentary; SDSNH 43873, complete left humerus; SDSNH 38256, damaged left humerus. All collected from the San Diego Formation.

Discussion.—This species is assigned to *Dusignathus* because it shares with the type species a shortened rostrum, narrow symphyseal "chin," and deep mandibular rami with a sinuous ventral border. *D. seftoni* differs from the type species primarily in overall size (larger), configuration of the tooth row (laterally convex in occlusal aspect), orientation of the roots of the postcanine teeth (in transverse cross-section the long axes of the roots are rotated medially progressively from the back of the tooth row to the front), and size of the upper and lower canines (both enlarged). The lower jaw of *D. seftoni* is very robust with a deeply excavated masseteric fossa and well-developed marginal process. The large genial tuberosity is swollen and excavated. The holotype skull of *D. seftoni* represents an immature (probably male) individual and has the distinctive nasal/frontal suture seen in *Gomphotaria* and referred material of *Pontolis* (see below) in which the nasals extend posteriorly as a wedge between the frontals (Fig. 3D).

The humerus of this species of *Dusignathus* is generalized compared to that of the Odobenini. The shaft is slender, the greater tuberosity extends above the proximal capitulum, the deltoid insertion is positioned on the elongated pectoral crest, and this crest descends with a marked flexion to the distal portion of the shaft.

$$\text{Dentition: } \frac{2I,\ 1C,\ 4P,\ 2M}{1I,\ 1C,\ 4P,\ 1M} \times 2 = 32$$

Gomphotaria Barnes and Raschke, 1991

Type species.—*Gomphotaria pugnax* Barnes and Raschke, 1991.

Distribution.—Late late Miocene of the eastern North Pacific.

Included species.—Type species only.

Emended diagnosis.—A large dusignathine walrus with roots of enlarged upper and lower canines finely fluted and covered with thick cementum, mastoid–paramastoid crest compressed anteroposteriorly and expanded dorsoventrally (autapomorphies of *Gomphotaria*), upper and lower canines greatly enlarged, squamosal fossa above the external auditory meatus relatively large (synapomorphies shared with *Dusignathus*), body large, and sagittal crest highly elevated and arched (synapomorphies shared with *Pontolis*, USNM 335567); postcanine teeth with bulbous crowns, thin enamel, and smooth narrow lingual cingula (synapomorphies at the level of the common ancestry of the Odobeninae and Dusignathinae); $I^{1,2}$ lost (convergent with *Odobenus*); marginal process of dentary weakly developed, overlap of nasal by ascending process of premaxilla relatively long, and ventral border of mandible straight (reversals to primitive condition).

Gomphotaria pugnax Barnes and Raschke, 1991

Gomphotaria pugnax Barnes and Raschke, 1991.

Holotype.—LACM 121508, nearly complete skeleton including skull, mandible, and most postcranial elements.

Type locality.—LACM locality 4631, Marblehead, San Clemente, Orange County, California.

Horizon and age.—Capistrano Formation; late late Miocene (Hemphillian NALMA correlative, ca. 5–8.5 Ma).

Diagnosis.—As for the genus.

Referred material.—JMTC 907-170, damaged rostrum with palate intact and teeth and/or alveoli for I^3, C^1, P^{1-4}, M^{1-2}. This specimen was collected from the Oso Sand Member of the Capistrano Formation and is currently assigned only a field number in the catalog system of John Minch and Associates, Mission Viejo, California. Eventually this specimen will be donated to the Orange County Natural History Foundation.

Discussion.—The holotype includes almost every skeletal element, making *Gomphotaria pugnax* the most completely known dusignathine. A baculum indicates a male. Many of the postcranial elements are characterized by pathological exostoses suggesting arthritis. The condylobasal length of 466 mm indicates an enormous pinniped, second in size only to *Pontolis magnus* (e.g., USNM 335567, condylobasal length of 600 mm). With its large and procumbent upper lateral incisors, enlarged and procumbent upper and lower canines with deeply fluted roots, vertically oriented palatine foramina, highly elevated and arched sagittal crest, and relatively small orbit, *Gomphotaria pugnax* is distinctive dentally and cranially. Dusignathine features include the broadly V-shaped invasion of the frontals by the nasals, enlarged upper and lower canines, and upper postcanine teeth with single vestigially bilobed roots. That the loss of I^{1,2} and retention of a large I^3 is not a result of the senility of the holotype is confirmed by the referred rostrum. In this specimen (JMTC 907-170), which lacks any of the exostoses of the type, the right I^3 is preserved in its alveolus and is large with a conical and well-worn crown. Wear is presumably the result of occlusion with the enlarged C$_1$. The premolars preserved with this specimen (P$^{2-4}$) all have nearly circular roots that are swollen and greater in diameter than the somewhat oval crowns. An alveolus for M^2 suggests that the reduced dentition of the type skull is pathological. The enamel on the postcanine teeth is thin as in *Dusignathus*. However, occlusal wear is apical and does not extend onto the anterior and posterior margins of the crown, as is seen in the type of *D. santacruzensis*. A distinct lingual cingulum is preserved on P^{3,4} and is marked by a slight posterolingual expansion. There are no accessory cusps or cuspules.

The humerus of *Gomphotaria* is generalized and, like that of *Dusignathus seftoni*, has a greater tuberosity that rises distinctly above the proximal capitulum. The humerus has a large and elongated pectoral crest, which descends abruptly to the distal portion of the humeral shaft. The deltoid tubercle is positioned on the lateral margin of the pectoral crest.

$$\text{Dentition: } \frac{1\text{I}, 1\text{C}, 4\text{P}, 1(2)\text{M}}{0\text{I}, 1\text{C}, 4\text{P}, 1\text{M}} \times 2 = 26(28)$$

Pontolis True 1905

Type species.—*Pontolis magnus* (True, 1905)

Distribution.—Late late Miocene of the eastern North Pacific.

Included species.—Type species only.

Emended diagnosis.—A large dusignathine walrus with elongated rostrum and marked interorbital constriction (possible autapomorphies of *Pontolis*), infraorbital foramen unenlarged, I$^{1-3}$ all present, M$^{1-2}$ double rooted, P$_{1-4}$ double-rooted, M$_{1-2}$ double rooted (reversals to conditions at base of the Odobenidae), sagittal crest greatly enlarged (apomorphy shared with *Gomphotaria*), mandible with sinuous ventral border (apomorphy shared with *Dusignathus*), mastoid process enlarged (homoplasy shared with the Odobenini), nasal/frontal suture V-shaped, and C^1 and C$_1$ large (dusignathine synapomorphies).

Pontolis magnus (True, 1905)

Pontoleon magnus True, 1905.

Pontolis magnus (True, 1905); True 1909; Kellogg 1922; Repenning and Tedford 1977; Barnes and Raschke 1991.

Holotype.—USNM 3792; complete basicranium and partial occiput of a damaged skull.

Type locality.—Sea cliffs near Empire, Coos County, Oregon.

Horizon and age.—Empire Formation, late late Miocene (Hemphillian NALMA correlative; ca. 5–7 Ma).

Diagnosis.—As for the genus.

Referred material.—The Emlong Collection at the USNM contains undescribed material here referred to *Pontolis magnus*. This material includes a skull and partial skeleton (USNM 335567), a nearly complete skull (USNM 314300), a rostrum (USNM 335554), a right dentary (USNM 335563), and isolated postcrania.

Description of referred material.—The following description is based primarily upon USNM 314300, a complete skull, lacking only the dorsal portion of the braincase including the sagittal crest and occipital crest. There are alveoli for I$^{1-3}$, C^1, P$^{1-4}$, and M$^{1-2}$. P$^{1-4}$ are all single-rooted with oval alveoli. P$^{3-4}$ alveoli have lateral septa (vestigially bifid roots). M^1 has two roots (posterior root bilobed), and M^2 has two separate roots of equal sizes. C^1 and C$_1$ are large relative to adjacent teeth but not tusklike. The rostrum is elongated and associated with a small braincase (relative to overall length of skull) and narrow interorbital constriction. The anterior outline of the braincase is triangular in dorsal aspect. The nasals are relatively elongated and extend as a V-shaped wedge between the frontals. The infraorbital foramen is not especially enlarged and is hidden by the swollen maxilla when viewed in anterior aspect. The frontal bone at the frontal/nasal suture is not raised above the dorsal level of the maxilla and nasal as in *Gomphotaria pugnax* and *Dusignathus seftoni*. The antorbital process is strongly developed and split by the maxilla/frontal suture (USNM 335554). The frontal lacks a supraorbital process. The temporal fossa is long and narrow. The zygomatic arch forms the widest part of the skull. The posterolateral border of the zygomatic process of the squamosal slopes ventrolaterally in the transverse plane, while anteriorly the process is long and slender and forms a simple overlapping contact with the jugal. The postorbital process of the jugal is relatively small. The sagittal crest is sharply keeled and has a sagittal groove running posteriorly to the cranial vertex. In USNM 335567, the sagittal crest is strongly developed (as in *Gomphotaria*) but does not extend above the general dorsal outline of the skull as viewed in lateral aspect. Instead, the roof of the braincase is depressed (in contrast to its more elevated position in *Gomphotaria*) and broadly convex at the level of the external auditory meatus. In USNM 335567, the lambdoidal crest flares posteriorly and overhangs the occiput, which is vertically oriented and marked by a strong occipital crest. The occipital condyles are small (relative to the overall size of the skull) whereas the mastoids are enlarged, resembling somewhat those of *Odobenus*. The palate is broad and slightly arched transversely. The hamular process of the pterygoid is delicate and extends posteriorly to the level of the posterior border of the glenoid fossa. The pterygoid strut is narrow, and the anterior border of the internal nares is smoothly curved. The auditory bulla is flattened with smooth external surfaces, and the basisphenoid is arched transversely.

Skull measurements of USNM 314300 (in mm): condylobasal length 528, braincase length 310, rostrum length 218, zygomatic width 255, mastoid width 237, interorbital width 47. Measurements of empty alveoli of USNM 314300 (anteroposterior diameter/transverse diameter, in mm): I^3 28/25, C^1 43/34, P^1 21/16, P^2 23/16, P^3 21/13, P^4 21/13, M^1 15/14, M^2 21/8.

The lower jaws here referred to *Pontolis* preserve a large caniniform canine, at least one incisor (I$_3$), P$_{1-4}$, and M$_{1-2}$. In USNM 335567 M$_{1-2}$ are missing. The crowns of P$_{2,3}$, as preserved in USNM 335563, are characterized by a single central cusp (= paraconid) and a strong lingual cingulum that extends around to the posterior margin of the tooth. The anterior portion of each tooth is worn to the extent that the paraconid is nearly lost. Whether or not there were any anterior cusps or cuspules is unclear. Overall, the dentary is elongated, with a distinct genial tuberosity, unfused and narrowly oval symphysis (in medial aspect), shallow horizontal ramus with a sinuous ventral border, well-developed marginal process, and large coronoid process without a deeply excavated masseteric fossa.

Referral of this material to *Pontolis* is based on the following features shared with the holotype: overall large size, narrow pterygoid strut, transversely convex braincase, smooth and flattened bulla, bulla smoothly joining with mastoid (i.e., a prominent groove between the stylomastoid foramen and hyoid fossa is lacking), large and pentagonal basioccipital, and lateral border of zygomatic process of squamosal sloping ventrolaterally in transverse plane. Both the holotype braincase and the Emlong fossils were collected from the Empire Formation at Coos Bay, Oregon.

Discussion.—*Pontolis magnus* was the first fossil pinniped to be named from the Pacific coast. The holotype, USNM 3792, is a large incomplete braincase, described and illustrated by Repenning and Tedford (1977:42–43; pl. 18, fig. 5). The important new material described here documents a truly tremendous animal—one skull (USNM 335567) measures 600 mm in condylobasal length. In contrast, skulls of modern adult males of *Odobenus rosmarus divergens* range between 380 and 430 mm long (Fay 1985).

Pontolis magnus is considered a dusignathine on the basis of its large upper and lower canines and V-shaped nasal/frontal suture. The retention of numerous dental plesiomorphies like separate roots on $M^{1,2}$, P_{1-4}, and $M_{1,2}$ and three upper incisors underlines the taxon's mosaic nature.

$$\text{Dentition: } \frac{3I,\ 1C,\ 4P,\ 2M}{1I,\ 1C,\ 4P,\ 2(0)M} \times 2 = 32(36)$$

Subfamily Odobeninae (*sensu* Repenning and Tedford, 1977)

Definition.—The monophyletic group containing the most recent common ancestor of *Aivukus* and *Odobenus* and all of its descendants.

Diagnosis.—Odobenids with frontal/maxillary suture transversely directed, postorbital process of jugal dorsoventrally expanded, C_1 less than 75% the size of C^1, postcanine teeth reduced to five, P^3 and P^4 with simple peglike crowns, P^4 with single circular root, first metacarpal with insertion for pollicle extensor muscle developed as a rugosity, and lower canine premolariform (odobenine synapomorphies).

Aivukus Repenning and Tedford, 1977

Type species.—*A. cedrosensis* Repenning and Tedford, 1977.

Distribution.—Late late Miocene of the eastern North Pacific.

Included species.—Type species only.

Characterization.—A medium-sized odobenid with frontal/maxillary suture directed transversely, postorbital process of jugal dorsoventrally expanded, C_1 less than 75% the size of C^1, $P^{3,4}$ with simple peglike crowns, first metacarpal with insertion for pollicle extensor muscle developed as a rugosity (odobenine synapomorphies), I^1 lost (apomorphy shared with *Dusignathus* and *Alachtherium*), C^1 not enlarged as tusk and lacking a central column of globular dentine, humerus with elongated and sharply keeled pectoral crest, and deltoid tubercle joined with pectoral crest (symplesiomorphies at the level of the Pinnipedia).

Aivukus cedrosensis Repenning and Tedford, 1977

Aivukus cedrosensis Repenning and Tedford, 1977; Barnes and Raschke 1991.

Holotype.—IGCU 901, a partial skull, partial left dentary, and partial front limb.

Type locality.—UCR locality RV 7309, Isla Cedros, Baja California Sur, Mexico.

Horizon and age.—Almejas Formation (lower portion), late late Miocene (Hemphillian NALMA correlative, ca. 5–8.5 Ma).

Characterization.—As for the genus.

Referred material.—Repenning and Tedford (1977:14) referred several postcranial elements, including a complete humerus (UCR 15243) and isolated carpal bones, to *A. cedrosensis*.

Discussion.—Repenning and Tedford (1977) described the type and referred material of *Aivukus cedrosensis* thoroughly. As noted by these authors and confirmed here, *Aivukus* is clearly an odobenine with its dorsoventrally elongated postorbital process of the jugal, frontal/maxilla suture transverse and nearly perpendicular to sagittal plane, lower canine reduced in size relative to the upper canine, and postcanine teeth peglike with single, nearly circular roots and heavy "jacket" of cementum. The mosaic nature of this taxon is evident in its retention of numerous plesiomorphies (relative to the Odobenini), including an elongated and slender rostrum, upper canine not ever-growing and lacking a central column of globular dentine, lower canine larger than Pc_1, mandibular symphysis unfused, and deltoid tubercle incorporated into the pectoral crest of the humerus (Fig. 7B).

Although Repenning and Tedford (1977:fig. 1) presented a complete restoration of the skull of *Aivukus*, portions of the skull are not preserved on the holotype. For example, the cranial roof is not preserved at the midline, and thus it is impossible to determine whether there was a sagittal crest (as in *Neotherium*, *Imagotaria*, *Pontolis*, *Gomphotaria*, and *Dusignathus*) or a flattened cranial vertex (as in *Alachtherium*, *Pliopedia*, *Valenictus*, and *Odobenus*). Also, the nasal/frontal suture is not discernible in the holotype, and the occipital condyles, pterygoids, palatines, auditory bullae, basioccipital, and most of the alisphenoid and nasals are missing. This incompleteness calls into question some of the odobenine features discussed by Repenning and Tedford (1977), such as the domed and crestless braincase, transverse nasal/frontal suture, broad pterygoid hamuli, and pentagonal basioccipital. My analysis indicates that *Aivukus* represents the least divergent odobenine walrus and is a possible ancestor of the tusked odobenines.

$$\text{Dentition: } \frac{2I,\ 1C,\ 4P,\ 1M}{?I,\ 1C,\ 4P,\ 1M} \times 2 = 28?$$

Tribe Odobenini new name

Definition.—The monophyletic group containing the most recent common ancestor of *Alachtherium* and *Odobenus* and all of its descendants.

Diagnosis.—Odobenines with the external narial opening elevated above the incisive margin, palate arched transversely and longitudinally, hard palate elongated (also occurs in the otariid *Otaria*), mastoid processes as widest part of cranium, zygomatic portion of squamosal blunt and robust, temporal fossa shortened, orbital vacuity posteriorly placed, upper canine with well-developed globular dentine column, C_1 less than 40% the size of C^1, P^1 medial to upper canine, upper postcanine teeth three or four, adult postcanine tooth crowns with cementum only (no enamel), mandibular terminus vascular, deltoid tubercle of humerus on extreme lateral side of pectoral crest or off crest, mastoid enlarged (also occurs in *Pontolis*), I^3 medial to upper canine (also occurs in *Dusignathus*), lower canine premolariform, tooth row between P^1 and M^1 laterally convex (also in *Dusignathus*), mandibular arch sharply divergent (also occurs in *Dusignathus*), palatine telescoped beneath alisphenoid, hamular process broad, pterygoid strut lost, lambdoidal crest with distinct flattened traction surface, sagittal crest lost (also variably seen in phocoids), and optic foramen funnel-shaped.

Pliopedia Kellogg, 1921

Type species.—*Pliopedia pacifica* Kellogg, 1921.

Distribution.—Late late Miocene of the eastern North Pacific.

Included species.—Type species only.

Emended diagnosis.—A medium-sized member of the Odobenini with lesser tuberosity of the humerus expanded medially (possible autapomorphy of *Pliopedia*), braincase broadly convex, sagittal crest absent, lambdoidal crest with flattened traction surface, occipital shield hemispherical, humerus with low pectoral crest descending gradually to distal end, and deltoid tubercle well separated from pectoral crest (synapomorphies of the Odobenini).

Pliopedia pacifica Kellogg, 1921

Pliopedia pacifica Kellogg, 1921; Repenning and Tedford 1977; Barnes and Raschke 1991.

Holotype.—USNM 13627, associated left humerus, radius, ulna, metacarpals, metatarsals, and phalanges.

Type locality.—Santa Margarita, San Luis Obispo County, California.

Horizon and age.—Paso Robles Formation, late late Miocene (Hemphillian NALMA correlative, ca. 5–6 Ma, Repenning and Tedford 1977:49).

Characterization.—As for the genus.

Referred material.—Repenning and Tedford (1977:49) referred a partial skeleton (USNM 187328, including a braincase, rib and portions of the right and left forelimbs collected from the Etchegoin Formation, late late Miocene, Hemphillian NALMA correlative of central California) to *P. pacifica*. This referral was made on the basis of the morphology of the humerus. Although Barnes and Raschke (1991:13) subsequently removed this specimen from *P. pacifica*, citing work in progress, I retain it in this taxon.

Discussion.—Repenning and Tedford (1977:49-53) discussed the type and referred material of *Pliopedia pacifica* thoroughly. The holotype itself consists of fragmentary material preserving little diagnostic morphology except a distal humeral articulation with the medial lip of the trochlea broader than the radial capitulum and a metacarpal I with a conspicuous pit for insertion of the pollicle extensor muscle (both odobenid synapomorphies). More important is the partial skeleton (USNM 187328) from the Etchegoin Formation. The lesser tuberosity of the right humerus of this specimen (Repenning and Tedford 1977:pl. 17) is unique in being medially expanded and positioned distinctly below the proximal capitulum. The greater tuberosity is at the same level as the capitulum. The humerus also exhibits several features characteristic of the Odobenini, including a pectoral crest that gradually joins the shaft distally and a deltoid tubercle well separated from the pectoral crest. The partial skull of USNM 187328 (Repenning and Tedford 1977:pl. 24, fig. 6) also exhibits several important features of the Odobenini, including a low and broadly rounded braincase, absence of a sagittal crest and its replacement by a sagittal sulcus, and a broad flattened and crescentic traction surface on the lambdoidal crest. The occipital shield is hemispherical in posterior aspect.

Pliopedia pacifica differs from *Alachtherium* in lacking a rectangular occipital shield and a deltoid tubercle joined with the pectoral crest of the humerus. It differs from *Prorosmarus* in lacking a deltoid tubercle joined with the pectoral crest of the humerus and from *Valenictus* in its humerus' lacking an enlarged entepicondyle. It differs from *Odobenus* in the lesser tuberosity of the humerus being medially expanded. Repenning and Tedford (1977:52) noted the strong resemblance between the referred braincase and that of *Odobenus*, yet they chose to place *Pliopedia* with the dusignathine walruses. It is clear from the phylogenetic analysis that *P. pacifica* is a member of the Odobenini and the oldest known member of this group. This assignment suggests that *Pliopedia pacifica* also possessed the elongated specialized tusks of the Odobenini.

Alachtherium du Bus, 1867

Type species.—*A. cretsii* du Bus, 1867.

Distribution.—Pliocene of the eastern North Atlantic Ocean.

Included species.—Type species only.

Emended diagnosis.—A large member of the Odobenini with humerus approximately 15% larger than that of *Odobenus rosmarus*, posterior outline of occipital shield rectangular, lower postcanine teeth more widely spaced than those of *Odobenus* (autapomorphies of *Alachtherium*); external narial opening elevated, palate elongated and vaulted, C^1 enlarged and tusklike, C^1 with central column of globular dentine, upper and lower postcanine teeth with single circular roots, mandibular symphysis elongated, mastoid process enlarged (synapomorphies of the Odobenini), mandibular symphysis unfused, I^3 transversely in line with I^2 at anterior end of the premaxilla (not displaced posteriorly, adjacent to P^1 and medial of C^1, as in *Odobenus*), external auditory meatus large and open in ventral aspect between postglenoid process and mastoid process (in *Odobenus* the two processes are closely appressed to one another), C^1 (tusk) more procumbent than in *Odobenus*, and coronoid process of mandible elongated (plesiomorphies relative to *Odobenus*).

Alachtherium cretsii du Bus, 1867

Alachtherium cretsii du Bus, 1867; van Beneden 1877; Kellogg 1922.
Trichechus antverpiensis Rutten, 1907.
Alachtherium antwerpiensis Hasse, 1910.
Odobenus antverpiensis van der Feen 1968; Erdbrink and van Bree 1986, 1990.

Holotype.—Complete right dentary (IRSNB M.168) illustrated by van Beneden (1877) and Berry and Gregory (1906).

Type locality.—Wyneghem, Fort I, Antwerp Basin, Belgium.

Horizon and age.—Scaldisian sands; early Pliocene.

Diagnosis.—As for the genus.

Referred material.—Van Beneden (1877) referred several Scaldisian walrus specimens, including a partial cranium (IRSNB M.169) and a complete humerus (IRSNB M.170), to this taxon.

Taxonomic history.—Rutten (1907) examined the partial cranium of Beneden (IRSNB M.169), concluding that it was incompatible with the holotype dentary. Rutten was concerned primarily with presumed size differences between the skull and dentary and with the large coronoid process of *A. cretsii* (Fig. 6D), which he suggested would be too massive to fit between the convex braincase and zygomatic arch. Rutten (1907) removed the Beneden cranium from his concept of *A. cretsii* and instead designated it the type of a new taxon, *Trichechus antverpiensis*.

Hasse (1910) described cranial (Fig. 4E) and postcranial material belonging to at least four individuals, both adults and juveniles, from the younger Merxemian (= Poederlian, upper Pliocene) sands north of Antwerp (van der Feen 1968). Like Rutten (1907), Hasse concluded that the type jaw of *A. cretsii* was incompatible with his new walrus material and so erected yet another new species, *Alachtherium antwerpiensis*.

Van der Feen (1968) illustrated and described a posterior cranial fragment collected from the mouth of the Scheldt River, Netherlands, referring to it as *Odobenus antverpiensis* (Rutten) but not discussing why it was not referable to the genus *Alachtherium* or the species *A. cretsii*.

Erdbrink and van Bree (1990) described and illustrated a nearly complete cranium (GMAU K-8052) from offshore Zeeland, Netherlands, referring it to *Odobenus antverpiensis* (Rutten) on the basis of its depressed (not ridgelike) sagittal suture, broad and high lambdoidal crest, weakly developed occipital crest, large size (relative to *O. rosmarus*), anterior position of I^3 (anterior to C^1, not posterior as in *O. rosmarus*), low (dorsoventral) position of the external narial opening (relative to the elevated position seen in *O. rosmarus*), and small peglike postcanine teeth with sharp edges. From illustrations of GMAU K-8052 it appears that this specimen is conspecific with the skull of *A. antwerpiensis* figured by Hasse (1910) and the cranial fragment used by Rutten (1907) as the holotype of *T. antverpiensis*. Similarities include the rectangular posterior outline of the occipital shield, broad and vaulted palate, large diastema between I^3 and C^1, sinuous postcanine tooth row (when the diastema is included as part of the tooth row's curvature), anteriorly placed incisors, and procumbent C^1. Differences between the skulls include five postcanine teeth in Hasse's skull vs. four in GMAU K-8052, retention of I^1 in GMAU K-8052 vs. loss of this tooth in Hasse's skull, and more anterior placement of Pc^1 (medial to C^1) in Hasse's skull vs. posterior placement of this tooth in GMAU K-8052. Erdbrink and van Bree (1990) concluded that *O. antverpiensis* (Rutten) is a senior synonym of *A. antwerpiensis* Hasse. Surprisingly, these authors failed even to mention *A. cretsii* and offered no reasons for not synonymizing *O. antverpiensis* (Rutten) with *A. cretsii* du Bus.

Reasons for lumping all taxa into *Alachtherium cretsii* include the largeness of both the type dentary (Fig. 6D) and type and referred crania (Fig. 4E) of *T. antverpiensis* Rutten, *A. antwerpiensis* Hasse, and *O. antverpiensis* (Rutten) (in van der Feen 1968; Erdbrink and van Bree 1990), sinuous lower and upper postcanine tooth rows (a tracing of the sinuous occlusal outline of the type jaw conforms to the sinuous occlusal outline of the upper jaw of both the Hasse skull and GMAU K-8052), and possession of two lower incisors in the type dentary of *A. cretsii* and two upper incisors in the skull of Hasse (Fig. 4E). The skull of Hasse also has a more elongated snout region than does that of *Odobenus*, which is compatible with the rather elongated symphyseal region in the type dentary of *A. cretsii*.

Possible reasons for retaining two species of *Alachtherium* include the early Pliocene age (Scaldisian) of the holotype dentary of *A. cretsii* vs. the late Pliocene age (Poederlian) of the Hasse (1910) material (*A. antwerpiensis*) and retention of five postcanine teeth vs. four in GMAU K-8052.

Discussion.—The features of *Alachtherium cretsii* linking it to the Odobenini include its elongated and ever-growing upper canine (with central column of globular dentine), C_1 reduced to size of the premolars, mastoid enlarged and descending ventrad to level of the hamular process of the pterygoid, sagittal crest lost and replaced by a sagittal sulcus marking the interparietal suture, palate elongated and longitudinally arched, pterygoid strut lost, lambdoidal crest flattened, and Pc^1 medial to C^1.

In general, *Alachtherium* preserves intermediate character states in the transition from the primitive dental condition of *Aivukus* to the derived condition of *Odobenus*. In adults of *O. rosmarus*, I^{1-2} are typically lost (Fay 1982), I^3 is displaced posteriorly to the medial side of C^1 and in line with the postcanine teeth, and Pc^1 is placed anterior and medial of C^1 (Fig. 4G). In *Alachtherium*, I^1 is variably present, I^2 is always present, I^3 is consistently positioned anterior to C^1, and Pc^1 is placed posterior to C^1 (Fig. 4E). Major differences are seen in the lower jaws, where *Odobenus* has a strongly fused and massive symphysis and a reduced coronoid process (Fig. 6F), in contrast to the unfused and slender symphysis and large coronoid process of *Alachtherium* (Fig. 6D).

The humerus (IRSNB M.170) of *Alachtherium* is longer than that of *Odobenus* (435 vs. 390 mm) and similarly slender, more slender than that of *Valenictus*. The pectoral crest is elongated but not sharply keeled. The deltoid tubercle is laterally displaced but still associated with the pectoral crest. The biciptal groove is broadly open, and the lesser tuberosity is distinctly below the proximal capitulum. The entepicondyle is not enlarged and is more quadrate than the triangular entepicondyle of *Odobenus*.

I retain *Alachtherium* as a genus distinct from *Odobenus* because of the differences noted in the postcanine teeth, the more procumbent canines, the more elongated rostrum, the broader palate, the less elevated external narial opening, the unfused and unswollen mandibular symphysis, and features of the humerus.

$$\text{Dentition: } \frac{2(3)\text{I, 1C, 4(5)Pc}}{\text{2I, 1C, 4Pc}} \times 2 = 28(32)$$

Prorosmarus Berry and Gregory, 1906

Type species.—*Prorosmarus alleni* Berry and Gregory, 1906

Distribution.—Early Pliocene of the western North Atlantic.

Included species.—Type species only.

Characterization.—A medium-sized member of the Odobenini with lower postcanine teeth closely appressed to each other (apomorphy shared with *Odobenus*); distal tip of lower jaw roughened and pitted, mandibular symphysis elongate and sloping, lower canine equal in size to Pc_1 (i.e., C_1 reduced), horizontal ramus in occlusal aspect laterally concave anteriorly, becoming convex in region of postcanines (synapomorphies of the Odobenini), postcanine teeth with single nearly circular roots and simple crowns (odobenine synapomorphies), and unfused mandibular symphysis (plesiomorphy shared with most pinnipeds).

Prorosmarus alleni Berry and Gregory, 1906

Prorosmarus alleni Berry and Gregory, 1906; Kellogg 1922; Repenning and Tedford 1977; Barnes and Raschke 1991.

Holotype.—USNM 9343, partial left dentary.

Type locality.—Beach at Yorktown, Virginia.

Horizon and age.—Yorktown Formation, early Pliocene (latest Hemphillian NALMA correlative, ca. 3.5–5 Ma).

Characterization.—As for the genus.

Referred material.—Left humerus (MCZ 7713; C. E. Ray in Repenning and Tedford 1977:13); numerous isolated skeletal elements in the USNM collections from the Lee Creek Mine (C. E. Ray, pers. comm.). All referred material collected from the Yorktown Formation.

Discussion.—The holotype dentary is missing the mandibular condyle, coronoid process, pterygoid process, and masseteric fossa. The horizontal ramus is deep dorsoventrally and moderately thick transversely. The unfused symphysis extends below the anterior border of Pc_3. There are many similarities with the holotype dentary of *Alachtherium cretsii*, including reduced and premolariform canine, possession of alveoli for four postcanine teeth (presumably P_{1-4}, Berry and Gregory 1906) and two incisors, single-rooted and circular postcanine alveoli, distinct but unswollen genial tuberosity, well-developed marginal process, large and deeply set mental foramen beneath intra-alveolar septum separating Pc_1 and Pc_2, and dorsally expanded and pitted incisive margin.

Important differences between the type dentaries of *P. alleni* and *A. cretsii* include smaller overall size, less upturned symphysis, position of mental foramen below Pc_1 rather than Pc_2, and postcanine alveoli closely appressed to each other and positioned squarely on alveolar rather than medial margin of dentary. C. E. Ray (pers. comm.) believes these and other features suggest a close relationship, perhaps conspecificity, between the two taxa. *Prorosmarus* may be the female of *Alachtherium*. Sexual dimorphism may be responsible for the greater intra-alveolar distance, larger overall size, and greater degree of symphyseal upturning seen in *A. cretsii*. Resolution of this issue must await discovery of diagnostic cranial material of *Prorosmarus* from the Yorktown Formation.

As discussed by Repenning and Tedford (1977:13), the left humerus (MCZ 7713) referred to this taxon falls within the size range of modern *Odobenus* humeri. It differs, however, in the position of the deltoid insertion, which is still located on the pectoral crest rather than being a separate tubercle on the lateral side of the shaft. Other differences include a wider bicipital groove, more robust distal extremity, and less triangular entepicondyle. Importantly, the pectoral crest is more keeled and descends with some flexure to the distal portion of the shaft. This flexion, however, is not as pronounced as in *Imagotaria*, *Dusignathus*, *Gomphotaria*, or *Aivukus*.

On the basis of these features, *P. alleni* is a member of the Odobenini close to the common ancestry of *Alachtherium* and *Odobenus*.

$$\text{Dentition: } \frac{?\text{I, 1C, }?\text{P, }?\text{M}}{\text{2I, 1C, 4P, 0M}}$$

Valenictus Mitchell, 1961

Type species.—Valenictus imperialensis Mitchell, 1961.

Distribution.—Late late Miocene and late Pliocene of the eastern North and Central Pacific.

Included species.—Valenictus imperialensis Mitchell, 1961, and *Valenictus chulavistensis* Deméré, 1994 (this volume).

Definition.—The monophyletic group containing the most recent common ancestor of *V. imperialensis* and *V. chulavistensis* and all of its descendants.

Emended diagnosis.— A member of the Odobenini with humeri characterized by pectoral crest broad, not a sharply keeled ridge, greater tuberosity thickened, entepicondyle greatly enlarged, shaft short and robust, and bicipital groove narrow (synapomorphies of *Valenictus*).

Valenictus imperialensis Mitchell, 1961

Valenictus imperialensis Mitchell, 1961; Mitchell 1968; Repenning and Tedford 1977.

Holotype.—LACM (CIT) 3926, nearly complete left humerus.

Type locality.—LACM (CIT) locality 472, Coyote Mountains, Imperial County, California.

Horizon and age.—Imperial Formation (Coyote Mountain Clays), late late Miocene to early Pliocene (Hemphillian NALMA correlative, 4–6 Ma).

Emended diagnosis.—A species of *Valenictus* with entepicondyle of humerus rounded, knoblike, and positioned distally and posterior outline of humeral shaft nearly straight (apparent autapomorphies of *V. imperialensis*).

Referred material.—Repenning and Tedford (1977:53) referred USNM 13643, the distal end of a right humerus collected from the San Joaquin Formation (latest Miocene to early Pliocene, probable Hemphillian NALMA correlative of inland central California) to *V. imperialensis*. As discussed below, close examination of this specimen suggests it is associated more closely with *Valenictus chulavistensis*.

Discussion.—Features shared with the modern walrus, *Odobenus*, include a greater tuberosity thickened and only slightly elevated above the proximal capitulum, a pectoral crest broad and not developed as a sharply keeled ridge, and a deltoid tubercle separated from the pectoral crest and located on the lateral margin of the shaft. The humerus is relatively stocky compared to those of *Odobenus*, *Alachtherium*, and *Imagotaria*.

Previous workers have assigned *Valenictus* to the Dusignathinae, perhaps because of its many unique derived features. Its possession of a deltoid tubercle located posterolateral to a low pectoral crest and a greater tuberosity elevated only slightly above the proximal capitulum, however, clearly demonstrate its affinities with the Odobenini.

The single specimen of *Valenictus imperialensis* is from a marine rock unit known for its distinctive assemblages of warm-water molluscan taxa of Caribbean and tropical Pacific affinities (Deméré 1993).

Valenictus chulavistensis Deméré, 1994

Valenictus chulavistensis Deméré, 1994 (this volume).

Type material.—Holotype, SDSNH 36786, a partial skeleton preserving the left side of the skull and mandible as well as nearly every postcranial element. Paratype, SDSNH 38227, a nearly complete skull with both canines.

Holotype and paratype locality.—SDSNH locality 3551, Chula Vista, San Diego County, California.

Horizon and age.—San Diego Formation, late Pliocene (Blancan NALMA correlative, ca. 2–3 Ma).

Diagnosis.—A large species of *Valenictus* with edentulous dentary, edentulous premaxilla and postcanine portion of maxilla, osteosclerotic long bones, astragalus with broad sulcus calcanei, very reduced collum tali, and coalesced navicular and sustentacular facet (autapomorphies of *V. chulavistensis*). Distinguished from *V. imperialensis* by the following features of the humerus: larger size, more sigmoidal posterior profile, sharply keeled supinator ridge, more robust and rectangular entepicondyle, and more obtuse angle between the shaft and the axis of the distal trochlea.

Referred material.—Numerous cranial, dental, and postcranial remains from the San Diego Formation (see Deméré 1994, this volume). The distal fragment of a right humerus (USNM 13643) from the San Joaquin Formation (latest Miocene to early Pliocene, probable Hemphillian NALMA correlative of inland central California), originally referred to *V. imperialensis* by Repenning and Tedford (1977:53).

Discussion.—Valenictus chulavistensis is known from almost every skeletal element (see Deméré 1994, this volume). Dentally, it is the most divergent odobenid, having lost all teeth except the enlarged upper canines (Fig. 4F). This taxon has the following synapomorphies of the Odobenini: upper canines enlarged and ever-growing, with three dental layers (globular dentine, orthodentine, and cementum), palate elongated and arched longitudinally as well as transversely, mastoid process as widest part of skull, temporal fossa shortened with blunt and robust zygomatic arch, hamular process of pterygoid broad, pterygoid strut lost, lambdoidal crest flattened, sagittal crest lost, and optic foramen funnel-shaped.

The mandible of *V. chulavistensis* is completely edentulous and delicate with a narrow but fused and strongly upturned symphysis (Fig. 6E). The alveolar margin is sharply keeled, and the occlusal outline is sinuous, accommodating the enlarged canines of the upper jaw.

The humerus of *V. chulavistensis* has the stocky shaft and enlarged entepicondyle characteristic of the genus. The distal end of a humerus from the San Joaquin Formation (USNM 13643) referred to *V. imperialensis* by Repenning and Tedford (1977) is better referred to *V. chulavistensis* because its entepicondyle is more cubic, the widest portion of its entepicondyle is positioned more proximally, and the long axis of its entepicondyle is rotated anterodorsally.

$$\text{Dentition: } \frac{\text{0I, 1C, 0P, 0M}}{\text{0I, 0C, 0P, 0M}} \times 2 = 2$$

Odobenus (Brisson, 1762)

Type species.—Odobenus rosmarus (Linnaeus, 1758).

Distribution.—Pleistocene and Holocene of the North Atlantic, North Pacific, and Arctic oceans.

Included species.—Odobenus rosmarus (Linnaeus, 1758); *Odobenus mandanoensis* Tomida, 1989; *Odobenus huxleyi* (Lankester, 1865); *Odobenus koninckii* (van Beneden, 1871).

Definition.—The monophyletic group containing the most recent common ancestor of *O. huxleyi* and *O. rosmarus* and all of its descendants.

Emended diagnosis.—A member of the Odobenini with mandibular symphysis fused and greatly reinforced, lower canine incorporated into postcanine tooth row, external nares well elevated above the incisive margin of the premaxilla, external overlap of premaxilla and nasal lost, C^1 enlarged as a tusk and oriented nearly vertically, I^{1-2} and I_{1-3} lost (sometimes present as an atavism), I^3 posteriorly placed (relative to C^1), external auditory meatus constricted anteroposteriorly (autapomorphies of *Odobenus*), C^1 a tusk and composed of three layers including a central column of globular dentine, palate elongated and vaulted, palate telescoped beneath braincase, hamular process of pterygoid enlarged and laterally directed, lambdoidal crest flattened, sagittal crest lost and replaced by a sulcus, temporal fossa shortened, and external narial opening elevated (synapomorphies of the Odobenini).

Odobenus rosmarus (Linnaeus, 1758)

Phoca Rosmarus Linnaeus, 1758
Odobenus rosmarus (Linnaeus, 1758): Harington 1984; Harington and Beard 1992; Harington et al. 1993; Fay 1982, 1985; Erdbrink and van Bree 1986, 1990
Trichechus virginianus De Kay, 1842
Trichechus huxleyi (in part): Rutten 1907

Holotype.—None designated.

Type locality.—None designated.

Horizon and age.—Pleistocene to Recent.

Diagnosis.—As for the genus.

Discussion.—Fay (1982) recognized two subspecies of *Odobenus rosmarus, O. r. rosmarus* from the North Atlantic and *O. r. divergens* from the North Pacific. Fossil and/or subfossil remains closely resembling modern *O. rosmarus* (= *Trichechus virginianus*) have been recovered from coastal deposits and the inner continental shelf of eastern North America (Ray 1975; Harington 1977; Harington et al. 1993; Parris 1983), and from the English Channel and North Sea (Rutten 1907; van der Feen 1968; Erdbrink and van Bree 1986). Included in this material are several complete and nearly complete crania as well as isolated tusks, mandibles, and assorted postcrania. Late Wisconsin remains of *O. rosmarus* have also been reported from British Columbia (Harington and Beard 1992) and California (Harington 1984). Erdbrink and van Bree (1986) reviewed English and Dutch Pleistocene walrus material and offered anatomical criteria for assigning it to *O. rosmarus*. Undescribed Pleistocene crania from the western Atlantic seaboard in USNM are conspecific with *O. rosmarus* (Ray 1992). *Odobenus rosmarus* is currently the only nominal species of *Odobenus* for which the skull (Fig. 4G) and mandible (Fig. 6F) are confidently known.

$$\text{Dentition: } \frac{1I,\ 1C,\ 3(4)Pc}{0I,\ 1C,\ 3Pc} \times 2 = 18(19)$$

Fay (1982) reported that some Pacific walruses have three incisors, four premolars, and two molars as an atavism.

Odobenus huxleyi (Lankester, 1865)

Trichechodon huxleyi Lankester, 1865.
Trichecus (*sic*) *huxleyi* Lankester 1880.
not *Trichechus huxleyi* Rutten 1907.
Trichechodon huxleyi (in part) Kellogg 1922.
Odobenus huxleyi van der Feen 1968; Erdbrink and van Bree 1986.

Holotype.—Partial upper canine, BMNH 46000.

Type locality.—Sutton, Suffolk County, England.

Horizon and age.—Red Crag (Waltonian), early Pleistocene (Erdbrink and van Bree, 1986).

Emended diagnosis.—A species of *Odobenus* known confidently only from tusks, which have cementum and outer orthodentine layers thinner than those of *O. rosmarus* (possible autapomorphies of *O. huxleyi*).

Discussion.—Lankester (1865, 1880) stated that *Trichechodon huxleyi* was distinguishable from *O. rosmarus* by the greater curvature and diameter of its tusks. Erdbrink and van Bree (1986) found that the supposed greater curvature and diameter of Lankester's tusks fall within the range of variation of modern *Odobenus rosmarus* and therefore are unreliable for distinguishing the two taxa. They noted instead that the cementum and outer orthodentine layers of the type and referred tusks of *O. huxleyi* are much thinner than those of *O. rosmarus* and so used this character complex as the sole diagnostic feature of *O. huxleyi*.

Since Lankester's original description, additional specimens have been referred to *O. huxleyi*, most notably a nearly complete cranium (with tusks) illustrated by Rutten (1907). In their review of North Sea fossil odobenids Erdbink and van Bree (1986) restricted the concept of *O. huxleyi* to the type dental material and several additional tusks dredged from the North Sea. Under their view, Rutten's and several other cranial specimens referred to *O. huxleyi* are instead assignable to *O. rosmarus*. It should be pointed out, however, that Erdbrink and van Bree (1986) also assigned specimens here referred to *Alachtherium* (i.e., *A. antverpiensis* = *A. cretsii*) to *Odobenus* (i.e., *O. antverpiensis*). These authors included in *Odobenus* all odobenids with tusks possessing a central column of globular dentine. Erdbrink and van Bree (1986) suggested that *O. huxleyi* may prove to be a senior synonym of *A. antverpiensis* if and when tusks having thin cementum and outer orthodentine layers and so positively assignable to the latter species are found. Since thin dental layers could actually have arisen in the common ancestor of *O. huxleyi* and *A. cretsii*, this feature alone may not be sufficient to diagnose a taxon, and *O. huxleyi* may not be diagnosable at all (i.e., a *nomen nudum*). In this report, the concept of *O. huxleyi* is that proposed by Erdbrink and van Bree (1986).

Odobenus koninckii sensu lato (van Beneden, 1871)

Trichechodon koninckii van Beneden, 1871
Trichechodon koninckii (in part) van Beneden 1877
Trichechodon huxleyi (in part) Kellogg 1922

Holotype.—Partial upper canine (original lost, but cast survives; IRSNB cast 2892; Rutten 1907).

Type locality.—Antwerp, Belgium.

Horizon and age.—Scaldisian sands, early Pliocene.

Emended characterization.—A species of *Odobenus* with four equally large lower postcanine teeth behind a canine of larger circumference.

Referred material.—Partial left dentary (van Beneden 1877; no catalog number).

Discussion.—The cast now serving as the basis for *Trichechodon koninckii* is not by itself diagnostic except in its preservation of the dental-layer synapomorphies of the Odobenini. Therefore Rutten (1907) and van der Feen (1968) dismissed *T. koninckii* as a *nomen nudum*.

This designation would be easy to accept had van Beneden (1877) not referred additional fossils to this taxon. Most important is a partial left dentary preserving alveoli for C_1–Pc_4 (van Beneden 1877: pl. 6, figs. 5–7). This specimen appears to have had a broad and fused symphysis (C. E. Ray, pers. comm.), a synapomorphy of *Odobenus*. Its other important features include nearly circular and equal-sized alveoli for Pc_{1-4}, very thin septa between the alveoli, straight tooth row with the alveolus for C_1 closely appressed to that of Pc_1, diameter of C_1 greater than those of Pc_{1-4}, and sigmoidal lateral outline of horizontal ramus in occlusal aspect. This character complex defines a taxon close to modern *Odobenus* and indicates that the genus may have evolved during the Pliocene. The taxonomic relationship of the referred dentary to the type of *O. koninckii* is unclear and may never be known unless more complete material is found. Thus I refer to this taxon as *O. koninckii sensu lato*.

Odobenus mandanoensis Tomida, 1989

Odobenus mandanoensis Tomida, 1989.

Holotype.—NSM-PV 18911, partial mandible preserving symphyseal portions of left and right rami with roots of left C_1, P_2, and right C_1.

Type locality.—Sand and gravel mine near village of Mandano, city of Kisarazu, Chiba Prefecture, Japan.

Horizon and age.—Mandano Formation, upper Pleistocene (ca. 0.5 Ma).

Emended diagnosis.—A species of *Odobenus* with symphysis widest above the mental foramen rather than below, portion of dentary lateral to alveoli for Pc_1 thicker than in *O. rosmarus*, dorsal longitudinal margin of symphysis gently sloping, and diastemata between C_1 and Pc_1 wider than in *O. rosmarus* (autapomorphies of *O. mandanoensis*).

Discussion.—This species' most notable feature is its massive and strongly fused mandibular symphysis, a synapomorphy of *Odobenus*. Tomida (1989) was not certain that his taxon differed from *O. huxleyi* but distinguished it from *O. koninckii sensu lato* (i.e., van Beneden's partial mandible) by its smaller symphyseal area and more steeply sloping dorsal longitudinal symphyseal margin.

Features of the Odobenini preserved in the holotype include the following: lower canine incorporated into postcanine tooth row, symphysis strongly fused and massive, incisive margin of symphysis with precanine constriction, lower incisors lost, right and left tooth rows forming angle of 40° to 42° at the symphysis, lower canine premolariform, and adult teeth lacking enamel. This taxon demonstrates that *Odobenus* was in the western North Pacific as early as 500,000 years ago.

$$\text{Dentition: } \frac{?\text{I}, ?\text{C}, ?\text{P}, ?\text{M}}{0\text{I}, 1\text{C}, 1\text{+P}, ?\text{M}} \times 2$$

SUMMARY

Computer-assisted phylogenetic analysis of fossil and living odobenids supports the monophyly of the group and recognizes two principal clades, the Dusignathinae and the Odobeninae. This phylogenetic framework suggests that odobenids evolved during the middle Miocene in the North Pacific Ocean and diversified during the later Miocene, dispersing to the North Atlantic Ocean by the early Pliocene. The earliest odobenids lacked enlarged upper canines, confirming that "tusks do not a walrus make." Tusks evolved independently in the dusignathine and odobenine lineages. Dusignathine walruses developed enlarged lower as well as upper canines, while odobenines evolved the greatly enlarged tusks seen in modern *Odobenus*. The evolution for social display of these enormous structures is associated with many other modifications of the skull and mandible. This high degree of divergence is recognized in the naming of a new taxon, the Odobenini, which contains the fossil genera *Alachtherium*, *Pliopedia*, *Prorosmarus*, and *Valenictus* as well as modern *Odobenus*.

ACKNOWLEDGMENTS

I gratefully acknowledge Clayton E. Ray (USNM), Lawrence G. Barnes (LACM), and John A. Minch (John Minch & Associates) for allowing me to study specimens in their care. This report benefited from discussions with Annalisa Berta, Lawrence G. Barnes, Matthew W. Colbert, and Clayton E. Ray. Matthew W. Colbert, Clayton E. Ray, Charles A. Repenning, and Blaire Van Valkenburgh provided critical reviews of the manuscript.

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Phylogenetic Relationships of Platanistoid River Dolphins (Odontoceti, Cetacea): Assessing the Significance of Fossil Taxa

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ABSTRACT.—The superfamily Platanistoidea (*sensu* Simpson 1945) includes four extant monotypic genera of mostly freshwater dolphins (*Inia geoffrensis*, *Pontoporia blainvillei*, *Lipotes vexillifer*, and *Platanista gangetica*) and approximately 20 fossil species. Character states diagnosing the Platanistoidea are almost entirely primitive, thus uninformative in revealing phylogenetic relationships. Recent phylogenetic analyses question the monophyly of the group and suggest that some of the taxa are more closely related to members of the Delphinoidea (i.e., extant and fossil dolphins, porpoises, narwhals, and belugas). Studies of soft-anatomical characters, including nasal passage anatomy and facial musculature, have elucidated relationships within the extant Odontoceti but have not resolved the status of the Platanistoidea. Although soft-anatomical characters often cannot be inferred from fossils, fossil taxa improve resolution, especially within the Platanistoidea, for the following reasons: morphological diversity seen in these fossils provides insight into the variability and distribution of some osteological characters, some fossil families (e.g., the Squalodontidae and Eurhinodelphidae) have been proposed as the nearest relatives of at least some of the extant Platanistoidea, and some of these fossil taxa represent groups temporally close to the ancestral node, allowing more accurate resolution of the ancestral condition at the internal nodes of the cladogram. If these fossil families are closely related to the Platanistoidea, their exclusion from phylogenetic studies could lead to incorrect polarity assessment, incomplete views of character evolution, and specious conclusions of relationships. Fossil taxa sometimes have been used, however, when their monophyly or phylogenetic position within the Odontoceti were in question. Recognizing nonmonophyletic groups may effectively exclude taxa from the analysis, again decreasing the probability of recovering the true phylogeny. The best inference of phylogenetic relationships will ultimately come from consideration of all available data, including fossil taxa, molecular data, and soft-anatomical characters, analyzed with rigorous phylogenetic methods.

INTRODUCTION

Platanistoid (*sensu* Simpson 1945) river dolphins include four extant monotypic genera of mostly freshwater dolphins found only in the Amazon (*Inia geoffrensis*), Yangtze (*Lipotes vexillifer*), and Ganges and Indus (*Platanista gangetica*) river systems and a restricted area of the southwest Atlantic Ocean (*Pontoporia blainvillei*). Additionally, approximately 20 fossil species, excluding fragmentary material, have been regarded as closely related to river dolphins (Muizon 1987:13, 1988a:162). Currently, the river dolphins are among the most endangered of all cetaceans (Brownell et al. 1989), yet their basic biology, including their systematic relationships, remains poorly known.

The taxonomy of the river dolphins has fluctuated for more than 100 years. Some researchers (Flower 1867; Winge 1921; Slijper 1936; Simpson 1945) have proposed a monophyletic origin for river dolphins, placing the genera either into one family, the Platanistidae, or into separate families within the same superfamily, the Platanistoidea, the latter arrangement emphasizing their great morphological differences. Others (Gray 1863, 1866; Miller 1918, 1923; Kellogg 1928) have regarded the extant river dolphins as polyphyletic, generally placing *Pontoporia* within the Delphinidae. During the second half of this century the river dolphins' monophyly has been widely accepted (Hershkovitz 1966; Kasuya 1973; Pilleri et al. 1982; Zhou 1982; Barnes 1985; Barnes et al. 1985; Gaskin 1985; for opposing views see Rice 1977; Fordyce 1983), despite the characters diagnosing the group, such as a long, narrow rostrum and elongate mandibular symphysis, being demonstrably primitive or equivocal at the level of the Platanistoidea. Thus the monophyly of river dolphins has not been established on the basis of shared derived features. Recent phylogenetic analyses question it (Muizon 1984, 1987, 1988a, 1991; Heyning 1989) and suggest that some genera are more closely related to members of the Delphinoidea, which include the dolphins, porpoises, narwhals and belugas. Yet none of these analyses has attempted to incorporate all available data (i.e., some analyses have not included fossils as terminal taxa, while others have excluded soft-anatomical characters).

Both Heyning (1989) and Muizon (1984, 1987, 1988a, 1991) have attempted to reconstruct the phylogenetic relationships of odontocete whales by using cladistic methodology, yet each used quite different approaches. Heyning (1989) analyzed the relationships of extant families of odontocetes by using a large number of soft-tissue characters, while Muizon (1984, 1987, 1988a, 1991), using osteological characters, focused on fossil taxa. These studies have resolved some odontocete relationships, but some of their hypotheses conflict. It is not my objective in this paper to compare these hypotheses to detect the effects of fossil taxa in phylogenetic studies, as the studies differ not only in the inclusion or exclusion of fossils but also in the choice of characters included, method of polarity assessment, and use of computer-assisted programs to generate most parsimonious trees. These studies simply represent the current state of knowledge of the relationships of odontocete whales, within the context of which I investigate the effect of the exclusion of fossils in resolving river dolphin relationships.

I have taken data on fossil taxa from Muizon (1984, 1987, 1988a, 1991), although his inclusion of nonmonophyletic fossil taxa and use of fossil taxa with unresolved relationships may undermine his hypotheses, as will be seen below.

PREVIOUS CLADISTIC STUDIES

With the addition of fossil taxa into a phylogenetic analysis of the Odontoceti, Muizon (1984) concluded that the river dolphins are paraphyletic (i.e., not including all of the descendants of their most recent common ancestor). The fossil families included in his studies, such as the Squalodontidae, Squalodelphidae, and Eurhinodelphidae, are important in their being more diverse osteologically than any extant odontocete family. When included in an analysis with extant odontocetes, their unique combination of primitive and derived character states introduced a greater degree of character conflict and imposed topological changes in the phylogenetic hypotheses. Among the extant river dolphins, Muizon (1988a, 1991) retained only *Platanista* in the Platanistoidea (Fig. 1a, Platanistidae). He placed *Pontoporia* and *Inia* in the Inioidea, the sister taxon to the Delphinoidea, *Lipotes* in the Lipotoidea, the sister taxon to the clade including both the Inioidea and Delphinoidea.

Soft-tissue characters of the nasal passage complex, used by

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In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
Proc. San Diego Soc. Nat. Hist. 29:125–133, 1994

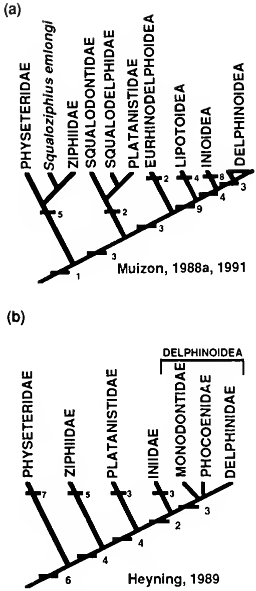

Figure 1. Alternative hypotheses of relationships of the Odontoceti. (a) Cladogram based on both extant and fossil taxa, redrawn from Muizon (1988a, 1991). The Inioidea include *Pontoporia* and *Inia*. (b) Cladogram based on 42 (including 18 soft-anatomical) characters of extant taxa only (from Heyning 1989). The Iniidae include *Inia*, *Lipotes*, and *Pontoporia*. Numbers next to bars indicate the number of synapomorphies supporting that clade.

Heyning (1989) in his analysis of extant odontocetes, also have resolved some relationships among extant odontocete families (Fig 1b). For example, Heyning (1989) cited the development of a vestibular sac as one of the synapomorphies (i.e., shared, derived character states) linking the Iniidae (including *Inia*, *Pontoporia*, and *Lipotes*) with the Delphinoidea to the exclusion of *Platanista*, also implying that the Platanistoidea (*sensu* Simpson 1945) are paraphyletic or polyphyletic. He did not address relationships within the Iniidae. Although both studies concluded that platanistoids are not monophyletic and separated *Platanista* from the remaining river dolphins, Heyning (1989) did recognize the other three river dolphins as a monophyletic taxon, the Iniidae, whereas Muizon (1988a) indicated that this grouping is itself paraphyletic. Nonetheless, Heyning (1989) stated that platanistoid relationships have not been resolved conclusively and emphasized the need for all platanistoid species to be reanalyzed.

Another and perhaps more significant difference in the two proposed hypotheses is in the relationship of ziphiids to physeterids. Four characters of the nasal passage (confluence of nasal passages, presence of a blowhole ligament, presence of premaxillary sacs, and development of the proximal sac into an inferior vestibule/nasofrontal sac/posterior nasal sac complex) were used by Heyning (1989) as synapomorphies uniting the Ziphiidae (beaked whales) with the clade including the Platanistidae (*Platanista* only), Iniidae, and Delphinoidea and excluding the Physeteridae. Soft-anatomical features were also among the character states he used to unite *Physeter* and *Kogia* into a monophyletic group, the Physeteridae (presence of a spermaceti organ and frontal and distal sacs), and to establish the monophyly of the Ziphiidae (presence of throat grooves). Yet Muizon (1984, 1991) recognized the Physeteridae and Ziphiidae as a monophyletic group. On the basis of features evident in fossil taxa, especially *Squaloziphius emlongi*, which he considered a ziphiid, Muizon (1984, 1991) determined that characters previously thought to be primitive for odontocetes, such as the absence of the lateral plates of the pterygoids, were derived in parallel in the clade including physeterids and ziphiids and the clade including the remaining odontocetes.

These examples demonstrate the need for a re-evaluation of the Platanistoidea, as well as odontocetes in general. Although neither soft-anatomical characters nor fossils resolved platanistoid relationships, the value of both has been clearly demonstrated.

EFFECTS OF EXCLUDING TAXA ON PHYLOGENY RECONSTRUCTION

Many have debated the usefulness of fossil taxa in phylogenetic analyses (Simpson 1961; Hennig 1966; Patterson 1981; Doyle and Donoghue 1987; Gauthier et al. 1988; Donoghue et al. 1989; Huelsenbeck 1991; Novacek 1992). While some (e.g., Simpson 1961) have advocated the special qualities of fossils, emphasizing ancestor–descendant relationships, others (e.g., Patterson 1981) have contended that fossils offer no additional information and should not affect the topology of a cladogram based solely on extant taxa. Yet Doyle and Donoghue (1987), in their phylogenetic analysis of angiosperms, and Gauthier et al. (1988), in their re-evaluation of amniote relationships, have demonstrated that the consideration of fossil taxa can affect hypothesized relationships dramatically. Huelsenbeck (1991), through the use of computer simulations, has proposed conditions under which fossils might provide both more and less resolution than extant taxa alone. According to Gauthier et al. (1988), "fossils should be most important in phylogenetic inference when the group of interest is old and only a few, highly modified, terminal taxa are extant." This statement agrees with Felsenstein's (1978) prediction that parsimony methods can be positively misleading (i.e., the method will not converge on the real phylogeny despite the addition of more data) in lineages in which the scaled lengths of branches leading to terminal taxa are much longer than those of internal branches. This situation is directly applicable to the river dolphins. Each of the four monotypic extant genera exhibits a unique combination of primitive and derived character states. In my own analyses, I have found for the river dolphins many more autapomorphies than characters elucidating relationships among them. These four extant species constitute less than 20% of the total number of known river dolphin species, even if only well-preserved fossil taxa are considered. Also, several families within the river-dolphin group, as defined by Muizon (1984) (e.g., Squalodontidae, Squalodelphidae), as well as in cetaceans in general [e.g., Archaeoceti, Eurhinodelphidae (= Rhabdosteidae), Cetotheriidae], are represented exclusively by fossil members, evidence that cetacean history conceals far more diversity than the order shows today. This lost diversity represents lost information.

Fossil taxa are important in systematics for the following reasons: first, fossil taxa may represent outgroups (i.e., taxa closely related to the group under study that are used to determine the direction of character evolution) phylogenetically closer to the ingroup than are extant forms. Similarly, fossil taxa, especially those temporally close to the ancestor, should be more representative of the condition at the ancestral node. If condition at the nodes are better known, the resulting phylogeny will better approximate the true phylogeny (Huelsenbeck 1991). Second, fossil taxa may provide information on intermediate character states, showing that some characters vary continuously, although they appear discontinuous in extant taxa. Without these fossil taxa such character states may be mistakenly interpreted as nonhomologous. Third, a fossil taxon that is a sister taxon of a living form may retain many plesiomorphic character states and may render alternative hypotheses of relationships more parsimonious (Doyle and Donoghue 1987; Gauthier et al. 1988; Donoghue et al. 1989). Potential problems resulting from the exclusion of fossil taxa can be illustrated by examples in platanistoid systematics.

Fossils as Outgroup Taxa

Outgroup taxa are used in phylogenetic analyses to determine the direction of character transformations, i.e., polarity of character states. If fossil taxa represent outgroups phylogenetically closer to the ingroup than any extant taxon, addition of these fossil taxa could change polarity assignments at the outgroup node. Because previous investigators have proposed that some river dolphins are more closely related to members of the Delphinoidea, the ingroup in investigations of the relationships of extant platanistoids must include the Delphinoidea. Therefore, the first outgroup should be the Ziphiidae, followed by the Physeteridae and, if necessary, the Mysticeti and terrestrial mammals (Heyning 1989). In Muizon's (1984, 1987, 1988a, 1991) studies including fossil taxa, the Agorophiidae (*sensu* Fordyce 1981), Squalodontidae, Squalodelphidae, and Eurhinodelphidae represent fossil groups more closely related to the ingroup than are some of the extant outgroups. The effect that these additional fossils can have on polarity assessment is illustrated by a particularly interesting and complex structure in cetaceans, the pterygoid bone.

Cetaceans possess a pterygoid that, in some members, is divided into medial and lateral lamina (Fig. 2). The condition of the lateral lamina of the pterygoid, extending posteriorly beyond the level of the pterygoid hamulus, varies widely in the Odontoceti, especially among some of the extant river dolphins, and homologies are unclear (Cozzuol 1989a). For this example, however, I will assume that all lateral lamina are homologous. The presence of the lateral lamina of the pterygoid has been interpreted as both plesiomorphic (Fraser and Purves 1960; Muizon 1984; Fordyce 1985) and apomorphic (Barnes 1985; Cozzuol 1989a). This character can be polarized differently depending on whether or not fossil taxa are considered (Figs. 3a, b). Among extant taxa, the lateral plate is present in mysticetes (Fraser and Purves 1960), *Platanista gangetica*, *Pontoporia blainvillei*, some species of the Phocoenidae (e.g., *Phocoenoides dalli*), and some individuals of *Lagenorhynchus albirostris* (Cozzuol 1989a). The pterygoids of the earliest-diverging extant odontocetes, the Physeteridae and Ziphiidae, lack a lateral lamina. The lateral lamina of mysticetes, creating a shallow fossa in the posterior margin of the pterygoid (Fraser and Purves 1960), differs greatly from that of any extant odontocete and may not be homologous. Therefore, by the outgroup method of Maddison et al. (1984), the lateral lamina of extant odontocetes is derived (Fig. 3a). Among fossil taxa, the pterygoid bears a lateral lamina in archaeocetes, agorophiids, ziphiids (*Squaloziphius emlongi*), squalodontids, squalodelphids, platanistids (*Zarhachis* and *Pomatodelphis*), and eurhinodelphids. If the structures are homologous and some of the fossil taxa are more closely related to the ingroup than to any extant outgroup taxon, as Muizon (1991) has suggested, the fossil taxa imply that the lateral lamina of the pterygoid could be primitive in the clade including the river dolphins and Delphinoidea (Fig. 3b).

Similarly, the size of the posterior process of the tympanic bulla is a character whose polarity can be interpreted differently when fossil taxa are included in or excluded from phylogenetic analysis. The tympanics of the Physeteridae and Ziphiidae (and Mysticeti) exhibit a large posterior process that becomes incorporated into the cranium between the squamosal and the exoccipital suture and is visible on the exterior of the skull. All other extant odontocetes except *Platanista* exhibit a much smaller posterior process that is no longer visible on the exterior of the cranium; *Platanista* has a posterior process somewhat intermediate in size. Outgroup comparison of extant taxa only implies that the large posterior process of the tympanic of physeterids, ziphiids, and mysticetes is primitive and the small posterior process is derived. Muizon (1984), however, found that the posterior process of *Platanista* resembles that of agorophiids and considered this moderately small posterior process as the plesiomorphic condition in odontocetes. Therefore, he considered the enlarged posterior process of physeterids and ziphiids derived, constituting a synapomorphy uniting the two families and and their fossil relatives into a monophyletic group. He considered the much smaller process of the Lipotoidea, Inioidea, and Delphinoidea to be a derived condition representing a synapomorphy of that clade.

A character traditionally used to unite the river dolphins is their elongated mandibular symphysis. Indeed, all of them possess a mandibular symphysis measuring over one-half of the total length of the mandible. Heyning (1989), however, found that agorophiids, eurhinodelphids, and *Steno* (a delphinid) also possess elongated mandibular symphyses. Because the origin and taxonomic distribution of an elongated mandibular symphysis was unclear, Heyning gave it less weight, though he considered this character derived, having evolved independently three times, in Physeteridae, Platanistidae, and Iniidae. If the relationships of fossil and extant odontocetes proposed by Muizon (1988a, 1991) are correct and the elongated mandibular symphysis is derived, the character must have evolved independently seven times, in agorophiids, physeterids, eurhinodelphids, platanistids, *Lipotes*, iniids, and *Steno*. If the elongated symphysis is primitive for toothed whales, however, its independent loss in *Kogia*, ziphiids, and delphinioids and reappearance in *Steno* requires only five steps. With the addition of fossil taxa it is no longer more parsimonious to use the presence of an elongated mandibular symphysis to unite any of the river dolphin species.

Fossil Taxa and Increased Diversity of Character States

Fossil taxa can also affect phylogenetic inferences because additional information on intermediate states of characters seen in some fossils may be used to link taxa that had not been considered closely related. Extant taxa may be highly derived, with homologous features lost or difficult to detect. Fossil taxa may illustrate the variability of some characters, aiding in determining their homologies. For example, *Platanista* and its fossil relatives exhibit an articular process on the periotic bone. This process is associated with a fossa in the squamosal bone and, in some taxa (e.g., the Platanistidae), fits so tightly into the fossa that the periotic cannot be removed without breaking the process. A similar process seen in another fossil family, the Eurhinodelphidae, appears to be homologous. *Zarhachis*, a fossil platanistid, however, exhibits both the articular process and the process seen in the Eurhinodelphidae, indicating that these processes may not be homologous (Muizon 1987).

Some fossil taxa, such as the Squalodontidae, exhibit intermediate or additional character states not seen in any extant taxon. Two

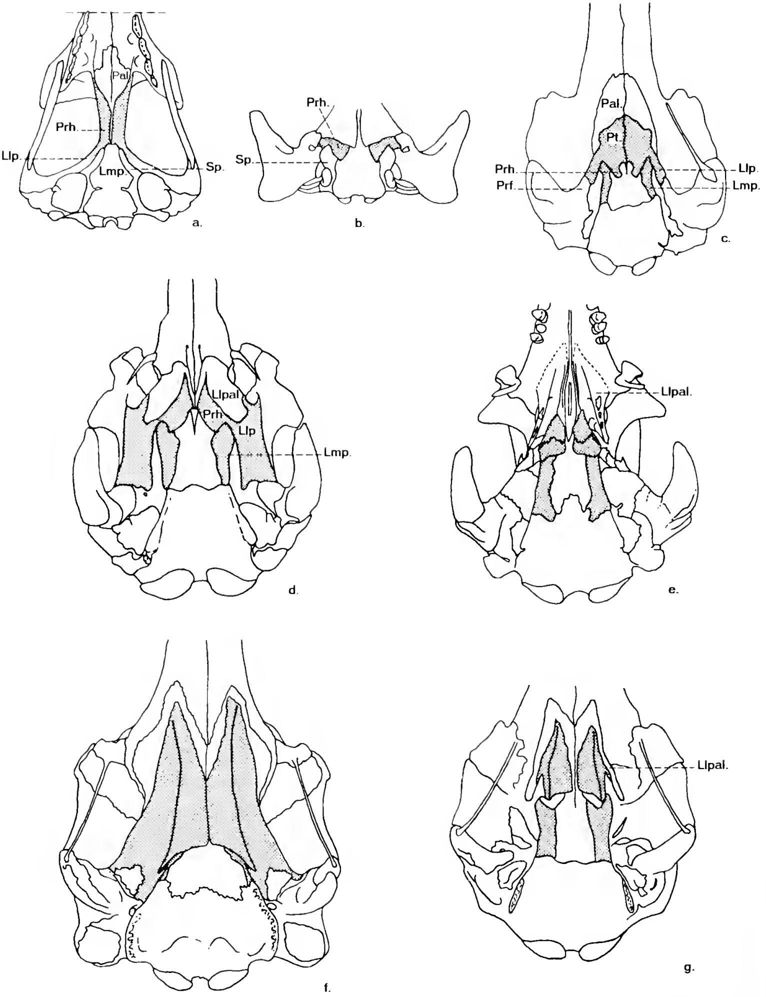

Figure 2. Ventral view of skulls showing different morphologies of the pterygoid and palatine bones in several species of cetaceans (modified from Muizon 1984). (a), Archaeocete (*Zygorhiza kochii*); (b), mysticete (*Balaenoptera musculus*); (c), eurhinodelphid (*Eurhinodelphis bossi*); (d), *Pontoporia blainvillei*; (e), *Inia geoffrensis*; (f), ziphiid (*Mesoplodon bidens*); (g), delphinid (*Lissodelphis peroni*). Llp, lateral lamina of the pterygoid; Llpal, lateral lamina of the palatine; Lmp, medial lamina of the pterygoid; Pal, palatine; Prf, falciform process; Prh, hamular process; Pt, pterygoid process; Sp, pterygoid sinus.

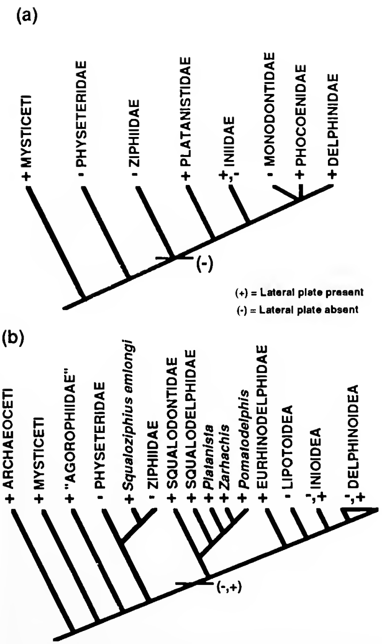

Figure 3. Distribution of states (in parentheses) of the lateral plate of the pterygoid in representative cetaceans. +, plate present; —, plate absent. (a), Cladogram based on extant taxa only (from Heyning 1989). At the outgroup node (bar) the plate is absent. (b) Cladogram based on both both fossil and extant taxa (from Muizon 1991). At the outgroup node presence or absence of the plate is equivocal.

characters, a subcircular fossa in the squamosal bone and an articular process of the periotic, are unique to the Platanistoidea (*sensu* Muizon 1987, 1991). The deep subcircular fossa is positioned posteromedial to the postglenoid process of the squamosal and dorsal to the periotic. It may be a result of the expansion of the peribullary sinus, a basicranial air sinus that surrounds the periotic and tympanic bones (Muizon 1987). The articular process, discussed above, is found on the lateral surface of the periotic at the junction between the posterior process and the body of the periotic. This process articulates with a fossa in the squamosal bone at the base of the postmeatal process. These characters are well developed in *Platanista*, fossil platanistids (*Zarhachis* and *Pomatodelphis*), and the Squalodelphidae. According to Muizon (1987), they occur in some members of the Squalodontidae (e.g., *Squalodon* and *Eosqualodon*) but are much less developed. Nonetheless, these characters have been used as synapomorphies diagnosing the Platanistoidea, as defined by Muizon (1987, 1991). In a phylogenetic analysis of extant taxa only, these characters would be considered autapomorphies of *Platanista*, thus offering no information about the phylogenetic relationships of *Platanista* within the Odontoceti. One important phylogenetic implication of this inclusion of fossil taxa (Muizon 1984,1987) is that it is no longer most parsimonious to retain *Platanista*, with its presumed fossil relatives (*Zarhachis*, *Pomatodelphis*, Squalodelphidae, and Squalodontidae), in the clade including the remaining river dolphins.

Fossils as Sister Taxa Retaining Plesiomorphic Characters

Fossils may affect the topology of a cladogram if they represent sister taxa retaining plesiomorphies. As discussed above, the evidence of fossils led Muizon (1987, 1991) to unite *Platanista* with *Zarhachis*, *Pomatodelphis*, the Squalodelphidae, and Squalodontidae and separate it from the remaining river dolphins, the Inioidea and Lipotoidea. He hypothesized that the Squalodontidae and Squalodelphidae are the sister taxa of *Platanista*, *Zarhachis*, and *Pomatodelphis* (Figs. 4a, b). Muizon (1987,1991) proposed this relationship on the basis of derived characters (e.g., subcircular fossa of the squamosal bone, articular process of the periotic), yet the Squalodontidae are otherwise primitive. To include *Platanista* and its fossil relatives in a clade with the remaining river dolphins implies a great number of reversals in the fossil taxa (Fig. 4a). For example, 12 characters of the Squalodontidae, such as heterodont dentition and unfused lacrimal and jugal bones, would have to be considered reversals. As a consequence, *Platanista*, with its fossil relatives, has been placed as the sister taxon to the clade including the Eurhinodelphidae, Lipotidae, Iniidae, and Delphinoidea (Fig. 4b). This arrangement implies that the characters shared by the platanistids, *Lipotes*, and *Inia* are convergences or plesiomorphies.

These examples illustrate that fossil taxa can indeed have a significant impact on the topology of a cladogram and should be considered in cladistic analyses.

ALTERNATE METHODS OF PHYLOGENETIC RECONSTRUCTION

Application of correct phylogenetic methodology (Hennig 1966; Eldredge and Cracraft 1980; Wiley 1980) is necessary to avoid erroneous inferences of relationships. Proper cladistic methodology includes the use of monophyletic groups as operational taxonomic units, polarization of characters on the basis of comparison with at least two outgroups that consist of the taxa most closely related to the ingroup (Watrous and Wheeler 1981; Maddison et al. 1984), and the use of computer-assisted algorithms (e.g., PAUP; Swofford 1990), especially when data sets are large or characters are inconsistent. To date, only one phylogenetic study (Heyning 1989) addressing platanistoid relationships has employed a computer program (PAUP, version 2.4.1), and it did not present a published matrix of character-state assignments. Any attempt to reproduce the results of such an analysis requires that such a matrix be reconstructed on the basis of character descriptions in the text that are not always complete. Very few studies sufficiently describe character states to the species level or describe intraspecific polymorphism, both of which are necessary for accurately reconstructing character matrices. Other studies (Muizon 1984, 1987) have included nonmonophyletic taxa (e.g., the Squalodontidae) or have used alternative, less reliable methods to polarize characters, such as assuming earlier taxa are more primitive. The following examples illustrate these problems in platanistoid systematics.

A significant problem in recognizing a nonmonophyletic taxon is that some members of that taxon may be more closely related to

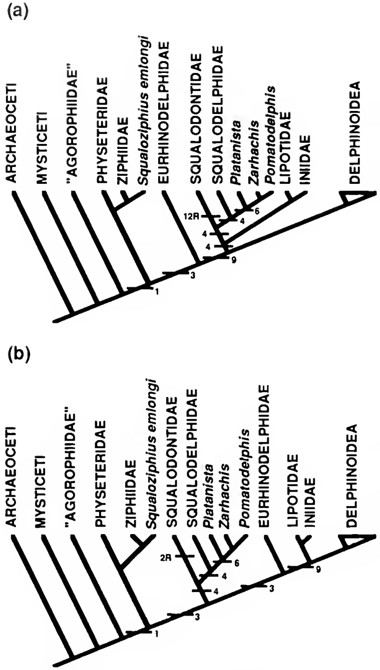

Figure 4. Alternative phylogenetic positions of *Platanista* and its fossil relatives (modified from Muizon 1988a, 1991). Muizon (1984, 1988a, 1991) has proposed that fossil taxa Squalodontidae and Squalodelphidae are most closely related to Platanistidae (*Platanista*, *Zarhachis*, and *Pomatodelphis*). Numbers, number of synapomorphies; R, reversals. (a), River dolphins constituting a monophyletic group, implying 12 reversals in the Squalodontidae. (b) It is more parsimonious to remove *Platanista* and its fossil relatives from the remaining river dolphins and place them as the sister taxon to the clade including the Eurhinodelphidae, Lipotidae, Iniidae, and Delphinoidea.

the ingroup than others. Not recognizing those members separately could have the same effect as excluding them from the analysis. Also, since a nonmonophyletic taxon can contain members of more than one monophyletic group, if the taxon is polyphyletic, such taxa may appear misleadingly diverse. As mentioned earlier, the increased diversity of character states seen in fossils can be useful in establishing homologies or uniting taxa. If these groups are nonmonophyletic, however, they could confound rather than resolve phylogenetic relationships. Alternatively, a paraphyletic taxon, by definition not including all descendants of a common ancestor, may appear misleadingly uniform. Since most phylogenetic studies of river dolphins (Muizon 1984, 1987, 1988a, 1991) have considered nonmonophyletic taxa, these problems need to be addressed.

Groups such as the Agorophiidae, Squalodontidae, and Eurhinodelphidae have not been demonstrated to be monophyletic but rather have been defined by plesiomorphic character states. Additionally, *Squaloziphius emlongi*, considered by Muizon (1991) to be an important early diverging ziphiid, is considered by others not to be closely related to the Ziphiidae (Heyning pers. comm.). Several of these taxa are considered by some researchers (Fordyce 1985) to be grades, and they are very possibly paraphyletic. The Agorophiidae and Squalodontidae, often described as primitive odontocetes, include stratigraphically early fossil taxa united largely by plesiomorphies such as heterodont dentition and incompletely telescoped skulls. Several of the taxa included in these families are represented by only fragmentary material. To date, no diagnosis of the Agorophiidae on the basis of derived character states has been attempted, and the group is in much need of study. Nevertheless, it has been used as an outgroup taxon in studies of platanistoid relationships (Muizon 1984, 1991; Heyning 1989).

Although Muizon (1987) stated that the Squalodontidae could be nonmonophyletic, he included that family in his redefinition of the Platanistoidea as the sister taxon of the Squalodelphidae and Platanistidae. The Squalodontoidea, as defined by Winge (1921), Rice (1967), Rothausen (1968), and Barnes (1985), include the Agorophiidae. Fordyce (1985) stated not only that agorophiids did not share a most recent common ancestor with squalodontids, but also that some genera within the Squalodontidae are more closely related to other taxa, such as the Squalodelphidae and Platanistidae. Cozzuol (1989b) believed the Squalodontidae to be polyphyletic and, in an attempt to resolve this problem, removed *Prosqualodon* from the family while including the eurhinodelphids. Later, Muizon (1991) proposed that a subset of the genera he had previously placed in the family (Muizon 1987) form a clade. The status of the Squalodontidae is still not completely resolved.

The monophyly of the Eurhinodelphidae is also in question and requires further study. Although Fordyce (1985) stated that this family has not been diagnosed on the basis of derived character states, Muizon (1991) listed one synapomorphy for it, lengthening of the premaxillary portion of the rostrum such that the rostrum extends farther anteriorly than the mandible. Another problematic family, the Acrodelphidae (*sensu* Abel 1905), contains species that have been placed in the Eurhinodelphidae or as the sister taxon to the Eurhinodelphidae (Muizon 1988b).

This also brings into question the monophyly of the Acrodelphidae. Barnes (1985) defined the family as including *Schizodelphis*, *Pomatodelphis*, and probably *Zarhachis* but recommended re-evaluation of it. Muizon (1988b) stated that the family had traditionally included *Acrodelphis*, *Schizodelphis*, *Eoplatanista*, *Champsodelphis*, and, according to some researchers, *Pomatodelphis* and *Zarhachis*. In his revision, he broke up the family Acrodelphidae, restricting it to the type specimen of *Acrodelphis* and leaving it as *incertae sedis*. He placed *Schizodelphis sulcatus* into the Eurhinodelphidae, stated that *Acrodelphis* is a junior synonym of *Champsodelphis*, placed *Acrodelphis ombonii* into a new genus, *Dalpiazina* [subsequently proposing it as a possible sister taxon to Squalodontidae (Muizon 1991)], placed *Champsodelphis tetragorhinus* into a new genus, *Medocinia*, included in the Squalodelphidae, and placed *Pomatodelphis* and *Zarhachis* into the Platanistidae. This example underscores the need for a re-evaluation at all levels. Under such circumstances where the taxonomy appears to be very unstable, it is best to disregard the current classification and regard each species, or specimen, as a separate operational taxonomic unit.

Not only is the monophyly of several taxa in question, so are their phylogenetic positions within the Odontoceti. This can cause problems in determining appropriate outgroups and reconstructing character states at ancestral nodes. Some workers (Barnes 1985; Fordyce 1985; Cozzuol 1989b) have stated that at least some squalodontids represent an early-diverging lineage within the Odontoceti. At least three alternative branching sequences of the Squalodontidae have been suggested (Fig. 5): (1) as the sister taxon to the clade including the Platanistidae and Squalodelphidae (Muizon 1987, 1991); (2) as the sister taxon to the Ziphiidae (Fordyce 1985); (3) as one of the earliest diverging lineages within the Odontoceti (Barnes 1985; Cozzuol 1989b; Heyning 1989). If at least some members of the Squalodontidae are demonstrated to have diverged before the Physeteridae and/or Ziphiidae, this again could change polarity assignments for lineages branching off subsequently and ultimately may affect the topology of the cladogram.

Similarly, the Eurhinodelphidae (Fig. 6) have been suggested as (1) the sister taxon to the Delphinida (*sensu* Muizon 1988a), which include the Iniidae, Lipotidae, and Delphinoidea (Muizon 1988a); (2) an early-diverging lineage that may have originated within the Squalodontidae (Barnes 1985; Cozzuol 1989b); or (3) members of the family Delphinidae (Kellogg 1928). Fordyce (1983) mentioned similarities between eurhinodelphids and platanistids but concluded that further study is required to determine if these similarities are synapomorphies. These radically different hypotheses of relationships emphasize the need for more study of this group. Misplacement of the Eurhinodelphidae or its recognition as a nonmonophyletic family could lead to incorrect polarity assignments.

As has been demonstrated earlier, appropriate choice of the outgroups serving as the basis for character polarity is vital to inferring phylogenetic relationships. The outgroup-comparison method has been demonstrated to be the most objective method for determining character-state polarity (Watrous and Wheeler 1981). When possible, more than one outgroup should be used and the branching sequence of outgroups should be determined on the basis of shared, derived features. Yet several cladistic studies have failed to polarize character states on the basis of more than one outgroup (e.g., Barnes 1985). Others often have resorted to the stratigraphic record, generally looking at the stratigraphically earliest members of the ingroup to assign polarities (Muizon 1984, 1987, 1988a, 1991). When fossil taxa within the ingroup are used, characters may be polarized incorrectly and the resulting phylogenetic relationships may be based on shared primitive characters.

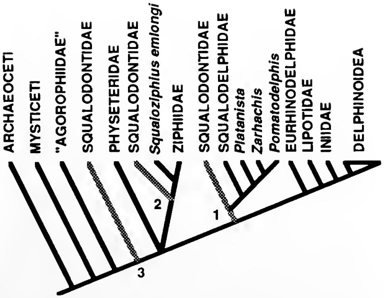

Figure 5. Alternative phylogenetic positions of the Squalodontidae, as proposed by various researchers. The family represents (1) the sister taxon of the Squalodelphidae and Platanistidae (Muizon 1987, 1991), (2) the sister taxon of the Ziphiidae (Fordyce 1985), or (3) an early-diverging lineage of odontocetes (Barnes 1985; Cozzuol 1989b; Heyning 1989).

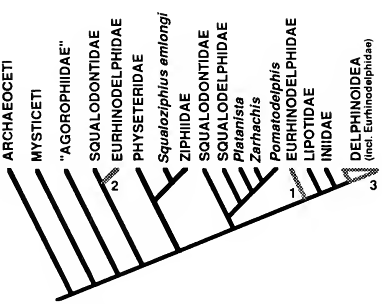

Figure 6. Alternative phylogenetic positions of the Eurhinodelphidae, as proposed by various researchers. The family represents (1) the sister taxon of the Delphinida (Muizon 1988a, 1991), (2) an early-diverging lineage originating within the Squalodontidae (Barnes 1985; Cozzuol 1989b), or (3) a subset of the Delphinidae (Kellogg 1928).

Finally, computer-assisted programs (e.g., PAUP, Swofford 1990) should be used to analyze phylogenetic relationships. The assumptions (e.g., whether or not characters were ordered or weighted) made during the computer analyses should be described. The matrix of character states used in the computer analysis should also be published. If character-state matrices cannot be reproduced accurately from the descriptions given in the text of a published phylogenetic analysis, the results of the analysis are not reproducible.

DISCUSSION

Clearly, much work still needs to be done before the phylogenetic relationships of many odontocete taxa are sufficiently understood. The problems regarding the phylogenetic position and/or monophyly of some fossil taxa, however, do not negate their importance in phylogeny. As the phylogenetic relationships of the earliest diverging lineages become further resolved and monophyletic groups are identified, assessments of character polarities and hypotheses of character evolution will change. This is especially relevant for cetaceans and river dolphins in particular, of which a large proportion of the species are extinct. It is important not to attribute special qualities to fossils or to overlook the inherent biases of the fossil record. The fossil record of cetaceans is skewed, since most fossil taxa are found in deposits originating in shallow seas or estuaries and very few pelagic species are known. The selective preservation of certain bony elements, such as periotic bones or teeth, is another source of bias. Fossils inherently lack certain characters available in extant taxa, such as soft tissue and DNA. As Heyning (1989) showed, such characters also provide important information for resolution of phylogenetic relationships and should be included in data sets even though they are lacking from fossil material. Lack of certain characters is not restricted to fossil taxa. Extant taxa may be effectively incomplete if some of their characters are so highly derived that homologies cannot be determined (e.g., nasal sacs of physeterids versus other odontocetes). The addition of fossil taxa will generally increase the number of missing characters in the data matrix. Missing character data will increase the number of equally parsimonious trees but should not give misleading trees. The increase in the number of equally parsimonious trees may be disconcerting; however, the quality of a phylogeny should not be based on its recovering a single most parsimonious tree, since that can be accomplished with relatively high reliability with randomized data, at least with molecular data (Hillis 1991; Hillis and Huelsenbeck 1992). The best approximation of phylogenetic relationships should consider all available data, including fossil taxa and soft-tissue characters, analyzed with rigorous and testable cladistic methodology.

ACKNOWLEDGMENTS

I especially thank A. Berta, D. Archibald, J. McGuire, L. Grismer, P. Mabee, R. Etheridge, and M. Simpson for thoughtful discussions and for helping me develop my ideas in the preparation of the manuscript. An earlier draft of this paper was improved through the comments of A. Berta, T. Deméré, J. McGuire, L. Grismer, and three anonymous reviewers. I thank J. Mead, C. Potter, T. Deméré, P. Unitt, S. Bailey, T. Daeschler, W. Fuchs, for lending or providing access to specimens used in this study. This work was funded in part by grants from the Society of Sigma Xi (Grant-in-Aid of Research), the Smithsonian Institution (Graduate Student Fellowship), the American Museum of Natural History Lerner–Gray Fund for Marine Research, and the Department of Biology at San Diego State University.

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Are the Squalodonts Related to the Platanistoids?

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ABSTRACT.—Traditionally, the superfamily Platanistoidea (Odontoceti, Cetacea) includes the four families of living river dolphins: the Platanistidae, Iniidae, Pontoporiidae, and Lipotidae. New studies regard the Platanistoidea as polyphyletic and classify the Iniidae, Pontoporiidae, and Lipotidae in the infraorder Delphinida, which also includes the Delphinoidea. Previously, I suggested that the Platanistidae, Squalodelphidae, Squalodontidae, and *Prosqualodon* are closely related and together form a monophyletic superfamily Platanistoidea. Here, I test the platanistoid affinities of the squalodonts by examining the possibility of close relationships with other groups of odontocetes such as the Delphinida, the Physeterida (more precisely the Ziphioidea), and the Eurhinodelphidae. For each grouping, several features regarded as key characters in odontocete phylogeny are considered and an attempt is made to establish synapomorphies with the Squalodontidae. However, none of the possible synapomorphies that could contradict the placement of the Squalodontidae within the Platanistoidea is satisfactory because either they are symplesiomorphies or the structures compared are nonhomologous. Furthermore, none of the synapomorphies that relate the Squalodontidae to the Platanistoidea have been observed in the other three groups. Consequently, no argument is found contradicting the platanistoid affinities of the Squalodontidae without considerably increasing the number of convergences. Several archaic odontocetes, including *Agorophius*, *Archaeodelphis*, *Xenorophus*, *Patriocetus*, and *Microzeuglodon* have not been included in the Platanistoidea mainly because diagnostic platanistoid features are not observable, either because of incompleteness or inadequate specimen preparation. It is probable that these archaic odontocetes do not belong to the Platanistoidea but represent early branches in the evolution of odontocetes. Further studies and discoveries are needed to clarify this point.

INTRODUCTION

The family Squalodontidae (*sensu* Simpson 1945) is a group of odontocete cetaceans that lived worldwide during the Oligocene and Miocene. Remains of squalodonts are especially abundant in upper Oligocene and lower to middle Miocene rocks of Europe (Jourdan 1861; Paquier 1894; Capellini 1903; Dal Piaz 1904, 1916; Gemmelaro 1920; Rothausen 1968), Asia (Mchedlidze 1984), North and South America (Lydekker 1894; Kellogg 1923; Cabrera 1926), Australia and New Zealand (Hall 1911; Benham 1935; Flynn 1948). Although abundant, squalodont remains are seldom well preserved. Complete or nearly complete skulls and/or skeletons are uncommon, and several generic names assigned to squalodonts are based on species whose type specimens are too incomplete to allow a meaningful comparison and, consequently, a reliable determination. Many species of squalodonts are based upon isolated teeth or jaw fragments that are inadequate for accurate determination given the high individual and interspecific variability of cetaceans. Although skull elements or partial skulls may be sufficient in other groups of cetaceans, because of the scarcity of derived features in squalodonts, very complete skulls are necessary in this group to provide an adequate basis for comparison. Furthermore, since several key features in odontocete phylogeny are related to the auditory region, that region should be known in association with the skull in the specimens used for phylogenetic reconstructions. For those reasons only five genera (*Squalodon*, *Eosqualodon*, *Kelloggia*, *Phoberodon*, and *Prosqualodon*) of the family Squalodontidae were considered in a previous phylogenetic analysis (Muizon 1991). These genera are represented by complete or nearly complete skulls and, in part, by nearly complete skeletons.

Furthermore, as noted above, the family Squalodontidae is a conservative group that retains several primitive features of the skull and postcranial skeleton. Derived characters appear to be rare, and the synapomorphies used to diagnose this family (Muizon 1991) could probably be interpreted as independent acquisitions in the various taxa and, if considered alone, are not very satisfactory.

These difficulties, related to the preservation of the specimens or inherent in the group, have made the understanding of squalodont relationships complex and contentious. Because of their lack of obviously derived characters, squalodonts have been placed with various groups of odontocetes. Abel (1914) regarded the Squalodontidae as descendants of the Agorophiidae and ancestors of the Physeteridae, Ziphiidae, Eurhinodelphidae, and Platanistidae (= Platanistoidea *sensu* Simpson 1945). Slijper (1936), contrary to Abel, regarded the Squalodontidae as ancestral to the Delphinidae (= Delphinoidea *sensu* Muizon 1988a) as well as to the Eurhinodelphidae and Platanistidae, and Rothausen (1968) admitted that the Delphinoidea and Platanistoidea had their origin in the Squalodontidae. In the phylogeny proposed by Thenius (1969), relationships among taxa are unclear, although he indicated that the Delphinoidea, Eurhinodelphidae, and Platanistidae are more closely related to the Squalodontidae than to the Physeteridae and Ziphiidae. Barnes et al. (1985) directly associated the Delphinoidea, Squalodelphidae, and Eurhinodelphidae with the Squalodontidae, whereas they did not recognize close relationships with the Platanistoidea, Ziphiidae, and Physeteroidea. Barnes (1990:20) regarded the Squalodontidae as the sister group of the Squalodelphidae, and he considered the Squalodontidae, Squalodelphidae, and Eurhinodelphidae (= Rhabdosteidae *sensu* Barnes 1990) as a monophyletic group that is the sister group of the Delphinoidea. The cladogram presented by Barnes (1990:20) can be a better basis for discussion than the phylogenetic tree of p. 10 of the same paper, as the author lists numerous characters to justify his position. He presented no character analysis, however, and the previous works (Kasuya 1973; Zhou 1982; Muizon 1984, 1985, 1987, 1988a,b; Heyning 1989) on that topic are not taken into account, although some characters listed by Barnes were described and mentioned as synapomorphies in some of these works.

The Agorophiidae have often been considered as either the primitive sister group of the Squalodontidae (Slijper 1936; Thenius 1969; Barnes et al. 1985) or ancestral to them (Abel 1914; Dal Piaz 1977). Winge (1921) included *Agorophius* within the Squalodontidae, and Rothausen (1968) regarded *Agorophius* as a member of the superfamily Squalodontoidea along with *Patriocetus*, *Microzeuglodon*, and *Agriocetus*. *Patriocetus* was erroneously regarded as a mysticete by Abel (1914) and Winge (1921). Whitmore and Sanders (1977) and Fordyce (1981) reviewed these primitive odontocetes and did not include them in the Squalodontidae. The family Agorophiidae has been restricted by Fordyce (1981) to include only *Agorophius pygmaeus*; however, several undescribed taxa that probably belong to this family are known.

Recently, I have discussed odontocete relationships (Muizon 1984, 1985, 1987, 1988a, 1991) and have interpreted the Platanistoidea (*sensu* Simpson 1945) as a polyphyletic group. The Platanistoidea (*sensu* Muizon 1984, 1987, 1991; Heyning 1989) are a monophyletic group represented by one living and several fossil taxa (see below). In previous works I have classified the Squalodontidae in the Platanistoidea (Muizon 1984, 1987, 1991).

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
Proc. San Diego Soc. Nat. Hist. 29:135–146, 1994

The purpose of this paper is to test this hypothesis by comparing it to alternative hypotheses of relationships with the Delphinida, the Physeterida, and the Eurhinodelphidae. In the following sections the terms Platanistoidea, Platanistidae, Squalodontidae, Squalodelphidae, Eurhinodelphidae, Physeterida, Physeteroidea, Physeteridae, and Ziphiidae are used *sensu* Muizon (1988b, 1991). My interpretation of platanistoid relationships and the character analysis that justifies it have already been presented elsewhere (Muizon 1984, 1985, 1987, 1988a, 1991). The cladogram presented in Figure 1 summarizes the main relationships among odontocetes I proposed previously.

Abbreviations.—AMNH, American Museum of Natural History, New York, USA; IGUP, Geological Institute of Padua University, Italy; MHNG, Muséum d'Histoire naturelle de Grenoble, France; MHNL, Muséum d'Histoire naturelle de Lyon, France; MNHN, Muséum national d'Histoire naturelle, Paris, France; MLP, Museo de la Plata, Argentina; USNM, United States National Museum of Natural History, Washington, D.C., USA.

SQUALODONTIDAE AND PLATANISTOIDEA

I have previously included the Squalodontidae within the Platanistoidea (Muizon 1987, 1991). Traditionally, this superfamily was regarded as a monophyletic group including the four living genera of river dolphins, *Platanista*, *Inia*, *Pontoporia*, and *Lipotes* (Winge 1921; Kellogg 1928; Slijper 1936; Simpson 1945; Hershkovitz 1966; Kasuya 1973). The authors of even recent works (Zhou 1982; Barnes 1985; Barnes et al. 1985; Barnes 1990), though disputing the position of genera within the superfamily, all accept the monophyly of the Platanistoidea (*sensu* Simpson 1945).

In a recent revision of fossil and living odontocetes, I concluded that this was not the case and that the only extant taxon that should be included in the family Platanistidae is *Platanista* (Muizon 1984, 1987). *Inia*, *Pontoporia*, and *Lipotes* should be classified within the Delphinida, mainly on the basis of several synapomorphies of the auditory and pterygoid regions (Muizon 1988a). It is noteworthy that Heyning (1989:33, 56–57), using different characters (including some of the soft parts), proposed a nearly identical interpretation, providing an independent test of my earlier hypothesis (Muizon 1984, 1985, 1987, 1988a).

The Platanistoidea (*sensu* Muizon 1984, 1987, 1991) include three or possibly four families: the Platanistidae, Squalodelphidae, Squalodontidae, and possibly Dalpiazinidae (Muizon 1987, 1988b, 1991). The Platanistidae include *Platanista*, *Zarhachis*, and *Pomatodelphis*. The Squalodelphidae include *Squalodelphis*, *Notocetus*, *Phocageneus*, and *Medocinia* (Muizon 1987, 1988b). Four genera, namely, *Squalodon*, *Kelloggia*, *Eosqualodon*, and *Phoberodon*, are preserved well enough to be recognized as belonging to the Squalodontidae (Muizon 1991).

The genus *Prosqualodon*, which lacks the synapomorphies of the squalodontid–squalodelphid–platanistid clade but possesses platanistoid synapomorphies (see Muizon 1991 and below), has been excluded from the Squalodontidae and is regarded as the sister group of all other Platanistoidea (Fig. 1).

Neosqualodon is probably a derived squalodont, but since none of the platanistoid features could be observed on the specimens referred to that genus (Dal Piaz 1904; Gemmellaro 1920), I do not include it in the family. Moreover, it is also possible that *Neosqualodon* does not belong in the Platanistoidea.

Sulakocetus, from the late Oligocene of the Caucasus, does not have the platanistoid synapomorphies of the scapula (see below) and consequently cannot be classified in this group. Judged from the illustrations provided by Mchedlidze (1984:pl. XIII) and Pilleri (1986:pl. V, 2), the premaxillae of *Sulakocetus* have a thickened

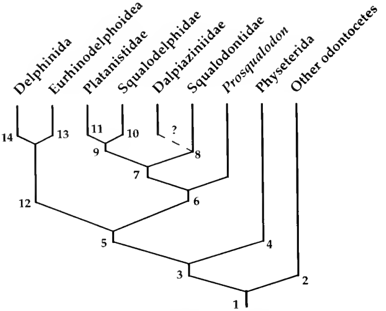

Figure 1. Phylogenetic relationships of the major groups of odontocetes. 1, Maxillae covering partially or totally the supraorbital processes of the frontals; large premaxillary foramina; posterior extension of the premaxillae contacting the frontals. 2, The designation "other odontocetes" refers to the early-diverging members of the order, including *Agorophius*, an undescribed agorophiid (USNM 256517), *Archaeodelphis*, *Microzeuglodon*, and *Xenorophus*, which have a less-telescoped skull and almost certainly do not represent a monophyletic taxon. 3, Posterior extension of maxillae and frontals, which almost contact occipital posteriorly, almost totally exclude the parietals from the dorsal surface of the skull (they do not articulate on the dorsal surface of the skull and often do not articulate at all), cover the temporal fossa, form a continuous crest (temporal crest) from the postorbital process to the nuchal crest, and demarcate a small square or trapezoidal frontal window on the vertex. 4, For definition of the Physeterida (Physeteroidea + Ziphoidea) see Muizon (1991). 5, Reduction of posterior process of tympanic, which is not exposed on exterior of skull in lateral view; development of posterior sinus; development of anterior spine on tympanic with salient anterolateral convexity separated from spine by a marked notch. 6, Reduction or loss of coracoid process on scapula; acromion located on anterior edge of scapula; diappearance of supraspinatus fossa on the lateral side of the scapula. 7, Palatine bone covered in middle by maxilla and pterygoids and divided into small anteroventromedial part and large posterodorsolateral area; presence of shallow subcircular fossa medial to spiny process of squamosal; presence of a foramen spinosum. 8, Lengthening of rostrum and dilation of its apex; increase in width of vomerian window on ventral side of rostrum; low, wide and regularly convex or flat dorsal process of periotic; opening of mandibular canal larger than in the Platanistidae, Squalodelphidae, and Eurhinodelphoidea; increase in size of anterior incisors, which lie horizontally; reduction of lateral lamina of pterygoid hamulus. 9, Tendency toward thickening of supraorbital process; development of supplementary articular mechanism with squamosal on lateral edge of periotic; appearance of deep subcircular fossa dorsal to spiny process of squamosal by deepening of shallow fossa observed in the Squalodontidae; loss of double roots on cheek teeth. 10 and 11, for definition of these taxa, see Muizon (1987). 12, Loss of articulation of tympanic with squamosal; palatine hollowed out by pterygoid sinuses but no lateral lamina of palatine present; expansion of pterygoid sinus outside pterygoid fossa in orbit and temporal fossa. 13, For definition of the Eurhinodelphoidea (Eoplatanistidae + Eurhinodelphidae), see Muizon (1991). 14, For definition of the Delphinida (Lipotidae + Inioidea + Delphinoidea) see Muizon (1988a). (For character analyses, see Muizon 1987, 1988a, and 1991).

posterior extremity that could be homologous with the premaxillary crest (defined by Moore 1968) observed in the Ziphiidae. If this is the case, *Sulakocetus* should be classified within the Ziphiidae since that structure has been regarded as the key character of the family (Moore 1968; Muizon 1991).

The genus *Eoplatanista* (middle Miocene of Italy) has previously been proposed as belonging in the Platanistidae (Pilleri 1985, 1989). However, as mentioned by Barnes et al. (1985) and as discussed by Muizon (1988b), *Eoplatanista* is not a platanistid. Pilleri's interpretation is poorly supported for the following reasons: (1) there is no discussion of the synapomorphies that diagnose the Platanistidae and Platanistoidea, (2) the synapomorphies of the Platanistidae and Platanistoidea as diagnosed by Muizon (1987, 1991, this paper) are not present in *Eoplatanista*, (3) *Eoplatanista* (family Eoplatanistidae) shares synapomorphies with the Eurhinodelphidae to form the superfamily Eurhinodelphoidea, which represents the sister group of the Delphinida (see Muizon 1988b, 1991), and (4) the tooth similarities between *Platanista* and the type specimen of *Eoplatanista italica* mentioned by Pilleri are the result of the old age of the individual and in some respects are also found in the specimens referred by Pilleri (1989) to a new genus, *Zignodelphis*. I regard *Zignodelphis* as a junior synonym of *Eoplatanista* (see Muizon 1988b).

The principal synapomorphies supporting the diagnosis of the Platanistoidea used here are based upon three anatomical regions: the scapula, the auditory region, and the palatine bone (see Muizon 1984, 1987, 1988a, 1991 for detailed discussion and character analysis).

Scapula.—The superfamily Platanistoidea is diagnosed by important morphological modifications of the scapula (Muizon 1984, 1987, 1991). The coracoid process is a small rounded protuberance (sometimes almost absent), and the acromion process is located on the anterior edge of the scapula in such a way that the supraspinatus fossa is very reduced or absent (it is possibly shifted medially in *Platanista*) (Fig. 2). These features are probably related to a change in use of the forelimb, which needs to be analyzed functionally. The loss of the supraspinatus fossa does not equate with the loss of the supraspinatus muscle since Pilleri et al. (1976) observed a supraspinatus muscle in *Platanista*. Therefore, the scapular synapomorphies of the Platanistoidea can be defined as (1) great reduction of the coracoid process and (2) great reduction or loss of the supraspinatus fossa, with the acromion process located on the anterior edge of the bone.

Among cetaceans, the plesiomorphic condition is found in the archaeocetes (the earliest known cetaceans), which have a scapula whose coracoid process is clearly fingerlike and straight (Kellogg 1936 and personal observations), an acromion located on the lateral side, and a well-developed supraspinatus fossa. However, the morphology of the coracoid process is derived in comparison to that of the outgroup (i.e., mesonychid condylarths, regarded as the closest relatives of cetaceans, Prothero et al. 1988). The scapula in the outgroup bears a small, rounded, and blunt coracoid process that is recurved medially (see USNM 299745, a partial skeleton referred to cf. *Mesonyx* sp. from the Bridger Basin, Wyoming).

In summary, cetaceans are diagnosed by the development of a straight fingerlike coracoid process of the scapula and by a tendency to reduce the supraspinatus fossa. Within cetaceans, the Delphinida (*sensu* Muizon 1988) are even more derived in having a coracoid process that is long, flattened, and often expanded at its apex. The absence of an elongated coracoid process in some cetaceans is also regarded as a derived feature. Among the odontocetes, reduction of the coracoid process, positioning of the acromion on the anterior edge of the scapula, and loss of the supraspinatus fossa occur in *Platanista*, *Notocetus*, *Squalodon*, *Kelloggia*, and *Prosqualodon*. Cozzuol and Humbert-Lan (1989:484) stated, *contra* Muizon (1987, 1991), that the type specimen of *Phoberodon arctirostris* has a scapula with a "conspicuous supraspinatus fossa which is larger than in the modern Ziphiidae" and that its acromion "is not on the anterior edge of the scapula"; furthermore, "the coracoid process (of the type specimen of *P. arctirostris)* is broken close to the base and its section permits us to infer that it was well developed." Cabrera (1926:387), however, noted that the coracoid process is represented merely by a small extension of the anterior border of the glenoid cavity. Furthermore, if the coracoid process is broken, I question its degree of development. The illustration (Cabrera 1926:fig. 8) suggests that the acromion is not located on the anterior edge of the bone. If Cozzuol and Humbert-Lan's observation is correct (unfortunately no illustration of the specimen was provided), then *Phoberodon* should be excluded from the Platanistoidea and, therefore, from the Squalodontidae. Like *Sulakocetus*, *Phoberodon* is a genus that needs revision and the discovery of better-preserved skeletons.

In several genera classified in the Platanistoidea, including *Zarhachis*, *Pomatodelphis*, *Squalodelphis*, *Phocageneus*, *Medocinia*, and *Eosqualodon*, the scapula is unknown. However, these genera possess other derived features of their auditory and pterygoid regions allowing their inclusion in this group (Muizon 1987, 1988b; see below).

The scapulae of *Inia*, *Pontoporia*, and *Lipotes* have a large coracoid process and an acromion located on the lateral side of the bone. Thus these genera lack the derived character states found in the Platanistoidea. On the contrary, their morphology is similar to that of the other Delphinida (Muizon 1988a).

A reduced coracoid process and an acromion located at the anterior edge of the scapula are features also present in the mysticetes *Balaena* and *Megaptera*. In these two taxa, however, the acromion is also very reduced (*Balaena*) or absent (*Megaptera*), while the acromion of the Platanistoidea is very large, as in other odontocetes. Consequently, the scapula of the Platanistoidea differs from that of *Balaena* and *Megaptera*, and it is probable that these differences represent different functional modifications. Reduction of the coracoid process is therefore interpreted as a convergence between mysticetes and odontocetes.

Auditory region.—The Platanistidae and the Squalodelphidae (*sensu* Muizon 1987) have been regarded as sister taxa mainly because both share a deep subcircular fossa located dorsal to the spiny process of the squamosal (Muizon 1987:fig. 3 and p. 5, Muizon 1991:fig. 11). The lack a subcircular fossa, the plesiomorphic condition, characterizes other cetaceans. As stated elsewhere (Muizon 1987, 1991), this structure could represent a simple extension of the peribullary sinus, which surrounds the periotic and part of the tympanic of odontocetes. It is noteworthy, however, that the subcircular fossa almost always possesses numerous foramina, implying an important function in blood supply, as hypothesized by Fordyce (this volume). A subcircular fossa is observed in *Platanista*, *Pomatodelphis*, *Zarhachis*, *Notocetus*, *Medocinia*, and *Squalodelphis*. A shallow subcircular fossa is also present in *Squalodon bariensis*, *S. calvertensis*, *S. tiedemani*, and *Eosqualodon latirostris*. In those species the foramina are present but larger and less numerous than in the Platanistidae and Squalodelphidae. Furthermore, in *Squalodon* and *Eosqualodon*, the subcircular fossa opens anteromedially in a groove (oriented anteromedially–posterolaterally) that leads into a small foramen located between the fossa and the foramen ovale. In *Squalodon calvertensis* (USNM 328343 and 214644) apparently this passage opens in the foramen ovale. The same foramen has been described in *Waipatia* by Fordyce (1994, this volume) as the foramen spinosum. In *Zarhachis* and *Pomatodelphis* a foramen spinosum is

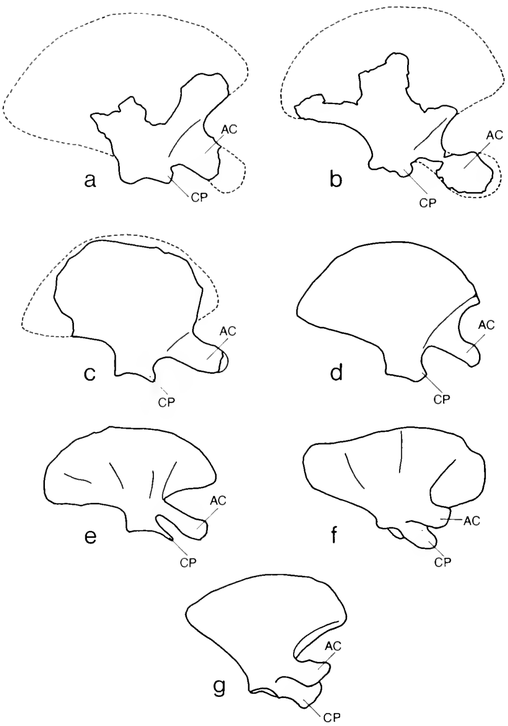

Figure 2. Lateral view of the scapula in some odontocetes. a, *Squalodon* (from USNM 22902); b, *Prosqualodon* (from AMNH 29022); c, *Notocetus* (from AMNH 29060); d, *Platanista* (from MNHN 1870-79); e, *Eurhinodelphis* (from USNM 11867); f, *Pontoporia* (from MNHN 1934-375); g, *Phocoena* (from MNHN 1982-137). All figures are schematic and not drawn to scale. AC, acromion; CP, coracoid process.

positioned between the subcircular fossa and the foramen ovale. In those genera, however, the groove is sometimes absent or reduced but never as deep as in *Squalodon*. In *Zarhachis flagellator* (USNM 10991), the ventral edge of the foramen is formed by the junction of two lips, indicating that a canal has been formed by the closure of the lips of a "gutter". Furthermore, in USNM 13768 (*Pomatodelphis* determined as *Zarhachis* by Muizon 1987), in which the internal side of the braincase is visible, the foramen apparently opens at least partially within the cranial cavity in the parietal, while in USNM 10911 (*Zarhachis*) the foramen spinosum clearly opens in the foramen ovale. In *Platanista* the foramen has disappeared because a large cranial hiatus has developed. Therefore, there seems to be some interspecific (or intraspecific) variation in the cerebral opening of the foramen spinosum. Nevertheless, I consider the shallow subcircular fossa of *Squalodon* and *Eosqualodon* to be homologous with that observed in the Platanistidae and Squalodelphidae because (1) it is located in the same position, dorsal to the spiny process (its lateral border being exactly dorsal, sometimes dorsolateral, to the base of the spiny process), (2) it bears a similar vascularization, suggesting that both functioned in blood supply, and (3) it is associated anteromedially with a similar foramen spinosum.

A vascularized subcircular fossa with a foramen spinosum has not been found in the Physeterida or in the clade consisting of the Eurhinodelphoidea and Delphinida. In *Kentriodon* and in some Recent Delphinidae a shallow depression is sometimes observed (as an individual variation) in a position close to that in *Squalodon*, but it is generally more medial. However, there is no foramen spinosum, and the position of the depression, when present, is variable. Therefore, it is likely that the condition sometimes observed in the Delphinoidea is not homologous but instead related to the presence of a cranial hiatus and to the important development in the Delphinoidea of the peribullary sinus, which tends to excavate the bones surrounding the periotic and the tympanic. In contrast, the subcircular fossa of the Platanistoidea seems to be associated with the circulatory system (Fordyce 1994, this volume). A subcircular fossa was not seen in *Eosqualodon langeweischei*, possibly because the tympanic and periotic of the specimen illustrated by Rothausen (1968) have not been removed from the skull. The same is true for *Kelloggia barbara* Mchedlidze (1984); however, the morphology of *Kelloggia* is very similar to that of *Squalodon*, and I suspect the former to be a junior synonym of the latter. A subcircular fossa is not present in *Prosqualodon australis* (AMNH 29022 and MLP 5-8 and 5-9). It is also noteworthy that *Phoberodon arctirostris* has no subcircular fossa (M. A. Cozzuol, pers. comm.), contrary to my earlier statement (Muizon 1991) that would confirm its exclusion from the Platanistoidea. The presence of a foramen spinosum in the Squalodelphidae could not be determined since no specimens were available for this study.

The families Platanistidae and Squalodelphidae also share a supplementary articular mechanism with the squamosal on the lateral edge of the periotic (Fig. 3). The plesiomorphic condition, absence of this articular mechanism, characterizes the Archaeoceti, Ziphiidae, Physeteridae, Eurhinodelphoidea (*sensu* Muizon 1988b), and Delphinida. This stucture is a hooklike articular process in the Platanistidae (*Platanista*, *Zarhachis*, and *Pomatodelphis*). In *Platanista* it is not possible to remove the periotic from the skull without breaking either the process or the corresponding fossa on the squamosal. In the Squalodelphidae, there is no true hooklike process but a less derived articular rim (as in *Notocetus* and *Phocageneus*) or a straight somewhat conical process (*Squalodelphis*). This feature has not been found in the Squalodontidae, but the periotic of *Squalodon bariensis* shows a preliminary stage in the development of the condition found in the Platanistidae and the Squalodelphidae. On the anterior border of the articular facet for the tympanic, the periotic of *S. bariensis* displays a groove extending from the fossa crus breve incudis to the apex of the process. This groove receives the spiny process of the squamosal, with which it articulates tightly (Muizon 1991:fig. 11, 12). The anterior crest that delimits the articular groove is elevated, and its posterior extremity forms a peg (Fig. 3A) that is in the same position as the articular rim and the hooklike process of the Squalodelphidae and Platanistidae. In fact, the supplementary articular mechanism observed in the Platanistidae and Squalodelphidae is the result of the important increase in size and thickness of the anterior crest of the articular groove for the spiny process of the squamosal. That interpretation is clear in a comparison of the periotics of *Squalodon calvertensis* (USNM 187315) and *Zarhachis flagellator* (USNM 26274). The condition observed in *Squalodon bariensis* is well marked in the holotype of *Squalodon calvertensis*, and I observed it (sometimes marked much better, with an incipient articular rim) in most of the specimens of the large collection of *Squalodon* periotics in the U.S. National Museum. That feature, although very common, is not constant in the genus *Squalodon*. Furthermore, it was not observed in the other squalodontid genera, since the periotic is either unknown (*Phoberodon arctirostris*) or it has not been removed from the skull (*Eosqualodon langeweischei* and *Kelloggia barbara*). The periotic of *Prosqualodon davidis* has been illustrated by Flynn (1948), but the figure does not show enough detail, and the holotype (and only known specimen) has been lost. The periotic referred by True (1909) to *Prosqualodon australis* does not have the articular modification observed in *Squalodon*. This periotic is not associated with a skull. However, several skulls of *Prosqualodon australis* (with associated periotics) recently collected in Patagonia confirm True's interpretation (Cozzuol, pers. comm.).

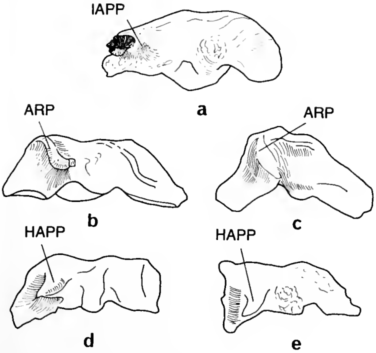

Figure 3. Lateral view of the periotic of some odontocetes. a, *Squalodon* (from MHNL Dr 15); b, *Notocetus* (from AMNH 29060); c, *Phocageneus* (from USNM 21039); d, *Pomatodelphis* (from USNM 187414); e, *Platanista* (from MNHN 1870-79). All figures are schematic and not drawn to scale. ARP, articular rim of the periotic; HAPP, hooklike articular process of the periotic; IAPP, incipient articular process of the periotic.

Palatine bone.—Previously, the Platanistidae were diagnosed by the structure of their palatine bones (Muizon 1987). In *Pomatodelphis* and *Zarhachis*, the palatines are not articulated ventrally on the palate as in most odontocetes; they clearly have migrated dorsolaterally and are surrounded by the maxilla and the pterygoid (which partially overlap them). In *Platanista* the condition is even more specialized, as the pterygoid totally overlaps the palatine and the posterior part of the maxilla (Kellogg 1924). The plesiomorphic condition in which the maxillae are totally separated from the pterygoids by the palatines is found in the Archaeoceti, in the Agorophiidae (new genus from the Oligocene of Oregon under study by E. Fordyce, USNM 256517), and in primitive Ziphiidae (e.g., *Squaloziphius emlongi*).

An interesting observation has been made on the further prepared skull of the holotype of *Squalodon bariensis* (Muizon 1991). The palatines of this specimen are clearly divided into a small ventromedial portion contacting the other palatine and a large posterolateral portion in a position similar to that in *Pomatodelphis* and *Zarhachis* (Fig. 4). The condition in *Squalodon* appears to be the consequence of a posterior extension of the maxilla, which partially overlaps the palatine, dividing it into two areas on the surface of the skull and contacting the pterygoid in its anterior region. Furthermore, as clearly seen in the lateral view of the skull of *S. bariensis* (Muizon 1991:fig. 10), the pterygoid also overlaps the ventral limit of the palatine. This arrangement, in which the palatine is split in

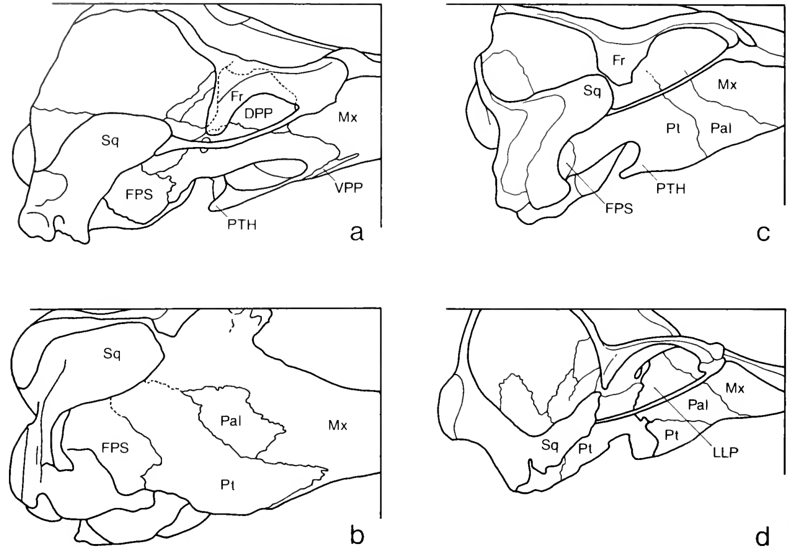

Figure 4. Lateral view of the skull in some odontocetes. a, *Squalodon* (from MHNL Dr 15); b, *Pomatodelphis* (from USNM 187414); c, *Eurhinodelphis* (reconstruction from various USNM specimens); d, *Delphinus* (from private specimen). All figures are schematic and not drawn to scale. DPP, dorsal part of the palatine; FPS, falciform process of the squamosal; Fr, frontal; LLP, lateral lamina of the palatine; Mx, maxilla; Pal, palatine; Pt, pterygoid; PTH, pterygoid hamulus; Sq, squamosal; VPP, ventral part of the palatine.

two parts by a posterior extension of the maxilla, is not common among odontocetes. It is regarded here as a first step toward the platanistid specialization in which the ventromedial part of the bone has disappeared. This feature was not observed in the Squalodelphidae, the sister group of the Platanistidae, probably as a consequence of the poor preservation of that suture on the four well-preserved skulls of the Squalodelphidae examined [*Notocetus vanbenedeni* (two skulls) and *Squalodelphis fabianii* (one skull), and *Medocinia tetragorhina* (one skull)]. It is probable that this character was present in the Squalodelphidae since, at the anterior region of the fossa for the hamular lobe of the pterygoid sinus, no trace of the palatine can be seen medially, a condition indicating that the bone has probably been displaced laterally as in the Platanistidae or covered by the maxilla or pterygoid in its medial part. The same observation can be made on the badly crushed skull of the holotype of *Medocinia tetragorhina* (Muizon 1988b:80). That feature was likely present in *Squalodon calvertensis* (holotype, USNM 10484, and USNM 328343) and is obvious in *Squalodon tiedemani* (USNM 183023 and 424070); however, it could not be observed in *Squalodon bellunensis* and *Phoberodon arctirostris* because of poor preservation of the skulls. Furthermore, the skulls of the holotypes of *Eosqualodon langewieschei* and *Kelloggia barbara* require further preparation to allow better observation of the palatine bones. In *Prosqualodon davidis* and *P. australis* the relationships of the palatine with the maxilla and the pterygoid are similar to those in nonplatanistoid odontocetes, and the maxilla does not overlap the palatine to contact the pterygoid. The reconstruction of the palatine suture of *Squaloziphius emlongi* (Muizon 1991:fig. 4), which is shown divided by a pterygoid–maxilla contact, is an editorial error; as indicated in the text (Muizon 1991:290), the maxilla–palatine suture shows the plesiomorphic condition of a "regular parabola opening posteriorly and whose branches run obliquely from the median suture to the anterior edge of the ventral opening of the infraorbital foramen"; in that species there is no contact between the maxilla and the pterygoid. Such a contact is seen in the Physeterida as individual variation in some specimens of *Kogia* (Fraser and Purves 1960:pl. 16), *Hyperoodon* (Fraser and Purves 1960:pl. 8), *Berardius* (Fraser and Purves 1960:pl. 9) *Ziphius* (Fraser and Purves 1960:pl. 10), and *Mesoplodon*. The condition seen in the Recent Ziphiidae (it is absent in all the fossil forms in which that region of the skull is preserved) is a result of the enlargement of the pterygoid, which overlaps the palatine anteriorly. It is also absent in the fossil kogiid *Scaphokogia*. In *Squalodon bariensis* and *S. tiedemani* (USNM 424070) the separation of both parts of the palatine is partially achieved by a posterior extension of the maxilla, which overlaps it and contacts the pterygoid. Consequently, the conditions observed in *Squalodon* and in the Physeterida are not homologous.

Muizon (1991:302) mentioned that the specimen from St. Paul-Trois-Châteaux (Department of Drôme, France; MHNG 5000) referred to *Squalodon bariensis* has a W-shaped suture of the palatine with the maxillae and, therefore, no contact between the maxillae and the pterygoids. This arrangement is due to the specimen's being a young animal in which the posterior extension of the maxillae had not yet fully developed.

RELATIONSHIPS OF THE DALPIAZINIDAE

The family Dalpiazinidae Muizon, 1988, is monotypic and represented so far by a single species, *Dalpiazina ombonii*. The diagnosis of this taxon and the description of the specimens referred to it have been presented previously along with discussions of its taxonomy and taphonomy (Muizon 1988b).

Before addressing the taxonomy and phylogenetic relationships of *Dalpiazina ombonii*, I must recount the great confusion existing in the associations of the specimens initially described by Longhi (1898) as belonging to *Champsodelphis ombonii*. Considering this, I have formally designated a lectotype for *D. ombonii*, IGUP 26405, a partial mandible associated with a fragment of maxilla (Muizon 1988b:64). The other specimens described by Longhi cannot be unequivocally referred to *Dalpiazina ombonii* and should not be taken into account for taxonomy or phylogeny (Muizon 1988b:62–66). I have also stated that the individual "B" described by Dal Piaz (1977:30) was composed of elements that, very probably, do not belong to the same taxon, and I have recommended that they be removed from the hypodigm (Muizon 1988b:66–67). The hypodigm of *Dalpiazina ombonii* should therefore be restricted to three specimens: (1) the lectotype of Longhi (1898), (2) the individual "A" of Dal Piaz (1977:27 and pl. I), a partial cranium and rostrum, a left periotic, and a cervical vertebra (Muizon 1988b:67–76), and (3) the individual "C" of Dal Piaz (1977:33 and pls. II, 19 and 20).

Specimens "A" and "C" of Dal Piaz show some features of the skull and periotic (which could be regarded as synapomorphies) that could indicate a relationship of *Dalpiazina ombonii* with the Squalodontidae (Muizon 1988b, 1991). This interpretation disagrees with that of Pilleri (1985, 1989), who classified *D. ombonii* within the Delphinoidea. I am reluctant to accept Pilleri's assessment for two reasons: (1) he has not explained his concept of the Delphinoidea and the synapomorphies he employed to diagnose that superfamily, and (2) the character states used to diagnose the Delphinoidea (Muizon 1988a; Heyning 1989; Barnes 1990) either are not observed (except for single-rooted teeth with conical crowns) in specimens confidently referred to *Dalpiazina ombonii* (see above) or are not preserved. Because of the high variability of cetacean teeth, they should not be used the sole character diagnosing a taxon (according to Pilleri's concept of delphinoid teeth, the majority of the teeth of young adult eurhinodelphids should be classified within the Delphinoidea). Consequently, I disagree with Pilleri's classification of *D. ombonii* in the Delphinoidea. "*Dalpiazella*" is an error by Pilleri et al. (1989:223–224) for *Dalpiazina*.

The *Squalodon*-like morphology of the periotic of *Dalpiazina ombonii* has been discussed by Muizon (1988b) and accepted by Fordyce (1994, this volume). However, it is uncertain whether the similarities of the periotics of *Dalpiazina* and *Squalodon* represent synapomophies, with the probable exception of the morphology of the dorsal process (see Muizon 1988b, 1991). Four character states that are possible synapomorphies relating *Dalpiazina* to the Squalodontidae (Muizon 1991) are (1) longer rostrum with enlarged apex, (2) wider vomerian window on the ventral side of the rostrum, (3) low, wide and regularly convex dorsal process of the periotic, and (4) opening of the mandibular canal larger than in the Platanistidae, Squalodelphidae, and Eurhinodelphoidea. Pilleri (1989:385) rejected the first synapomorphy, arguing that it is also present in the Delphinidae. The condition observed in some short-snouted delphinids (Globicephalinae) is different from that of the Squalodontidae and *Dalpiazina*. In the Globicephalinae, the rostral portions of the maxilla and premaxilla are equally long and both reach the apex of the shortened rostrum; on the long rostrum of the Squalodontidae and *Dalpiazina* the maxilla is shorter than the premaxilla and never reaches the apex. The anterior widening of the premaxillae on the rostrum of the Globicephalinae is due to the strong development of the melon, which characterizes that subfamily. Consequently, the condition in the Globicephalinae is not homologous with that of the Squalodontidae and *Dalpiazina*.

The hypothesized close relationship between the Dalpiazinidae and the Squalodontidae suggested in earlier works (Muizon 1988b, 1991) remains poorly supported since none of the platanistoid synapomorphies mentioned above were observed on the available specimens because of their poor preservation. Consequently, the Dalpiazinidae are a possible sister group of the Squalodontidae, although this hypothesis has yet to be confirmed.

SQUALODONTS AND OTHER ODONTOCETES

In the following section I compare the Platanistoidea with the three other major groups of odontocetes: the Delphinida, the Physterida, and the Eurhinodelphoidea.

Delphinida.—The Delphinida have been diagnosed by Muizon (1988a:164) on the basis of nine synapomorphies: (1) acquisition of a lateral lamina on the palatine, (2) virtual loss of the posterior region of the lateral lamina of the pterygoid, (3) excavation of the posterodorsal portion of involucrum of the tympanic, (4) reduction of the anterior process of the periotic, (5) development of a ventral swelling and tubercule on the periotic, (6) increase in size of the processus muscularis of the malleus, (7) enlargement of the transverse apophyses of the lumbar vertebrae as triangular blades, (8) anterior inflexion of the anteroventral angle of the sigmoid process of the tympanic, and (9) frontals narrower than (or as wide as) nasal on vertex. A continuous lateral lamina of the pterygoid is observed in *Pontoporia*; however, this condition has been regarded as a reversal in some Pontoporiidae (Barnes 1985; Muizon 1988a).

The oldest known fossil Delphinida belong to the family Kentriodontidae Barnes, 1978, a taxon whose definition and relationships with the superfamily Delphinoidea are complex (Muizon 1988a). Some taxa known by well-preserved specimens come from the middle Miocene of North and South America and include the genera *Kentriodon*, *Delphinodon*, *Liolithax*, *Lophocetus*, and *Atocetus*. *Oligodelphis* is from the late Oligocene of the Caucasus; however, in the specimens referred to this genus none of the synapomorphies of the Delphinida are preserved. Other fossil Delphinida from the Miocene represented by well-preserved specimens are the lipotid *Parapontoporia* and the iniid *Ischyrorhynchus*.

In their phylogenetic tree, Barnes et al. (1985: fig. 1) considered the Squalodontidae and the Delphinoidea closely related. However, none of the synapomorphies of the Delphinoidea (Muizon 1988a) have been found in the Squalodontidae and consequently their inclusion in the Delphinida cannot be supported. If the Squalodontidae were regarded as the sister group of the Delphinida, the platanistoid synapomorphies (e.g., reduction of coracoid process and supraspinatus fossa on the scapula, maxilla covering the palatine bone, and presence of a shallow subcircular fossa) would have to be considered convergences. No synapomorphies have been found to relate the Squalodontidae to the Delphinida or even to the Delphinoidea. Such a hypothesis would require too many parallelisms and reversals to be acceptable. Only a few authors have suggested a close relationship between the Delphinoidea and the

Squalodontidae. Winge (1921) stated that the Delphinidae had their origin in the Platanistidae, a family in which he included the four living genera of river dolphins. Winge's interpretation (1921:46) is based principally on his concept of the taxon Platanistidae. If one considers that three of the four extant genera that he included (i.e., *Inia*, *Pontoporia*, and *Lipotes*) belong to the Delphinida and that the Inioidea (Iniidae + Pontoporiidae) are the sister group of the Delphinoidea, his interpretation is understandable. Under my interpretation of the Platanistoidea, which excludes the Iniidae, Pontoporiidae, and Lipotidae, no close relationship between the Delphinoidea and the Platanistoidea, and thus the Squalodontidae, can be established.

Physeterida.—This infraorder includes two superfamilies, the Physteroidea and the Ziphioidea, and is regarded here as a monophyletic taxon. However, Heyning (1989) and Heyning and Mead (1990), from analysis of the morphology of the air sacs and nasal tracts as well as osteological data, did not recognize a close relationship between these superfamilies and regarded the Physeteroidea as the sister group of the remaining extant families of odontocetes. According to this interpretation the Physeterida are paraphyletic. These authors noted that the physeteroid morphology of the nasal tracts, although highly specialized, retains several primitive features. This interpretation may be correct; however, because of the spectacular modification due to scaphidiomorphy (development of a large supracranial basin) of this region of the physeteroid skull, it is also possible that the plesiomorphic features of the nasal tracts recognized by Heyning and Mead actually represent apomorphic features (reversals) imposed by its hyperspecialization (for instance, the morphology of the premaxilla of the middle Miocene *Orycterocetus crocodilinus* indicates that the bone could very well have contained a small premaxillary sac). Furthermore, Heyning's interpretation implies convergence of the five synapomorphies used to define the Physeterida (Muizon 1991:fig. 5). The monophyletic alternative is accepted here, although it is clear that a careful comparison of the synapomorphies supporting each interpretation is needed.

It is noteworthy that Heyning's (1989) cladogram considers only living odontocetes. The exclusion of fossil taxa from phylogenetic reconstructions is a subjective choice that certainly introduces errors that cannot be compensated for by computer-generated cladograms, since it may result in a more parsimonious cladogram markedly different from one that includes both living and fossil taxa. The significance of fossils in the reconstruction of phylogenetic relationships has been demonstrated by several authors (Gauthier et al. 1988; Donoghue et al. 1989; Novacek 1992), and it has been recommend that no phylogeny should ignore the fossil record. The introduction of fossil taxa in phylogeny allows better definition of character states and homoplasies and consequently provides more information for phylogenetic reconstruction.

Of the three characters presented by Heyning (1989:fig 39) to diagnose the nonphyseterid odontocetes, one (character 16, the presence of premaxillary sacs) is present in the Agorophiidae, which still retain joint parietals on the vertex and nasals overhanging the bony nares but have the maxilla covering the supraorbital process of the frontal, the key synapomorphy of the odontocetes. The two other characters (blowhole ligament and nasal passages confluent) are soft-anatomical characters and cannot be evaluated among fossil odontocetes. The feature "temporal fossa roofed over by expansions of the maxillae," retained by Heyning (1989:fig 39, character 22) as a synapomorphy of the Ziphiidae and Delphinoidea, is also found in the middle Miocene physeterid *Orycterocetus crocodilinus* and platanistid *Zarhachis flagellator*, while it is very poorly developed in the early Miocene ziphiid *Squaloziphius emlongi* and middle Miocene kentriodontid delphinoid *Kampholophos serrulus*. Furthermore, the feature "facial asymmetry" (Heyning 1989:fig. 39, character 4) cannot be retained as an odontocete synapomorphy since it is absent in several fossil odontocetes [e.g., *Agorophius*, an undescribed agorophiid (USNM 256517), *Patriocetus*, and *Archaeodelphis*]. Consequently, the introduction of the Agorophiidae or of fossil taxa of extant families into Heyning's cladogram also introduces character conflicts that can be resolved by including the Physeteroidea and the Ziphiidae in the same monophyletic taxon.

Abel (1914) proposed a phylogeny of cetaceans that suggests a close relationship between the Squalodontidae and the Ziphiidae. It is true that the Ziphiidae show several similarities with the Squalodontidae, such as the anterior extension of the pterygoid contacting the maxilla (as an individual variation), overlapping the palatine, and dividing the palatine on the palate (see above).

In *Squalodon bariensis* the ventrolateral portion of the pterygoid hamulus is reduced. This can be regarded as the first step toward the condition observed in the living ziphiids, in which the pterygoid hamulus has lost its lateral lamina (the polarity of that character state has been discussed by Muizon 1984). Study of the fossil ziphiids *Ninoziphius* and *Squaloziphius* indicates that the pterygoid condition observed in living ziphiids is the result of reduction of the lateral lamina that is present but vestigial on the edges of the pterygoid hamulus of *Ninoziphius platyrostris* (early Pliocene of Peru) and partially closes the hamular fossa laterally in the older *Squaloziphius emlongi* (early Miocene of Washington State, USA). Furthermore, the condition in *S. emlongi* shows that in ziphiids the reduction of the lateral lamina of the pterygoid is first achieved by reduction of its posterior part, lateral to the basioccipital. The second step is observed in *Ninoziphius platyrostris*, in which the anterior portion of the lateral lamina of the pterygoid (i.e., the lateral lamina of the pterygoid hamulus) has also disappeared. However, the condition of the pterygoid in *Squalodon bariensis* indicates that the reduction of the lateral lamina would be initiated by loss of its hamular portion, which is contradicted by data provided by the fossil ziphiids. The condition in *Squalodon* must therefore be regarded as independent of that in ziphiids.

The premaxillae of the Squalodontidae and *Prosqualodon* contact the frontals posteriorly on the vertex (Fig. 5). The same feature is present in the Ziphiidae, *Squaloziphius*, *Ziphirostrum*, *Choneziphius*, *Ziphius*, *Hyperoodon*, and almost always in *Mesoplodon* (at least on the left side of the skull). A premaxilla–frontal contact is also seen in the Eurhinodelphidae, Eoplatanistidae, Platanistidae, Squalodelphidae, and Dalpiazinidae. This character is absent in the Delphinida (although it is observed occasionally as a result of individual variation), in the Berardiini [*Berardius*, *Tasmacetus*, *Ninoziphius* (undescribed specimen)], and in the Physeteridae. It is also present in some mysticetes. Apparently a premaxilla–frontal contact is absent in archaeocetes and thus is derived in cetaceans. However, it is noteworthy that all early odontocetes show a premaxilla–frontal suture (*Agorophius*, *Patriocetus*, *Xenorophus*, and *Archeodelphis*). Furthermore, the oldest known ziphiid, *Squaloziphius emlongi*, possesses this feature. Consequently, it seems reasonable to infer that, within the odontocetes, the plesiomorphic state is a contact between the premaxilla and frontal. The apomorphic condition in odontocetes is the loss of the articulation, which is interpreted as having evolved convergently in several groups. In the Delphinida, the apomorphic condition is the consequence of reduction of the posterior apex of the premaxillae, which is extreme in the Phocoenidae. In the Berardiini it is probably related to the increase in size of the nasals, and in the Physeteridae it is probably related to the development of a large supracranial basin (scaphidiomorphy).

Consequently, the two features mentioned above (i. e., reduction of the lateral lamina of the pterygoid and presence of a premaxilla–frontal suture) that could be regarded as synapomorphies of the

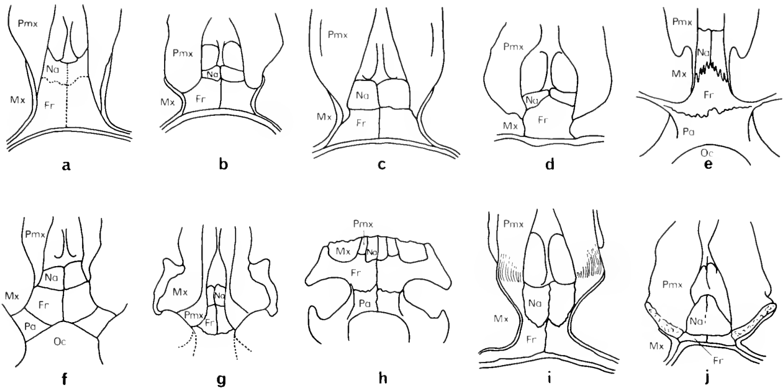

Figure 5. Dorsal view of the vertex in some odontocetes. a, *Squalodon* (from MHNL Dr 15); b, *Prosqualodon* (from Kellogg 1928); c, *Eurhinodelphis* (from USNM 8842); d, *Zarhachis* (from USNM 10911); e, *Agorophius* (from Fordyce 1981); f, *Patriocetus* (from K. Rothausen, unpublished thesis, 1965); g, *Xenorophus* (from Kellogg 1923); h, *Archaeodelphis* (from Kellogg 1928); i, *Squaloziphius* (from USNM 181528); j, *Ziphirostrum* (from Kellogg 1928). All figures are schematic and not drawn to scale. Fr, frontal; Mx, maxilla; Na, nasal; Oc, occipital; Pa, parietal; Pal, palatine; Pmx, premaxilla.

Squalodontidae and the Ziphiidae cannot be accepted. Furthermore, the absence in each family of synapomorphies of the other reinforces the hypothesis that there is no close relationship between the Squalodontidae and Ziphiidae.

Fordyce (1985) suggested a close, possibly sister-group, relationship of the Squalodontidae and Ziphiidae, basing his assessment on four derived features: (1) relatively deep rostrum, (2) teeth inserted on the lateral flanks of the rostrum, (3) robust zygomatic process, and (4) twisted transversely inflated anterior process of the periotic. However, the distribution of these character states among other odontocetes suggests that they cannot be retained as synapomorphies. As defined by Fordyce, the feature "deep rostrum" is imprecise; it should mention at which level of its length the rostrum is deep. If the depth of the rostrum is measured at its base, the feature cannot be used since it also occurs in archaeocetes, in several primitive odontocetes (e. g., *Xenorophus*), in an undescribed agorophiid (USNM 256517), and in most eurhinodelphids. If the character is defined as "rostrum deep in its anterior half," the synapomorphy cannot be used since it occurs in some Physeteroidea (*Scaphokogia*) and because it is not constant in the Ziphiidae (*Squaloziphius emlongi*, *Ninoziphius platyrostris*, and *Berardius* have a fairly flat rostrum). Furthermore, because of the wide variation among odontocetes in the morphology of the rostrum, character states based upon its shape or length should not be used at higher taxonomic levels. The second character proposed by Fordyce is unclear since teeth are inserted on the lateral flanks of the rostrum in all odontocetes. The third character, the strong zygomatic process, is found not only in the Ziphiidae but also in all Platanistidae, Squalodelphidae, *Prosqualodon*, and, to a certain extent, in the Agorophiidae. On the contrary, the zygomatic process' being robust, long, and slightly recurved ventrally could represent a synapomorphy of the Platanistoidea (*sensu* Muizon 1987, 1991). In the Ziphiidae this feature is much less marked (except in *Squaloziphius*, where its tremendous size is more a consequence of enlargement of the postglenoid process and represents an autapomorphy), and the process is never as long and always strongly recurved ventrally. It is also possible that the robustness of the process observed in the Squalodontidae represents a symplesiomorphy since a large zygomatic process is also found in some primitive odontocetes such as *Agorophius*, an undescribed agorophiid (USNM 256517), and *Patriocetus*. However, this hypothesis seems less probable as in these genera the process is generally less robust than in the Platanistoidea. The fourth proposed derived feature, the morphology of the anterior process of the periotic, is also found in the Platanistidae and Squalodelphidae, which have the same transversely inflated anterior process. It is true that the ventrally twisted anterior process is not found in those two families, but it is always observed in the Squalodontidae, Eurhinodelphoidea, and Physeterida. In summary, three of the four derived features listed by Fordyce (1985) are problematic.

Eurhinodelphidae.—This extinct family of odontocetes is the best candidate, besides the Platanistoidea, for a close relationship with the Squalodontidae. The Eurhinodelphidae and the superfamily Eurhinodelphoidea (Eurhinodelphidae and Eoplatanistidae) represent plausible morphological descendants of the Squalodontidae. However, the Eurhinodelphidae do not share any convincing synapomorphies with the Squalodontidae or with the Platanistoidea (*sensu* Muizon 1987). One possible synapomorphy is the presence of a contact between the premaxillae and the frontals. However, as discussed above, this is probably a symplesiomorphy among odontocetes, and the delphinoid condition, in which only the nasals contact the premaxillae, is an apomorphy.

Furthermore, the Squalodontidae, Platanistidae, Squalodelphidae, and *Prosqualodon* have a strong anterior spine on the tympanic, a feature also present in the Eurhinodelphoidea and Lipotidae. This character is absent in the Archaeoceti, an undescribed agorophiid (USNM 256517, under study by E. Fordyce), the Physeterida, and the Delphinoidea. Absence of the anterior spine in earlier-diverging groups (Archaeoceti and Agorophiidae) indicates that that condition is plesiomorphic, and thus the presence of the spine is apomorphic. However, the absence of an anterior spine on the tympanic in the Delphinoidea would contradict that interpretation. In fact, among the Delphinida (*sensu* Muizon 1988a), the Lipotidae, the earliest-diverging lineage, have a strong anterior spine; the Inioidea, the next lineage to diverge (sister group of the Delphinoidea), have a very reduced spine, and the Delphinoidea lack spines (the projections sometimes observed in *Tursiops* and *Globicephala* are regarded as hyperossification due to old age, since they are totally absent in young adults). Consequently, it seems that the tendency in the Delphinida is reduction of the anterior spine. If one admits that the absence of a spine is the plesiomorphic state, one must admit that the condition in the Delphinida is a reversal. The acquisition of a strong anterior spine on the tympanic has been regarded as a synapomorphy of the group Platanistoidea + Eurhinodelphoidea + Delphinida (Muizon 1991). Consequently, the common occurrence of an anterior spine in the Squalodontidae and in the Eurhinodelphidae is a symplesiomorphy within that group.

The Eurhinodelphidae, as well as the Eoplatanistidae, do not show any of the synapomorphies of the Platanistoidea (Muizon 1987; 1991); they have a scapula with a large coracoid process and a well defined supraspinatus fossa (Fig. 2e). Furthermore, the palatine morphology, the subcircular fossa, and the modification of the posterior process of the periotic that relate the Squalodontidae to the platanistid–squalodelphid clade are absent in the Eurhinodelphoidea. In other respects, the Eurhinodelphoidea have been regarded (Muizon 1991) as the sister group of the Delphinoidea on the basis of three synapomorphies: (1) loss of articulation of the tympanic with the squamosal, (2) palatine hollowed out by the pterygoid sinus with no lateral lamina of the palatine, and (3) expansion of the pterygoid sinus outside of the pterygoid fossa and into the orbit and temporal fossa.

This interpretation, however, is contradicted by the morphology of the involucrum of the tympanic, which is very similar in the Eurhinodelphoidea and Ziphioidea. In both groups the dorsal face of the involucrum shows a well-developed indentation that is never present to this extent in other odontocetes (Fig. 6). This feature has not been found in the Physeteroidea, indicating that the Eurhinodelphoidea could represent the sister group of the Ziphiidae, not of the Physeterida. It is also possible that the modified bulla of the Physeteroidea has altered the expression of that feature. In fact, the Eurhinodelphoidea do not show any of the five synapomorphies of the Physeterida (Muizon 1991), and, therefore, if one admits the monophyly of the Physeterida, the morphology of the involucrum in the two groups must be regarded as convergent. The involucrum is olive-shaped to conical in the Platanistoidea and Squalodontidae and has neither the indentation observed in the Eurhinodelphoidea and Ziphioidea nor the sigmoid shape of the Delphinida (Fig. 6).

DISCUSSION AND CONCLUSIONS

Three alternate hypotheses that relate the Squalodontidae to nonplatanistoid groups have been tested; none has proven satisfactory since their acceptance would increase the number of convergences. Furthermore, the characters used to support a relationship of squalodonts to nonplatanistoid taxa have been demonstrated to be symplesiomorphic, homoplastic, or not homologous. Consequently, the hypothesis that squalodontids are platanistoids (Muizon 1987) is more parsimonious.

Contrary to what is generally accepted, I have excluded *Prosqualodon* from the family Squalodontidae mainly because of the lack of a partial covering of the palatine by the maxilla and lack of a subcircular fossa in the roof of the middle ear cavity (Muizon 1991). This genus, which has the typical platanistoid scapula (Muizon 1987), must, however, be included in the superfamily and represents the sister group of all other Platanistoidea. Cozzuol and Humbert-Lan (1989) have related the genus *Prosqualodon* to the Delphinida mainly on the basis of what they have observed to be a lateral lamina on the palatine of the holotype of *Prosqualodon australis* and some unpublished specimens. Such a duplication is also mentioned by Flynn (1948). However, I consider that *Prosqualodon* lacks a true lateral lamina. Instead, both palatines present a small lateral crest, a consequence of the posteroventral excavation of the palatines (due to the pterygoid bone's being hollowed by the pterygoid sinus). The pterygoids of *Prosqualodon* are not opened anteriorly and the pterygoid sinus does not contact the palatine as it does in the Delphinida. A similar lateral crest of the palatine is observed in the skull of the type of *Squaloziphius emlongi* (see Muizon 1991), in the Squalodontidae, and in some specimens of the Eurhinodelphidae (*Schizodelphis barnesi*, USNM 187130). Consequently, the condition in *Prosqualodon* may be

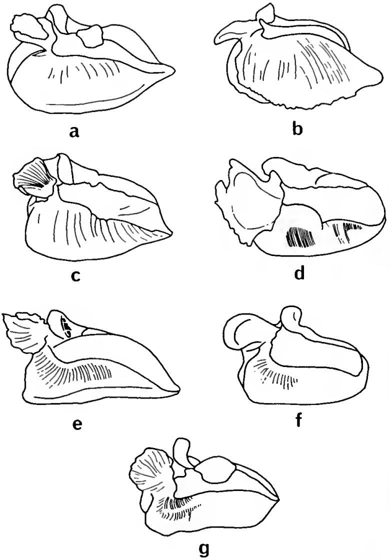

Figure 6. Dorsomedial view of the involucrum of the tympanic of some odontocetes. a, *Squalodon* (from MHNL Dr 15); b, *Platanista* (from MNHN 1870-79); c, *Eurhinodelphis* (from MNHN AMN 69); d, *Lipotes* (from AMNH 5333); e, *Ziphius* (from MNHN 1962-152); f, *Pontoporia* (from MNHN 1934-375); g, *Delphinus* (from private collection). All figures are schematic and not drawn to scale.

convergent with that of the Delphinida, but I do not regard them as homologous and do not accept the classification of *Prosqualodon* among the Delphinida as proposed by Cozzuol and Humbert-Lan (1989). Furthermore, *Prosqualodon* lacks a ventral rim on the ventrolateral side of the anterior process of its periotic, the involucrum of its tympanic is not sigmoid as in all the Delphinida, and on its vertex the frontals are wider than the nasals (for character analysis see Muizon 1988a).

Nevertheless, this interpretation of squalodont relationships is weakened by some of the Squalodontidae not being sufficently well known. In fact, the skulls of the type specimens of *Eosqualodon langewieschei* and *Kelloggia barbara* need further preparation to disclose their auditory and pterygoid regions. Furthermore, as stated above, the auditory region of *Prosqualodon* is poorly known, and the only periotics referred to that genus are those attached to the skull of the type of *P. davidis*, which is now lost (Fordyce 1982:49), and that of *P. australis*, figured by True (1909).

The platanistoid relationships of the squalodonts I advocate here are not new, having been proposed previously (Abel 1914; Slijper 1936; Rothausen 1968). The last author suggested that the Platanistoidea (*sensu* Simpson 1945) arose in the late Oligocene between the Patriocetidae and the Squalodontidae, in which he included *Prosqualodon*.

In this study, as in previous works (Muizon 1987; 1991), I have not considered several archaic taxa including *Patriocetus*, *Agorophius*, *Archaeodelphis*, *Xenorophus*, *Agriocetus*, and *Microzeuglodon*. As shown by Fordyce (1981), most of these taxa are odontocetes, and their primitive morphology indicates only a "pre-squalodontid" grade of evolution. *Patriocetus* is probably an archaic squalodontid or platanistoid. *Agriocetus*, known by only a single poorly preserved skull, could be a squalodontid or platanistoid but is too little known to be taken into account here. The six genera mentioned above must be classified within the odontocetes since they possess what I regard as the key synapomorphy of the group, the posterodorsal extremity of the maxillae partially or totally overlapping the supraorbital process of the frontals and extending posteriorly behind the preorbital process. This condition does not exist in other cetaceans, i.e., archaeocetes and mysticetes, including the Aetiocetidae.

The taxa mentioned above have been included by Rothausen (1968) in the superfamily Squalodontoidea. However, they represent several primitive stages in the early evolution of the odontocetes, and it is likely that they do not belong to the same monophyletic taxon. *Agorophius*, *Archaeodelphis*, and *Microzeugolodon* differ from the Squalodontidae in having the parietals still visible on the vertex dorsally (this observation cannot be made on *Xenorophus*, in which this part of the skull is not preserved) (Fig. 5). Consequently, they show a less advanced telescoping of the skull than do the other odontocetes, making them resemble the archaeocetes more than the Squalodontidae. For this reason, they probably represent early branches in odontocete phylogeny, and I do not think that they should be classified in the Squalodontidae. The vertex of other more typical odontocetes (more derived in this respect) is characterized by a more posterior extension of the maxillae and frontals, which almost exclude the parietals from the dorsal surface of the skull (they do not articulate on the dorsal surface of the skull and often do not articulate at all). The posteriorly expanded maxillae and frontals also cover the temporal fossa, form a continuous crest (temporal crest) from the the postorbital process to the occipital crest, and demarcate a small square or trapezoidal frontal window on the vertex.

Furthermore, some of these odontocetes of "pre-squalodontid" grade are represented by incomplete skulls, some of them totally lacking the rostrum or braincase, and the pterygoid and auditory regions are almost always absent or very damaged. Their poor preservation, as well as their scarcity, make phylogenetic analysis difficult. As shown by Fordyce (1981), the phylogenetic relationships of these primitive odontocetes are obscure, and more complete specimens are needed to clarify their evolutionary history and systematics.

ACKNOWLEDGMENTS

Special thanks are due to A. Berta, T. A. Deméré, and E. Fordyce for fruitful discussions and numerous comments that helped to improve the manuscript and to S. L. Messenger and J. E. Heyning, who reviewed the manuscript and provided useful comments. I also thank C. E. Ray, who read the manuscript, and A. Dagand, who made the illustrations.

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Waipatia maerewhenua, New Genus and New Species (Waipatiidae, New Family), an Archaic Late Oligocene Dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand

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ABSTRACT.—*Waipatia maerewhenua*, from the Otekaike Limestone (late Oligocene), Waitaki Valley, New Zealand, is a new genus and species in a new family Waipatiidae (Odontoceti: Platanistoidea) near the base of the radiation of platanistoids. Its features include skull about 600 mm long; rostrum long and narrow; incisors long, procumbent, and gracile; cheek teeth heterodont and polydont; maxillae telescoped back over frontals toward supraoccipital; parietal narrowly exposed on vertex; pterygoid sinus fossa restricted to basicranium; and palatine broad and not invaded by pterygoid sinus fossa. Features of the tympano-periotic, periotic fossa, and foramen spinosum indicate platanistoid relationships. *Waipatia maerewhenua* is more closely related to the Squalodelphidae and Platanistidae than to the Squalodontidae. Of the similar small dolphins previously identified as Squalodontidae, *Microcetus ambiguus* (late Oligocene, Germany) and *Sachalinocetus cholmicus* (early or middle Miocene, Sakhalin) are possible waipatiids. *Microcetus hectori* (earliest Miocene, New Zealand) is a probable squalodelphid. *Prosqualodon marplesi* (early Miocene, New Zealand) is transferred to *Notocetus* (Squalodelphidae) as *Notocetus marplesi* (new combination). *Sulakocetus dagestanicus* (late Oligocene, Caucasus) is probably a waipatiid close to *W. maerewhenua*. These taxa reveal an early radiation of the Platanistoidea by the late Oligocene.

INTRODUCTION

This article describes a new family, new genus, and new species of late Oligocene marine platanistoid dolphin from New Zealand. Heterodont dolphins from Oligocene and Miocene rocks worldwide have played a key role in interpretations of cetacean evolution because they are transitional in grade between archaic Cetacea (Archaeoceti) and extant odontocetes. *Waipatia maerewhenua* meets traditional concepts of the Squalodontidae, a family often used for heterodont odontocetes, but is more closely related to the Squalodelphidae and Platanistidae than to the Squalodontidae. It is an early member of the platanistoid radiation that led to diverse Miocene taxa and ultimately to the two extant species of "river dolphins" of the genus *Platanista*; the latter represent the last of the Platanistidae and, probably, the superfamily Platanistoidea. *Waipatia maerewhenua* thus has implications for odontocete history and for defining and delimiting the Squalodontidae, Squalodelphidae, and Platanistoidea.

The article has three main sections: (1) a description reviewing morphology and commenting on other taxa as needed to help interpret homology, (2) a comparison covering broader aspects of morphology, homology, and function, and (3) cladistic relationships. A new combination, *Notocetus marplesi* (Dickson, 1964) (Platanistoidea: Squalodelphidae), is used throughout for the so-called *Prosqualodon marplesi* of New Zealand.

MATERIAL AND METHODS

Descriptions are based on the right or left side, whichever is more informative, with differences between right and left mentioned only if asymmetry is evident. Unreferenced statements about morphology are based on personal observations. The specimen was prepared with pneumatic chisels and scrapers. Fine details were prepared under a microscope with an ultrasonic dental scaler and an air-abrasive unit; some sutures could not be traced fully because the cancellous bone is friable and not permineralized. Photographs were taken with a 35-mm Asahi Pentax camera with a 50-mm macro lens. Illustrations derived from photographs are not corrected for parallax.

Acronyms used here are NMNZ Ma, marine mammal catalog in the National Museum of New Zealand, Wellington, New Zealand; OM C and OM A, catalogs in Otago Museum, Dunedin, New Zealand; OU, fossil catalog in Geology Museum, University of Otago, Dunedin, New Zealand; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Platanistoidea Simpson, 1945

Family Waipatiidae, new

Type genus.—Waipatia, new genus.

Included genera.—Waipatia, new genus, only.

Diagnosis of family.—As for the only included species, *Waipatia maerewhenua*, in the only included genus, *Waipatia*, below.

Comment.—The family probably includes *Sulakocetus dagestanicus* Mchedlidze, 1976 (late Oligocene, Caucasus), and may include species of *Microcetus* and *Sachalinocetus*; these are discussed below.

Genus *Waipatia*, new

Type species.—Waipatia maerewhenua, new species.

Included species.—Waipatia maerewhenua, new species, only.

Diagnosis. — As for the only included species, *Waipatia maerewhenua*, below.

Etymology.—From the Maori name Waipati, a place near the type locality. Probable derivation: wai, water; pati, shallow. Regarded as indeclinable. Pronunciation: wai-pa-ti, with *a* pronounced as in English "far," and *i* as in "he."

Waipatia maerewhenua, new species

Figs. 2–8, 9b, 10a–k, 11, 12, 13a–g

Material.—Holotype only, OU 22095: a skull with 23 teeth in place, both mandibles, 17 loose teeth, left tympanic bulla, right periotic, left periotic lacking anterior process, atlas, natural cast of anterior of axis, and anterior thoracic vertebra. Collected by R. Ewan Fordyce, A. Grebneff, and R. D. Connell, January 1991.

Type locality.—North-facing cliff near Waipati Creek, 5 km west-southwest of Duntroon and 1.2 km north of "The Earthquakes," North Otago (Fig. 1). Grid reference: NZMS [New

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
Proc. San Diego Soc. Nat. Hist. 29:147–176, 1994

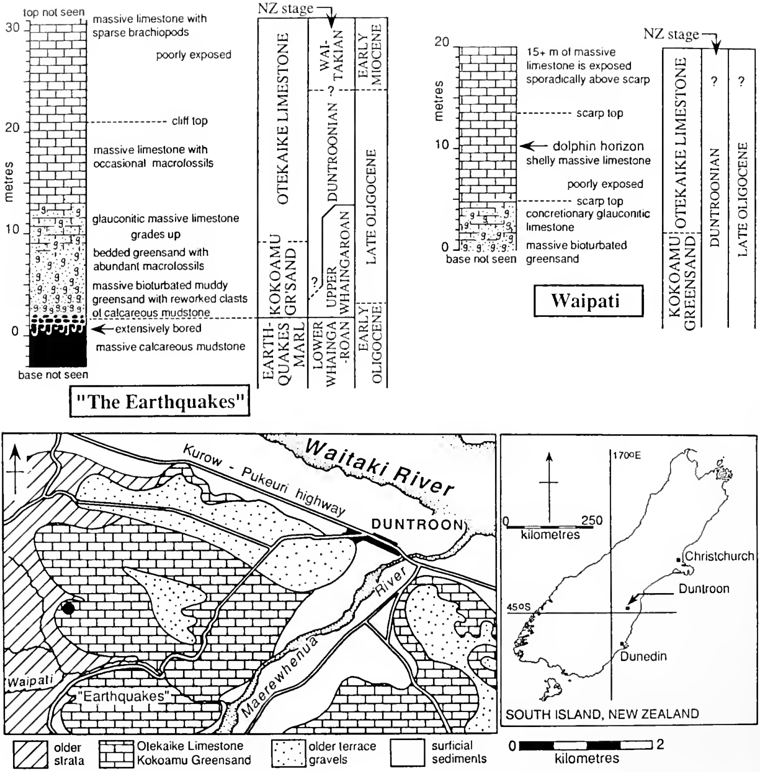


Figure 1. Locality map, geological map, and stratigraphic sections. Dot marks type locality of *Waipatia maerewhenua*. The "Earthquakes" section based on Hornibrook (1966), Fordyce et al. (1985), and Fordyce and M.A. Ayress field data. The Waipati section from Fordyce's field data; detailed microfossil dates unavailable for Waipati. Correlations between "Earthquakes" and Waipati sections are lithostratigraphic. Upper parts of both sections, exposed discontinuously on sloping hillsides, are measured less reliably than lower parts. Geological map based on Gage (1957).

Zealand Mapping Series] 260 metric sheet 140 (1987): 222912; near latitude 44° 51.5' S, longitude 170° 37.25' E. See Gage (1957: Geological Map No. 2).

Horizon and age.—Massive limestone with sparse macrofossils (Maerewhenua Member), 8–9 m above the base of the Otekaike Limestone Formation (Fig. 1). Fossil record number 140/f284 (New Zealand fossil record file, Geological Society of New Zealand). Matrix lacks *Globoquadrina dehiscens*, a planktonic foraminiferal index species for the Waitakian Stage; this species appears nearby in the upper Otekaike Limestone (Hornibrook et al. 1989). Other foraminifera in the sample indicate a Duntroonian to Waitakian age. The upper Duntroonian Stage is likely; this is equivalent to late or latest Oligocene, about 24–26 Ma (Hornibrook et al. 1989). Nearby, at "The Earthquakes," the stratigraphic sequence is established better (Fig. 1; Fordyce et al. 1985; Gage 1957; Hornibrook 1966; Hornibrook et al. 1989), reinforcing an upper Duntroonian determination. Here, the lower Otekaike Limestone represents the Duntroonian Stage (late to latest Oligocene), while Waitakian faunas (earliest Miocene) appear 13–14 m above the base of the limestone.

Diagnosis.—Odontocete with slightly asymmetrical skull of medium size (condylobasal length approximately 600 mm), attenuated rostrum, heterodont polydont teeth, and basicranium of archaic grade. Placed in the Platanistoidea because the periotic has an incipient articular process, the anterior process is roughly cylindrical in cross section and deflected ventrally, and the tympanic bulla has an incipient anterior spine, anterolateral convexity, and ventral groove extending anteriorly as a series of long fissures. Allied with the Squalodelphidae and Platanistidae, rather than the Squalodontidae, because the long asymmetrical posterior apex of the premaxilla extends posterior to the nasal to wedge between the elevated edge of the maxilla and frontal on vertex, the cheek teeth are small, the incisors are relatively delicate and procumbent, the premaxillary sac fossa is relatively wide and expanded medially to form a significant prenarial constriction, the pterygoid sinus fossa is in the alisphenoid and/or basioccipital dorsolateral to the basioccipital crest and posteromedial to the foramen ovale, the lateral groove affects the external profile of the periotic, rendering it sigmoidal in dorsal view, the dorsal ridge on the anterior process and body of the periotic is associated with a depression near the groove for the tensor tympani, the profile of the anteroexternal sulcus of the periotic is recurved and concave dorsally, and the squamosal carries a smoothly excavated periotic fossa associated with an incipient subcircular fossa (enlarged foramen spinosum) dorsal to the periotic. More derived than described Squalodelphidae, Platanistidae, and Dalpiazinidae in that the mandibles have a shorter unfused symphysis, the sinus fossa in the alisphenoid and/or basioccipital is larger, and the anterior process of the periotic is relatively larger and more inflated transversely, with a blunter apex reflected more abruptly ventrally.

Etymology.—From the Maori name Maerewhenua, name of a river near the type locality. Probable derivation: maere, perhaps from maru, shelter, or maero, the original inhabitants; whenua, country or land. Regarded as indeclinable. Pronunciation: mae-re-whe-nua, with *a* pronounced as in English "far," *e* as "ea" in English "leather," *wh* usually as "f" but sometimes as "wh" as in "when," *u* as double "o" in English "moon."

General description.—The skull is nearly complete; it lacks the apex of the rostrum, the pterygoids, and all but the bases of the jugals. There is a little shear (structures on the right side lie anterior to those on the left) but no major diagenetic distortion; the brain case is slightly crushed. The asymmetry of the nasals, frontals, premaxillae, and base of the rostrum appears real. The skull was found upside down; the right mandible lay bent over the rostrum with its body perforated by maxillary teeth. The earbones and 17 partial or whole teeth were loose in the matrix around the skull. About 1.5 m^2 was excavated without revealing the rest of the skeleton.

Cranium.—The cranium (that portion of skull posterior to the antorbital notches) is about as long as it is wide. In lateral view (Fig. 2e), the orbit is little elevated above the base of the rostrum. The external nares open from subvertical narial passages about level with the postorbital processes of the frontals. At the level of the nasals, the face is up to 30–35 mm deep, indicating well-developed maxillo-naso-labialis (facial) muscles (Fig. 2). Facial muscle origins, formed by the maxilla, are relatively long and narrow and not expanded or deepened posterolaterally; the posterior of the face is shallow. The maxilla and frontal only partly roof the relatively large temporal fossa (Figs. 2a, b). A prominent temporal crest with a long straight postorbital border bounds all of the dorsal edge of the fossa; within the fossa the braincase is not obviously inflated. The intertemporal constriction is reduced, with a narrow band of parietals exposed dorsally. The supraoccipital lies well forward, not encroached upon by facial elements.

Rostrum.—The rostrum is relatively long, wide at its base at the antorbital notches, and attenuated anteriorly (Figs. 2a, 3a). Each antorbital notch, which transmitted the facial nerve, is open anteriorly but is shallow dorsoventrally. A prominent antorbital (preorbital) process extends forward to bound the notch laterally. Anterior to the right notch, the rostral margin of the maxilla flares out to form a marked flange missing on the left (Figs 2a, 4a, 5a). The right notch is deeper and more U-shaped than the left. As viewed laterally (Fig. 2e), the premaxilla forms all of the dorsal profile; the ventral surface of the rostrum, formed by the maxilla, is roughly flat, and the rostrum thins only a little apically. In ventral view (Fig. 2c), the anterior half of the rostrum is grooved medially, while posteriorly it is gently convex. Palatal ridges are indistinct, and there are no rostral fossae for pterygoid sinuses. In dorsal view, the open mesorostral groove is wide posteriorly but narrow anteriorly. Other profiles of the rostrum are shown in Figs. 2 and 4.

Premaxilla.—Anteriorly, the premaxilla is narrowest in dorsal view at mid-rostrum, where it bounds and slightly roofs the mesorostral groove. Further forward, the premaxilla forms the apical 55+ mm of the rostrum. The dorsal rostral suture with the maxilla is prominent but not deep. The premaxilla forms an internarial constriction medially, where the premaxillary sac fossa is widest between the level of the nares and premaxillary foramina. Anteriorly, the fossa is nearly horizontal in transverse profile; it narrows and is elevated behind the prenarial constriction. Each premaxillary foramen is single; the right is longer than the left and lies more posteriorly, but both open anterior to the antorbital process. The anteromedial and, particularly, the posterolateral premaxillary sulci are prominent (Fig. 4a), but the posteromedial sulcus is shallow and indistinct. The nasal plug muscle probably originated on the narrow shelf of the premaxilla that overhangs the mesorostral groove anteromedial to the premaxillary foramen. Much of the outer margin of the premaxilla lateral to the premaxillary sulci carries a low thick rounded ridge. In dorsal view, the lateral edge of the premaxilla is gently convex around the region of the external nares. Lateral to each naris and within the premaxilla is a long median premaxillary cleft (new term; Figs. 4d, 5b), perhaps a vascular feature, which ascends posteriorly toward the junction of premaxilla, maxilla, nasal, and frontal at the vertex. The cleft lies just internal to the prominent medial facial crest formed by the maxilla and premaxilla and does not strictly mark the boundary between the posterolateral plate and posteromedial splint of the premaxilla. On the left, the premaxillary cleft grades forward into the posterolateral sulcus.

The premaxilla is split or bifurcated posteriorly into a more dorsal, posteromedial thin ascending process (splint) and a more ventral posterolateral plate (*sensu* Fordyce 1981). The posterolateral plate is developed where a thin portion of the premaxilla external to the posterolateral sulcus overlaps the maxilla; this plate is conspicuous in lateral view (Figs. 4c, 6b) but is indistinct from above (Figs. 4d, 5b). The narrow posteromedial splint extends behind each nasal to wedge between the maxilla and frontal, thus separating the nasal from the maxilla. The left and right splints are asymmetrical (Figs. 4d, 5b).

Maxilla.—Rostral profiles of the maxilla are shown in Figs. 2a, b, e and 4a–c. At least one maxillary foramen opens in the shallow depression between the maxillary flange and antorbital notch, and two or three foramina also open around each notch, but numbers are uncertain because the bone surface is damaged. Contacts with the frontal and lacrimal can be localized only to within a few millimeters. The right antorbital process, formed by the lacrimal, is not covered by the maxilla. Ventrally, the maxilla forms most of the surface of the rostrum; it extends back between the subhorizontally

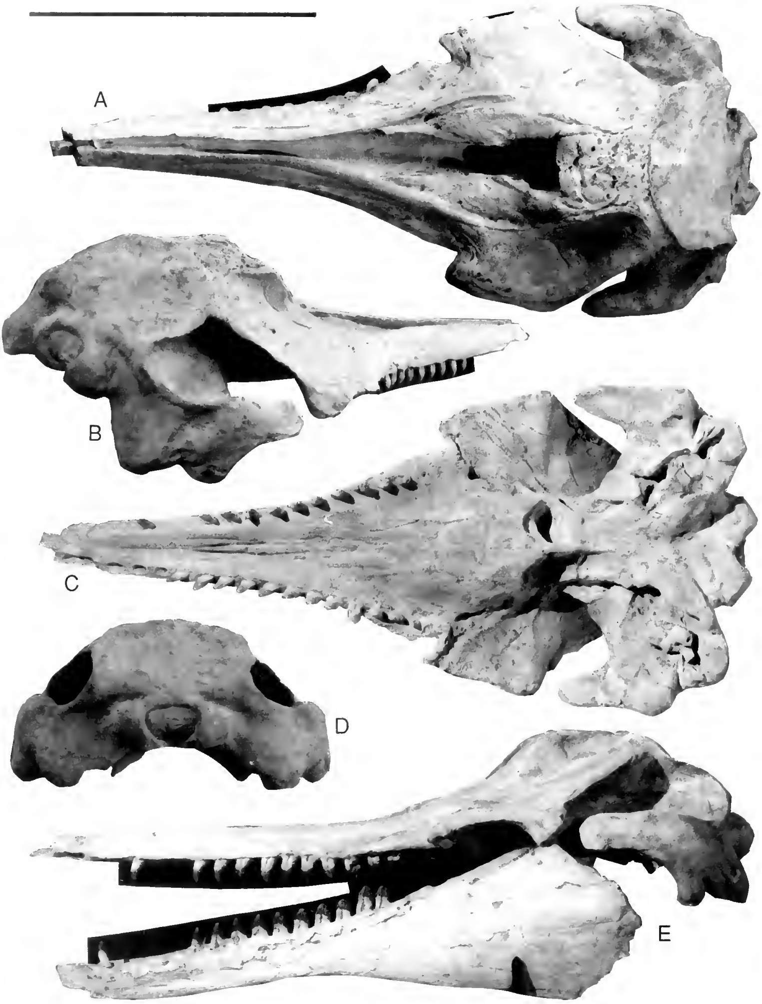


Figure 2. *Waipatia maerewhenua*, holotype, OU 22095. Skull, coated with sublimed ammonium chloride. All to same scale; scale = 200 mm. A, dorsal; B, right posterolateral; C, ventral; D, posterior; E, left lateral of skull and left mandible.

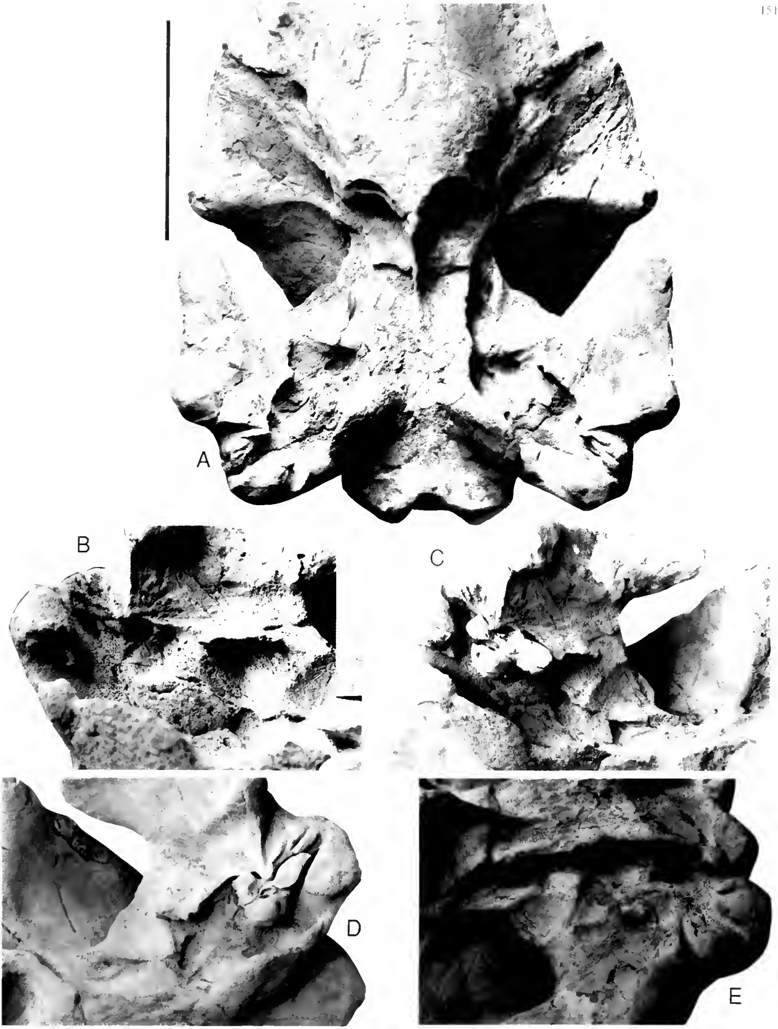


Figure 3. *Waipatia maerewhenua*, holotype, OU 22095. Skull, coated with sublimed ammonium chloride. A, ventral view, posterior of basicranium, right side. Scale = 100 mm. B–E all to same scale; ruler divisions are 1 mm. B, ventromedial view, posterior of basicranium, right side. C, ventral view, posterior of basicranium with periotic in place, right side. D, ventral view, posterior of basicranium with periotic in place, left side. E, ventrolateral view, posterior of basicranium showing pterygoid sinus fossa posteromedial to foramen ovale, right side.

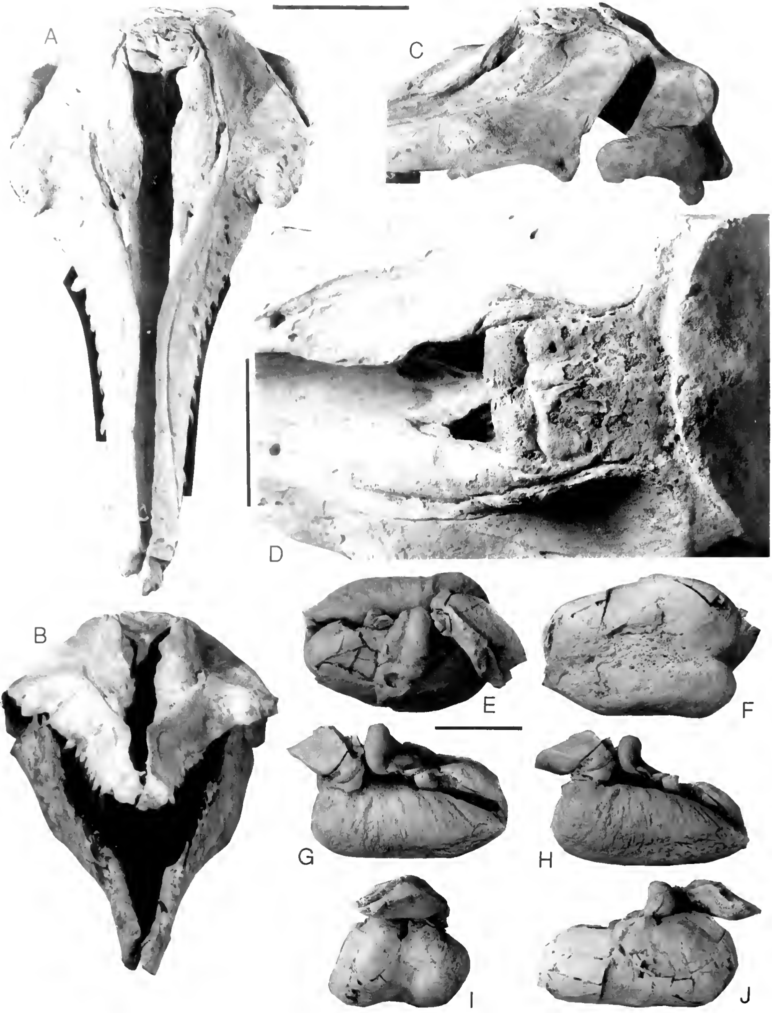


Figure 4 *Waipatia maerewhenua*, holotype, OU 22095. A–D, skull, coated with sublimed ammonium chloride. A–C at same scale; scale = 100 mm. A, anterodorsal; B, skull with articulated mandibles, anterior and slightly dorsal view (mandibles are distorted so that symphysis does not articulate properly); C, left anterolateral; D, detail of vertex. Scale = 50 mm. E–J, holotype, left tympanic bulla, coated with sublimed ammonium chloride. Scale = 20 mm. E, dorsal, F, ventral; G, oblique dorsolateral of medial face. H, medial; I, posterior; J, lateral.

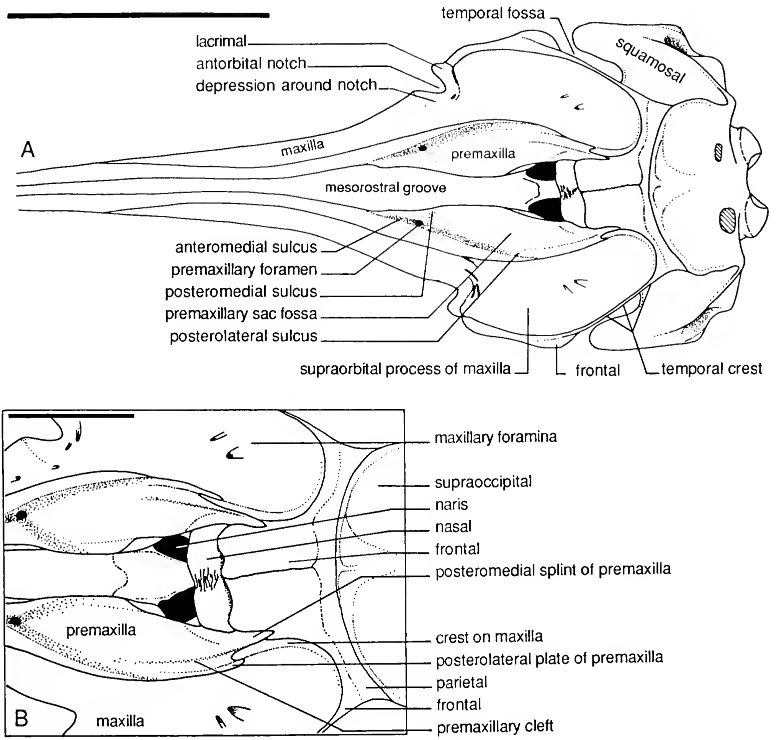


Figure 5. Reconstructions of dorsal view of skull of *Waipatia maerewhenua*. A, general profile. Scale = 200 mm. B, detail of vertex. Scale = 50 mm.

directed infraorbital foramen and the palatine but does not contribute to the anterior wall of the orbit (Figs. 2c, 3a, 7a).

The cranial part of the maxilla (e.g., Figs. 2a, 4a, c) forms a long narrow supraorbital process that covers all of the frontal but for a thin lateral band over the orbit and curves in gently behind the nasals. Although the maxilla is slightly thickened just behind the antorbital process, there is no facial crest. Each supraorbital process has two centrally placed posteriorly directed maxillary foramina about level with the postorbital process of the frontal; these foramina supplied blood vessels and nerves to the facial muscles. The maxilla carries anteriorly directed grooves, not obviously vascular, anterior to the maxillary foramina. Posteriorly, the rounded apex of the maxilla is separated from the supraoccipital by a thin band of the frontal and parietal. Though the maxilla is subhorizontal over the orbit, it becomes steeper posteromedially, with a markedly concave surface. The maxilla rises abruptly at the vertex to form a barely elevated maxillary crest that contacts the premaxilla (anteriorly) and frontal (posteriorly) (Figs. 4c, 5b), just behind the bifurcation of the premaxilla.

Palatine.—Broadly exposed palatines form the posterior portion of the palate between the choanae (posterior nares) at about the level of the most posterior cheek tooth (Figs. 2c, 3a, 7a). The palatines are continuous transversely across the convex palate, not narrowed or split by contact of the pterygoids with the maxillae. Contacts with the maxilla and frontal are localized to within a few millimeters; the sutures appear to be simple. The palatine sulci on the maxilla extend back toward the palatines, but the maxillary–palatine suture is preserved too poorly to tell whether a palatine foramen is present. Medially the palatines contact each other to form an indistinct flat palate bounded by faint palatal crests. Each

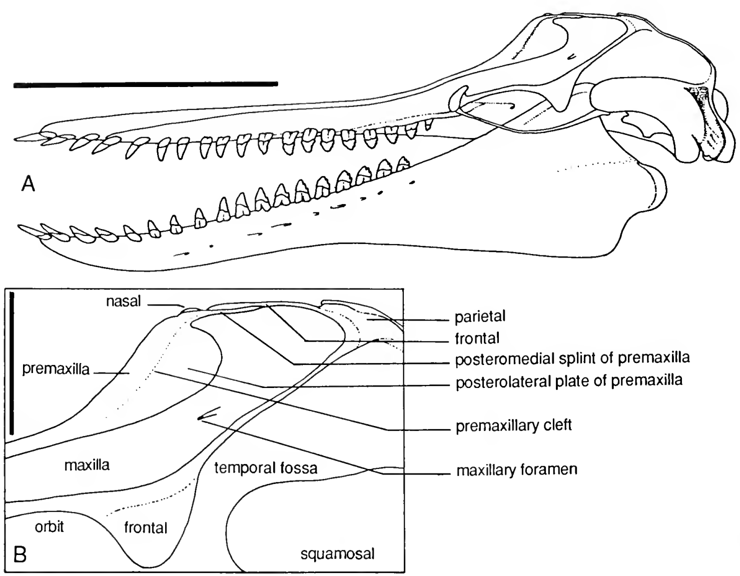


Figure 6. Reconstructions of lateral view of skull of *Waipatia maerewhenua*. A, general profile. Scale = 200 mm. B, detail of face. Scale = 50 mm.

palatine is prominently excavated posteroventrally, just below the choana, with a shallow, crescentic depression at the pterygopalatine suture (Fig. 3a). The palatine lacks a lateral (outer) lamina.

Pterygoid and pterygoid sinus.—Neither pterygoid is preserved. The loss of the pterygoids reveals an overlying large channel for the maxillary branch of the trigeminal nerve (V_2), which ran from near the foramen ovale internally out via the foramen rotundum to the orbit (Figs. 3a, 7a). The long lateral margin of the basioccipital, basisphenoid, and vomer in front of the basioccipital crest indicates that the inner lamina of the pterygoid was long; an anterior facet on the basioccipital crest indicates contact with the pterygoid. Since the basisphenoid and vomer are wide (Fig. 3a), the inner lamina of the pterygoid was probably narrow, not expanded medially. There is no evidence of a well-developed bony lateral lamina of the pterygoid associated with the subtemporal crest; the subtemporal crest is the abrupt ventrointernal margin of the temporal fossa (here mainly formed by alisphenoid) that extends from near the choanae toward the squamosal, to separate the basicranium from the temporal fossa and orbit. This well-preserved crest lacks a thin bony ridge, which would be expected if a pterygoid lateral lamina had extended ventral to the crest, and lacks a definite suture for the pterygoid. Furthermore, the falciform process of the squamosal (Figs. 3a–e, 8a, b) lacks evidence of contact with the pterygoid.

A relatively large hemispherical pterygoid sinus fossa is present; despite its name, this fossa lies mainly in the alisphenoid. The missing pterygoid probably formed the anterior part of the fossa. The fossa apparently did not extend anteriorly or dorsally beyond the pterygoid, and there is no evidence of a fossa in the palatine (Figs. 2c, 3a). Farther dorsally, the palatine and/or frontal just below the orbital infundibulum lacks any channel for an orbital extension of the pterygoid sinus; the orbit lacks fossae. Behind the orbit, the prominent subtemporal crest (Fig. 7a) further indicates that the pterygoid sinus was confined to the skull base. Smooth bone surfaces posterior to the main pterygoid fossa indicate other lobes of the sinus. Probable fossae include the large depression in the alisphenoid anterior to the groove for the mandibular nerve (V_3) and a smooth depression between the foramen ovale and falciform process. A fossa, presumably for a large posteromedial lobe of the pterygoid sinus, lies posteromedial to the foramen ovale around the carotid foramen. Sutures here are fused; the fossa probably involves the alisphenoid, basisphenoid, and the dorsal part of the basioccipital crest (Figs. 3e, 8a).

Nasal.—Nodular, anteroposteriorly short, wide nasals are crudely rectangular in dorsal view, with a convex anterior margin and a biconcave posterior margin (Figs. 2a, 4a–d). In vertical profile the anterior edge is rounded. Each nasal extends posterolaterally between the frontal and premaxilla, markedly so on the left. The interdigitating internarial suture and, particularly, the nasofrontal suture are depressed but not deep or narrow. The nasals only slightly overhang the external nares.

Mesethmoid.—The mesethmoid forms much of the borders of the narial passages below the nasals (Figs. 4d, 5b). Anteromedially,

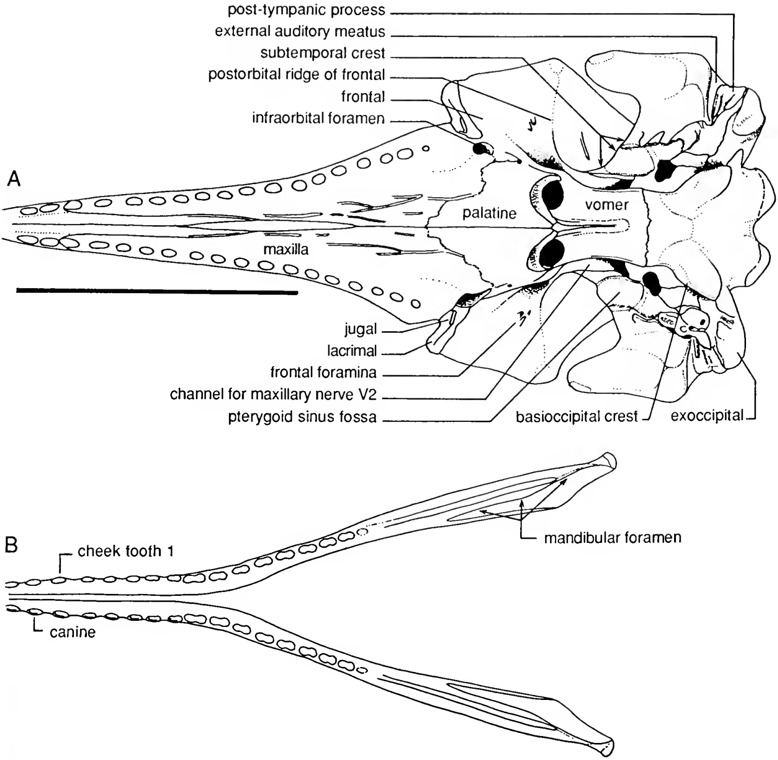


Figure 7. Reconstructions of *Waipatia maerewhenua*. Scale = 200 mm. A, ventral view, skull; B, dorsal view, mandible.

it forms a low rim on the narial passage at the posterior of the mesorostral groove, where it is probably fused with the vomer and/or presphenoid. Further posterodorsally, the mesethmoid forms an ossified internarial septum about 10 mm wide. The dorsal surface here and further ventrally in the mesorostral groove is diffuse and probably carried cartilage that formed a septum between the soft tissues of the nares and also filled the mesorostral groove. The mesethmoid does not significantly support the nasals (Fig. 4b). Behind and laterally, a narrow groove (for the olfactory nerve?) ascends to a diagonal depression (for the olfactory foramen?).

Vomer.—This lines the mesorostral groove, with a thin sliver exposed ventrally on the palate (Figs. 2c, 7a) between the maxillae. Further posteriorly (Fig. 3a), the sagittal part of the vomer separates the choanae, where the narial passages turn abruptly dorsally toward the external nares. The horizontal part of the vomer extends at least 65 mm posterior to the palatine, almost level with the foramen ovale, to cover the basisphenoid and broadly roof the basicranium. The margins of the horizontal part are subparallel posteriorly but flare out anteriorly as the choanae widen.

Lacrimal.—The lacrimal is exposed to dorsal view (Figs. 2a, 4a–c) at the antorbital process, where it forms the lateral margin of the antorbital notch. Sutures are ill defined because thin edges on the maxilla are preserved poorly. The lacrimal is thin both dorsoventrally and anteroposteriorly, is transversely wide, is directed anterolaterally, and has only a small ventral exposure. Ventrally, the transversely wide, anteroposteriorly narrow broken base of the

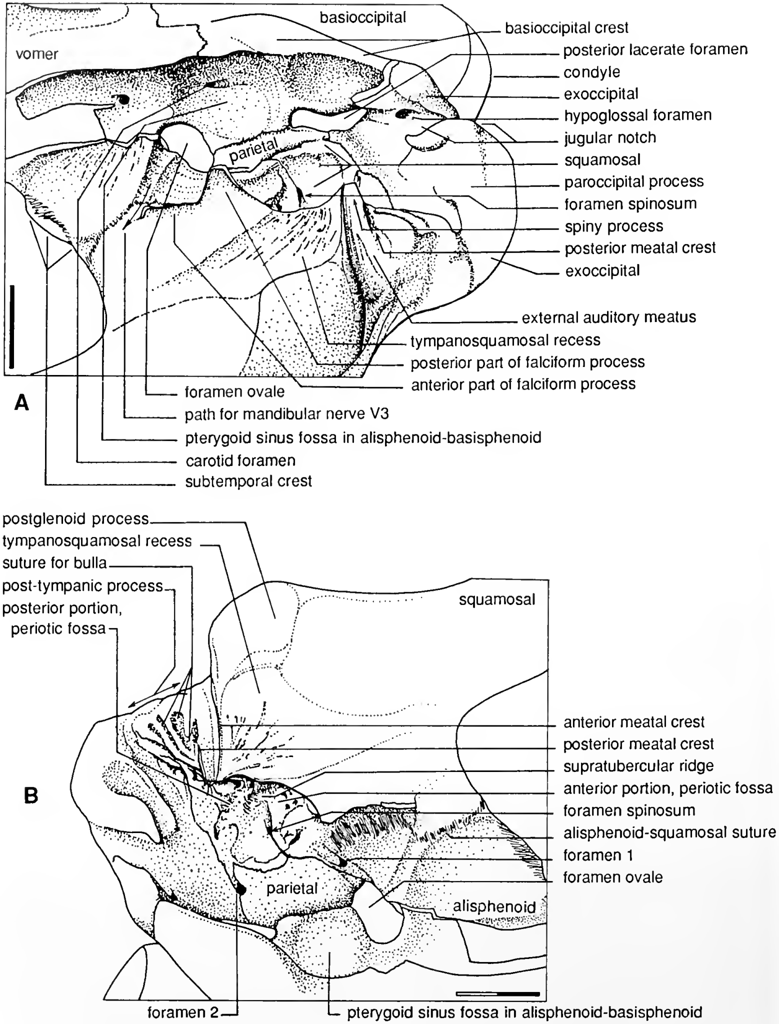


Figure 8. Interpretations of details of basicranium of *Waipatia maerewhenua*. Scale = 20 mm. A, ventrolateral, right side with ventral uppermost, showing position of fossa for pterygoid sinus in alisphenoid and basioccipital posteromedial to foramen ovale. B, ventral and slightly medial aspect, right side showing periotic fossa, presumed foramen spinosum, and other structures around periotic.

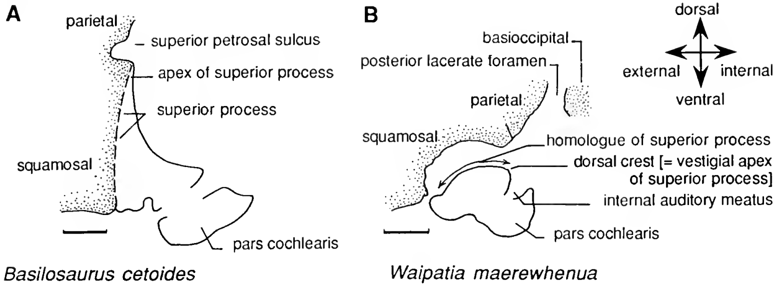


Figure 9. Schematic cross section of the basicranium at the level of the periotic in *Basilosaurus cetoides* (redrawn from Pompeckj 1922: pl. 2) and *Waipatia maerewhenua*, showing changes in relationship of periotic, squamosal, and parietal. Scale = 10 mm. A, *Basilosaurus cetoides*; B, *Waipatia maerewhenua*.

jugal lies immediately behind the antorbital notch. There is no clear evidence of a lacrimal canal.

Frontal.—The frontals have a long (ca. 45 mm) rather tabular exposure on the vertex behind the nasals (Figs. 4d, 5b). Since other bones on the skull are fused to the degree expected in a subadult or adult specimen, the distinct interfrontal suture is noteworthy. The frontals are markedly asymmetrical, with the left wider and shorter than the right. There are no supraorbital foramina (the large hole visible in Fig. 4d is a tool mark). The depressed suture with the parietals is partly fused; an interpretation appears in Fig. 5b. Farther laterally (Fig. 2b, 4c), the frontal is barely exposed dorsally along the postorbital margin of the face.

Ventrally, the frontal forms most of the shallow elongate orbit. The preorbital ridge is low and indistinct, without an antorbital process, and barely separates the orbit from the infraorbital foramen (Fig. 3a). The lateral margin of the frontal is thin; farther medially, two or three confluent small frontal foramina open laterally in the roof of the orbit near the prominent postorbital ridge (Figs. 3a, 7a). Posteromedially, the postorbital ridge appears to contact the alisphenoid. Behind the ridge and below the posterior of the face, the frontal forms a large posteroventrally directed origin for the temporal muscle.

Parietal.—A narrow slightly depressed band of parietal is exposed across the vertex between the frontal (Figs. 4d, 5b) and the nuchal crest of the supraoccipital. No obvious postparietal foramina or interparietal are present. A short robust temporal crest formed by the parietal separates the vertex from the temporal fossa at an intertemporal constriction. The parietal forms the slightly inflated anterolateral wall of the brain case (= medial wall of the temporal fossa), where it is markedly concave dorsally but convex farther ventrally toward the subtemporal crest.

A nodular exposure of parietal is present in the basicranium dorsomedial to the periotic and immediately internal to the squamosal (Figs. 3a–c, 8a, b), where it faces ventromedially. The parietal thus lies immediately dorsal and internal to the dorsal crest of the periotic (Figs. 8a, b, 9a, b); such juxtaposition is concomitant with the lack of a discrete subarcuate (subfloccular) fossa on the periotic and a change in the structure or position of the superior petrosal sulcus. Here the parietal lacks evidence of large cavities (presumed vascular sinuses) of the sort present anterior to the periotic in the archaeocete *Basilosaurus cetoides* (USNM 6087; Kellogg 1936: figs. 5, 6). Medially, the parietal contacts an extensive horizontal sheet of apparently fused basisphenoid (anteriorly) and basioccipital (posteriorly); the contact of these three elements separates the foramen ovale anteriorly from the posterior lacerate foramen and clearly isolates the periotic from the cranial cavity (Figs. 3b–e, 8b, 9b). The term cranial hiatus, used by Fraser and Purves (1960) for structures here, seems redundant; furthermore, a perusal of literature indicates that the term is used in an ambiguous and misleading way. Posteromedially, the parietal borders the posterior lacerate foramen, while farther laterally it has a long suture with the exoccipital that includes the small foramen 2 of Fig. 8b. The long suture with the alisphenoid anterolaterally is formed by a narrow fissure that runs obliquely from the foramen ovale to open at the foramen spinosum (Figs. 3a–c, 8a, b) dorsal to the periotic.

Squamosal.—In dorsal view, the zygomatic process parallels the axis of the skull at the maximum width of the cranium. The process reaches forward to about level with the back of the nasals but does not reach the level of the postorbital processes of the frontals. The crest of the zygomatic process is rounded transversely but nearly flat anteroposteriorly (Figs. 4a, c). Posteriorly, above the external auditory meatus and post-tympanic process, the zygomatic process carries a large fossa (Figs. 2b, d, e) that angles forward almost to the level of the postglenoid process; this fossa forms an origin for some or all of the sternomastoideus, scalenus ventralis, longus capitis, and mastohumeralis muscles (cf. Howell 1927; Schulte and Smith 1918). Dorsally, at the apex of the fossa, the broad crest of the zygomatic process passes abruptly into a narrow lambdoid crest that curves inward and up onto the supraoccipital. Between the parietal and zygomatic process, the dorsal surface of the squamosal carries a broad shallow depression that forms the floor of the temporal fossa. The apex of the zygomatic process is rather short and rounded.

The ventral surface of the squamosal is complex. In ventral view (Figs. 3a–e) the zygomatic process has a steep external face and gently rounded internal face, with a short narrow facet for the jugal at its apex. Posteriorly, a distinct ridge at the outer margin of the tympanosquamosal recess for the middle sinus marks the inner edge of the glenoid fossa. The ridge and recess extend ventrolaterally onto the robust postglenoid process, where the recess is widest; here the skull lacks a postglenoid foramen and the anterior transverse ridge associated with this foramen. Near the spiny process (*sensu* Muizon 1987), the surface of the recess carries a few shallow striae, presumably vascular, but there are no clear foramina (Figs. 3b, d). Anteriorly, the boundaries of the recess are indistinct, without any marked dorsal excavation.

Anteriorly, the squamosal–alisphenoid suture is indistinct (Fig. 8b). Contacts are not clear beyond foramen 1 of Fig. 8b. There is no pterygoid process of the squamosal at the subtemporal crest, but the falciform process (Figs. 3a–e, 8a) is well developed. This process has a long base and is bifurcated; an anterior portion extends out as a thin platelike subhorizontal spike ventral to the path of the mandibular nerve (V_3), while a posterior portion curls ventrally and inwards along the apex of the anterior process of the periotic. Both parts of the falciform process are thin distally and show no sign of contact with the pterygoid.

The smooth squamosal forms a sporadically vascularized and spacious periotic fossa (new term) above the periotic and lateral to the parietal (Figs. 3a, b, e, 8b, 9b). The periotic fossa extends anteroposteriorly about 22 mm from the base of the falciform process almost to the exoccipital, and transversely about 20 mm from the inner edge of the tympanosquamosal recess to a crest on the inner margin of the squamosal. The latter crest apposes the ventrally adjacent dorsal crest of the periotic (Figs. 9b, 11b), close to the parietal.

The periotic in *W. maerewhenua* approximates the squamosal at the posterior process (which, though finely porous dorsally, is not fused), lateral tuberosity, and part of the anterior process (Figs. 3c, d). For the most part, the squamosal and periotic are widely separated dorsally, leaving a spacious cavity between the periotic fossa and the periotic (Fig. 9b). There are two ventrolateral fissures that open into this cavity immediately anterior and immediately posterior to the lateral tuberosity, between the external edge of the periotic and the inner edge of the tympanosquamosal recess (Fig. 3c).

The periotic fossa (Figs. 3a, b, 8b, 9b) is split into two portions by a roughly vertical supratubercular ridge (new term; Figs. 3b, 8b) 11–12 mm anterior to the spiny process. A larger anterior portion lies dorsal to the anterior process of the periotic, while the smaller posterior portion lies dorsal to the body of the periotic. The anterior portion of the periotic fossa probably transmitted the middle meningeal artery, which entered the periotic fossa via the fissure immediately anterior to the lateral tuberosity (between the anterior process and the inner edge of the tympanosquamosal recess; Figs. 3c, d), passed above the periotic, and entered the large foramen spinosum. Given the voluminous cavity between the periotic and periotic fossa, the artery may have given rise to a rete that filled the anterior part of the periotic fossa. A near-obliterated fissure that marks the path of the foramen spinosum (Figs. 3a, b, 8a, b) runs forward across the squamosal and along or near the parietal–alisphenoid suture toward the foramen ovale. The anterior part of the periotic fossa and the large foramen spinosum are provisionally regarded as homologous with the subcircular fossa *sensu* Muizon (1987) of *Notocetus vanbenedeni* Moreno, 1892.

In the smaller posterior portion of the periotic fossa, behind the supratubercular ridge, the wall of the squamosal is excavated dorsal to the spiny process. The excavation may represent an incipient cavity for the articular process of the periotic (as seen in *Zarhachis flagellator*; e.g., Muizon 1987). The posterior portion of the periotic fossa could have housed a rete, a lobe of the middle sinus extending dorsally from near the spiny process, or a part of the posterior sinus. It is not clear how the posterior part of the periotic fossa relates to the large posterior sinus fossa shown by Muizon (1987: fig. 3a) for *Notocetus vanbenedeni*.

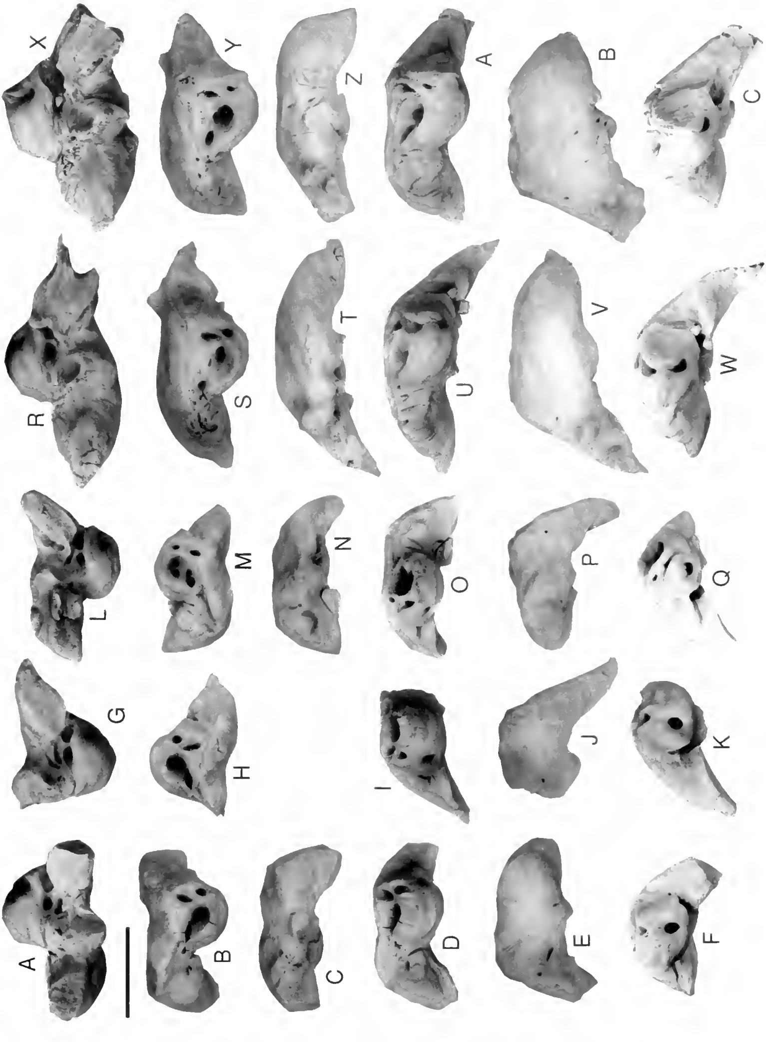
The external auditory meatus (Figs. 3a–e) is narrow, widens laterally and ventrally, and deepens externally; it has a steep anterior wall. Medially, the meatus is separated from the tympanosquamosal recess by a sharp anterior meatal crest (new term; Fig. 8b) that extends from the postglenoid process to the spiny process; in the Archaeoceti, a topographically identical and presumably homologous crest lies behind the vestigial postglenoid foramen. The posterior wall of the meatus slopes gently back to a low posterior meatal crest (new term; Figs. 8a, b), behind which lies the post-tympanic process (*sensu* Pompeckj 1922: pl. 2; = post-meatal process of Muizon 1987) of the squamosal (Fig. 8). The anterior edge of the posterior process of the bulla overlaps the posterior meatal ridge to form part of the meatus. Also, an anterodorsal projection from the posterior process of the bulla overlaps the spiny process. Three fissures in the post-tympanic process receive ridges on the posterior process of the bulla and the posterior (mastoid) process of the periotic (Figs. 3, 8a, b). *Waipatia maerewhenua* is amastoid, with a posterior process of the periotic that lies 9–10 mm internal to the skull wall, covered ventrally by bulla and hidden from lateral view. Behind the articulated periotic is a narrow cleft, open ventrally, by which the facial nerve perhaps left the skull.

Periotic.—The incomplete periotics together provide a clear idea of their structure. As this element seems one of the most diagnostic single bones among the Cetacea, I consider it here in detail. Morphological terms here largely follow Barnes (1978), Fordyce (1983), Kasuya (1973), Kellogg (e.g., 1923a), and Pompeckj (1922).

Distinctive features of the periotic (Figs. 10a–k, 11a–d) include, in summary, the large, robust, inflated anterior process with a subcircular cross section, an indistinct anterior keel, prominent anterointernal sulci (new term; see below), and a blunt apex. The lateral tuberosity and fossa incudis are prominent. The deep, laterally compressed, pyriform internal auditory meatus has a rather small posterior tractus, a very narrow anterior portion, and a supplementary opening (for the greater petrosal nerve?) off the facial canal (= Fallopian aqueduct of Kellogg) anterior to the internal auditory meatus. The smooth subspherical pars cochlearis is relatively large and dorsoventrally deep. The subcircular dorsal aperture for the cochlear aqueduct is small and thick-lipped, while the aperture for the endolymphatic duct is primitively slitlike. A dorsal crest (new term; Fig. 11b) forms the vertex of the dorsal surface. There is a narrow, smooth facet on the attenuated posterior process. Though each periotic is incomplete, it is likely that the axis (as viewed dorsally with the ventral face sitting on a flat plane) is sigmoidal, as is seen in *Notocetus marplesi*. Overall profiles are shown in Figs. 10a–k and Figs. 11a–d; details follow.

Of the two horizontal anterointernal sulci (Fig. 11d) on the internal face of the anterior process, the dorsal sulcus ends posteriorly at a vertical canal that opens (Figs. 11a, d) farther dorsally on the anterior process. One of these sulci may carry the lesser petrosal nerve. In lateral view (Fig. 10c), the axis of the anterior process is reflected down, so that the anterior bullar facet (that part of the anterior process normally in contact with the processus tubarius of

Figure 10. Periotics of *Waipatia maerewhenua*, squalodontids, and other presumed platanistoids. All coated with sublimed ammonium chloride. All life size; scale = 20 mm. A–K, *Waipatia maerewhenua*, holotype, OU 22095. A–F, right periotic. A, ventral; B, dorsal; C, lateral and slightly ventral; D, medial; E, lateral and slightly dorsal; F, posteromedial; G–K, left periotic; G, ventral; H, dorsal; I, medial; J, lateral; K, posteromedial. L–Q, *Notocetus marplesi*, holotype, left periotic, C.75.27. L, ventral; M, dorsal; N, lateral and slightly ventral; O, medial; P, lateral; Q, posteromedial. R–W, un-named squalodontid, right periotic, OU 22072. R, ventral; S, dorsal; T, lateral and slightly ventral; U, medial; V, lateral; W, posteromedial, showing reniform fenestra rotunda. X–C', unnamed squalodontid, right periotic, OU 21798. X, ventral; Y, dorsal; Z, lateral and slightly ventral; A', medial; B', lateral; C', posteromedial.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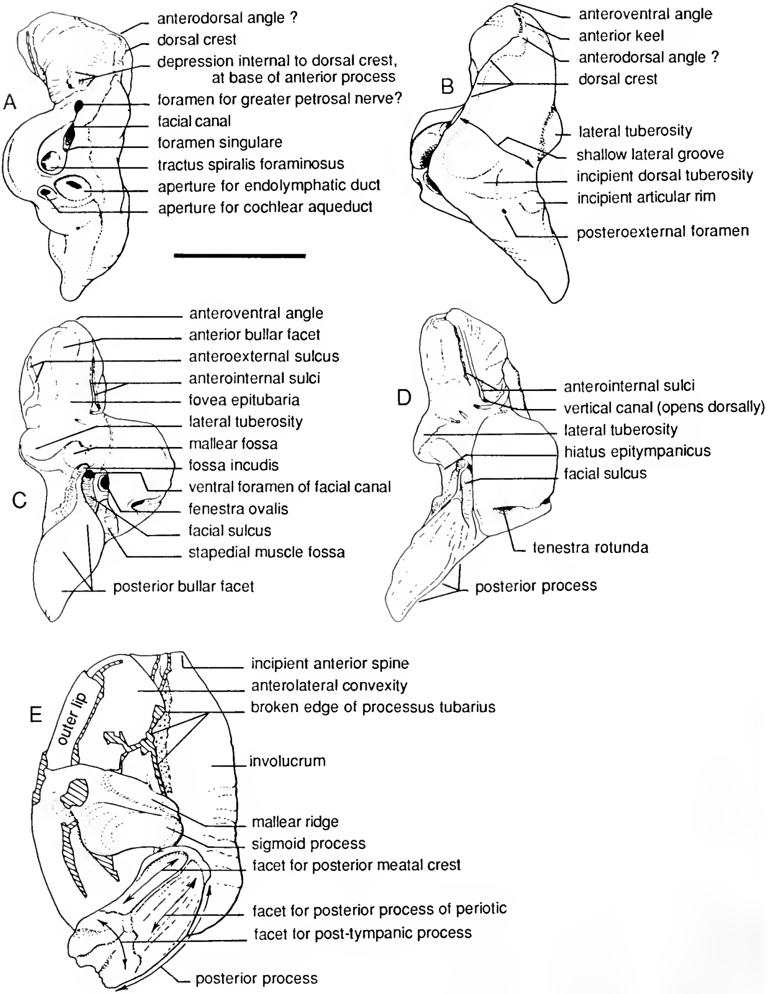

Figure 11. Camera lucida sketches interpreting the key features of the periotic and tympanic bulla of *Waipatia maerewhenua*. Scale = 20 mm. A–D, right periotic, with lateral tuberosity and posterior process reconstructed from left periotic. A, dorsomedial; B, dorsal to dorsolateral; C, ventral; D, ventrolateral; E, left tympanic bulla, dorsal.

the bulla; new term; Fig. 11c) is steeply inclined; the apex of the periotic appears blunt rather than attenuated. There are traces of an anterior keel on the anterior process. A prominent nodule on the inner face may represent a vestigial anterodorsal angle (*sensu* Fordyce 1983); the presumed anteroventral angle is blunt, not acute. The slightly damaged anterior bullar facet is a long shallow groove bounded laterally by smooth bone rather than by a thickened parabullary ridge (new term, possibly equals "distinct ventral rim" or "ventral swelling" of Muizon 1987: 7). More posteriorly, the fovea epitubaria (*sensu* Pompeckj 1922: 58, 66–67, pl. 2; = epitubarian fossa) is wide, shallow, and depressed medially. (Muizon 1987 used the term epitubarian fossa for what I term the anterior bullar facet.) A well-developed anteroexternal sulcus on the lateral face of the anterior process is visible in ventral view (Figs 10a, 11c); its recurved, dorsally concave profile is marked in external view (Fig. 10c). The sulcus may mark the path of a loop of middle meningeal artery ventral to the periotic.

The origin for the tensor tympani muscle is an indistinct cleft between the base of the anterior process and the perpendicular anterior face of the pars cochlearis. The pars cochlearis (Figs. 10a, b, d, f) is moderately inflated with abruptly rounded anterointernal and posterointernal angles; the posterointernal angle lacks a nodule. There is no obvious promontory sulcus. The small suboval fenestra rotunda is elongated vertically but is not reniform or fissured dorsomedially (Fig. 10f). Dorsally on the pars cochlearis, there is a faint raised rim on the long narrow internal auditory meatus, and an indistinct groove, perhaps a path for the inferior petrosal sinus, runs medial to the rim. Within the meatus, a rather narrow subcircular posterior tractus for the acoustic nerve is separated by a cleft from the deep narrow fissure into which open the small foramen singulare and slightly larger internal or dorsal aperture for the facial canal. A supplementary foramen opening 2–3 mm anterior to the internal auditory meatus (Figs. 10b, 11a) marks a canal (perhaps for the greater petrosal nerve) originating from the facial canal.

Externally, the dorsal surface of the body of the periotic has a long dorsal crest, indistinct posteriorly, but better developed anteriorly where it runs forward from the level of the facial canal on to the anterior process (Figs. 10b, 11b). Because of its topographic relations, I identify the crest as a homolog of the apex of the superior process of Archaeoceti (Fig. 9a,b). There is no obvious superior petrosal sinus or subarcuate (subfloccular) fossa internal to the crest. Between the lateral tuberosity (*sensu* Barnes 1978; = ventral tuberosity of Muizon 1987) and the posterior process, a broad shallow lateral groove (Figs. 10b, e, 11b) ascends the external face, rising toward the level of the dorsal opening of the facial canal. This lateral groove complements a depression in the squamosal, so that a cavity lies between the periotic and squamosal.

Ventrally on the body, the dorsoventrally compressed lateral tuberosity has a prominent subhorizontal crest (Figs. 10g, j) that closely follows the edge of the squamosal (Fig. 3d). Farther posteriorly, the hiatus epitympanicus is indistinctly biconcave (Figs. 10a, c). The anterior of this depression receives the spiny process (*sensu* Muizon 1987) at the internal limit of the external auditory meatus, while the shallow articular groove at the anterior of the base of the posterior process (Fig. 10a) receives the posterior border of the spiny process. Of other ventral features on the body, the mallear fossa has an indistinct posteroexternal boundary and carries a prominent foramen at its inner margin. The fossa incudis is prominent at the anterior end of a meandering shallow groove. The subcircular fenestra ovalis lies far dorsal to the surface of the pars cochlearis. The ventral (epitympanic) opening for the facial canal opens anteroexternal to the level of the fenestra ovale, while the shallow facial sulcus for the facial nerve disappears before the end of the fossa for the stapedial muscle. Ridges separate this large, concave, rugose, and rather narrow fossa from both the fenestra ovalis and the groove for the facial nerve.

On the posterior process (Figs. 10a, g), the facet for contact with the tympanic bulla is long, narrow, smooth, and attenuated, and does not extend dorsally onto the posteromedial face of the posterior process. Dorsally, two raised regions on the base of the posterior process may be homologous with more prominent structures on other platanistoids (Fig. 11b). An indistinct bulge on the dorsal surface of the posterior process is probably homologous with the dorsal tuberosity (*sensu* Muizon 1987). Further ventrally is a small posteroexternal foramen (new term; Figs. 10e, 11b), a persistent feature amongst archaic Cetacea, although of uncertain function. Below the posteroexternal foramen is a bulge on the base of the posterior process above the articular groove that is probably homologous with the articular rim (*sensu* Muizon 1987) or the peglike articular process of other Platanistoidea.

Tympanic bulla.—The bulla (Figs. 4e–j, 11e) is crushed. In dorsal or ventral view (Figs. 4e, f), it is roughly heart-shaped, with a convex outer margin, bilobed posterior face, and straight (posteriorly) to gently curved (anteriorly) involucrum. There is an incipient anterior spine and an anterolateral convexity (*sensu* Muizon 1987) on the outer lip, but there is no obvious anterolateral notch. Posteriorly, an interprominential notch separates the blunt inner prominence (medial lobe) and the narrower, deeper, slightly longer and more sharply rounded outer prominence (lateral lobe) (Figs. 4i, j). There is no obvious horizontal ridge between the prominences or across the inner prominence. In posterodorsal view, the interprominential notch is deep; below, it passes into a deep wide ventral groove that runs forward to about level with the sigmoid process (Fig. 4f). Farther forward, the groove is shallow and marked by fine to coarse fissures and small foramina; it extends to the apex of the bulla. The rough surface of the groove perhaps marks the attachment of the fibrous sheet known to cover the skull's base in some extant Cetacea (Fraser and Purves 1960). Although anteriorly the involucrum is depressed abruptly into the tympanic cavity (Fig. 4d), it is broad and not obviously invaded by an internally expanded tympanic cavity. Coarse striae of uncertain function cross the dorsal surface of the involucrum, radiating from about the position of the sigmoid process. The striae finish at a series of subhorizontal creases that traverse the inner face of the involucrum (Fig. 4h) and could be associated with tissues of the peribullary sinus known to occupy the space between the involucrum and the basioccipital crest in some extant Odontoceti (Fraser and Purves 1960).

As viewed laterally (Fig. 4j), the sigmoid process has an abruptly curved posteroventral profile; in anterior view the profile is rounded. The crushed lateral furrow is shallow. There is a robust oblique mallear ridge (new term) to which the malleus fuses internally at the base of the sigmoid process. The conical process, obscured by the sigmoid process, has a flat posterior face and may be anteroposteriorly compressed. A wide gap, now distorted, separates the conical process from the posterior process. The distorted long posterior process articulates with the squamosal in two ways (Fig. 11e); anterolaterally, the process carries a groove that overlaps the posterior meatal crest of the squamosal, while the thinner distal 12+ mm of the process has a ridged subhorizontal suture (Figs. 4i, j) that articulates with the post-tympanic process of the squamosal (Figs. 8a, b). In lateral view of the skull (Fig. 6a), the posterior process of the bulla is just visible ventral to the post-tympanic process. The elliptical foramen is open, deep, and narrow. When the bulla is articulated, there is a large cavity, presumably for the peribullary sinus, between the bulla and the basioccipital crest.

Supraoccipital.—The supraoccipital, which slopes forward at about 40° from horizontal, is roughly symmetrical, broad, and rather flat (Figs. 2a, b). Its blunt rounded anterior margin forms a nuchal crest elevated 3–4 mm above the parietal. A broad, low, and slightly asymmetrical anterior median ridge (Fig. 2a) bounds faint anterolateral depressions. Convex lambdoid crests are present laterally. Posteriorly, each crest descends abruptly toward the squamosal.

Basioccipital.—Behind the vomer, the basioccipital forms a shallow arcade that deepens posteriorly as the basioccipital crests diverge. Each crest is short (Fig. 3a) relative to the basicranial length. The crest is transversely thick and robust, with a thin ventral margin. Anterolaterally, just behind the carotid foramen, the dorsal base of the crest carries part of a large shallow hemispherical fossa for part of the pterygoid sinus (Figs. 3e, 8a). A small carotid foramen (Fig. 8a) indicates the anterior extent of the basioccipital, but there is no clear suture here with the alisphenoid or basisphenoid.

Exoccipital.—The hind surface of the exoccipital is gently convex, other than near the pedicle for the condyle where the surface is deeply excavated. The condyloid fossa is excavated deeply into the braincase; the condyle has a rather small articular surface and a prominent pedicle. The exoccipital is closely applied to the squamosal along its dorsal and lateral edges, with rounded borders and rather curved lateral and ventral profiles. Dorsally, the suture with the supraoccipital is fused (Figs. 2b, d).

Ventrally, the exoccipital forms the posterior portion of the so-called basioccipital crest, immediately internal to the shallow jugular notch and the internally placed hypoglossal foramen (Figs. 3a–e, 8a). The paroccipital process is robust, with a prominent but unidentified groove (Figs. 3a–c, right side) trending dorsomedially across the anterior face. Farther dorsally, the region between the exoccipital and squamosal–periotic is quite spacious, though there is no distinct fossa for a posterior sinus. Laterally, the exoccipital contacts the post-tympanic process of the squamosal (Fig. 3a).

Alisphenoid, basisphenoid, orbitosphenoid.—The alisphenoid forms part of the subtemporal crest, but is otherwise not exposed within the temporal fossa. Anteriorly, the alisphenoid forms most of what remains of the pterygoid sinus fossa. Posteriorly, the alisphenoid is notched at a large foramen ovale. The complex posterolateral suture with the squamosal is shown in Fig. 8b. The alisphenoid carries a broad, shallow groove for the mandibular nerve (V_3), which runs obliquely from the foramen ovale outward beyond the falciform process. Immediately anterior to this groove, the alisphenoid carries a large shallow hemispherical depression, probably for a lobe of the pterygoid sinus. The basisphenoid is probably fused with the alisphenoid; no sutures are apparent. Posteriorly, the carotid foramen marks the likely limit of the basioccipital. The orbitosphenoid is not distinct.

Teeth.—*Waipatia maerewhenua* is heterodont (Figs. 2e, 6a) and polydont. The right maxilla carries 16 alveoli (12 teeth are in place), suggesting 19 teeth in each upper tooth row. Alveoli in the right mandible indicate at least 16 and probably 19 teeth in the lower tooth row. Smooth procumbent single-rooted anterior teeth carry a crown formed by a single sharp and delicate denticle (Figs. 13 a, b). These subhorizontal apical teeth grade back into anterior cheek teeth with high crowns, small posterior accessory denticles, and fused double roots, in turn succeeded posteriorly by vertically positioned posterior cheek teeth with low, rather blunt and robust crowns that carry prominent posterior accessory denticles and strong ornament (Figs. 12a–f, 13c, d). The posterior diastemata are rather narrow, so that the upper and lower teeth probably did not interdigitate much. Apices of the posterior cheek teeth are worn from tooth-to-tooth contact.

No anterior teeth are in place in the subhorizontal alveoli of the premaxilla and mandible. Features of the presumed incisors (Figs. 13a, b, bottom) include a high smooth crown, subcircular in cross section with barely developed keels, and a somewhat inflated root that forms most of the height of the tooth. The largest tooth (maximum height, apex of crown to apex of root, 76+ mm), presumably I^1, has a gently sigmoid profile; its crown is subcircular in cross section. This large tooth was probably quite procumbent. Smaller and more recurved single-rooted teeth, presumably I^2, I^3, and C, have lower crowns that are recurved buccally and compressed laterally with indistinct keels. In lateral view, the axes of these teeth are recurved back, so that they were less procumbent than the apical teeth.

Features of the cheek teeth are shown in Figs. 12a–f and 13a–d. The axes of the upper cheek teeth are strongly recurved lingually (Fig. 4b), while the lower cheek teeth are roughly straight. The posterior two or three lower cheek teeth are inclined slightly outward, while the other cheek teeth are inclined lingually. Those cheek teeth in place are emergent, with the crown well clear of the alveolus. Crowns of the middle to posterior cheek teeth (Figs. 12a, b) are conspicuously compressed, with a high triangular main (apical) denticle, two or three posterior denticles, but no anterior denticles. The apical denticle becomes smaller posteriorly in the tooth row as the accessory denticles become larger, and the third denticle is better developed on the lower teeth. Buccal ornament is indistinct, but lingual ornament is strong and, basally, associated with a cingulum on most cheek teeth (Figs. 13c, d). In the double-rooted teeth, the roots are fused for at least one third of their length; anteriorly, roots are divergent, while posteriorly they are roughly parallel. The last upper cheek tooth is small and single-rooted with a coarsely ornamented subconical crown (Figs. 13c, d, upper left).

Mandible.—The reconstruction of the mandibles (Fig. 7b) is a visual "best fit," determined through aligning the mandibles with each other, with the glenoid cavities, and with the rostrum. The reconstructed profile in dorsal view is a Y shape, with a symphysis 110–120 mm long.

Conspicuous features of each mandible (Figs. 6a, 7b, 12c–f) include the relatively long tooth row, 16+ alveoli, the gently curved dorsal profile in which the long, narrow, and deep body passes back into the low coronoid process, the ventrally and laterally inflated "pan bone" (= outer wall of large mandibular foramen, or "mandibular fossa"), and the relatively short unfused mandibular symphysis. Both mandibles are incomplete. With the left jaw articulated on the skull, the tooth in the third preserved alveolus occludes behind the position of the upper left canine; I identify it provisionally as cheek tooth 1. Left lower cheek teeth 5–14 are in place, and there may have been a small cheek tooth 15; right lower cheek teeth 5–10 are in place.

The dorsal and ventral profiles of the body (Figs. 12c–f) are roughly parallel; the apical 80–90 mm of the ventral surface bends dorsally forward of the level of the fifth alveolus. The body deepens markedly behind cheek teeth 11–12, after which the pan bone is progressively inflated.

The long shallow apical groove on the internal face of each mandible probably indicates an unfused symphysis in which the bones were not closely apposed in life. The left mandibular foramen opens 140–150 mm anterior to the condyle (Figs. 12d, e). A robust ridge marks the posterodorsal edge of the foramen just below the coronoid process, where the foramen is about 90 mm deep. There is an equally robust ridge ventrally above the angular process. Internally, the condyle is slightly excavated, while its worn outer surface protrudes a little beyond the external profile. No distinct fossae are apparent for jaw muscle insertions; presumably insertions were as in extant Odontoceti (e.g., Howell 1927). Positions of the nine mental foramina are shown in Fig. 6a.

Vertebrae.—The atlas (Figs. 13e–g) is slightly distorted through crushing and shearing, and surface bone is eroded in places. It is moderately thick, not compressed anteroposteriorly, and not fused to the axis. The eroded base of the neural spine is not massive or inflated. Anterior and posterior facets for contact with the skull and axis diverge gently in lateral view. The anterior facets are shallow and indistinctly separated ventrally; the posterior facets are barely raised above the adjacent bone. The

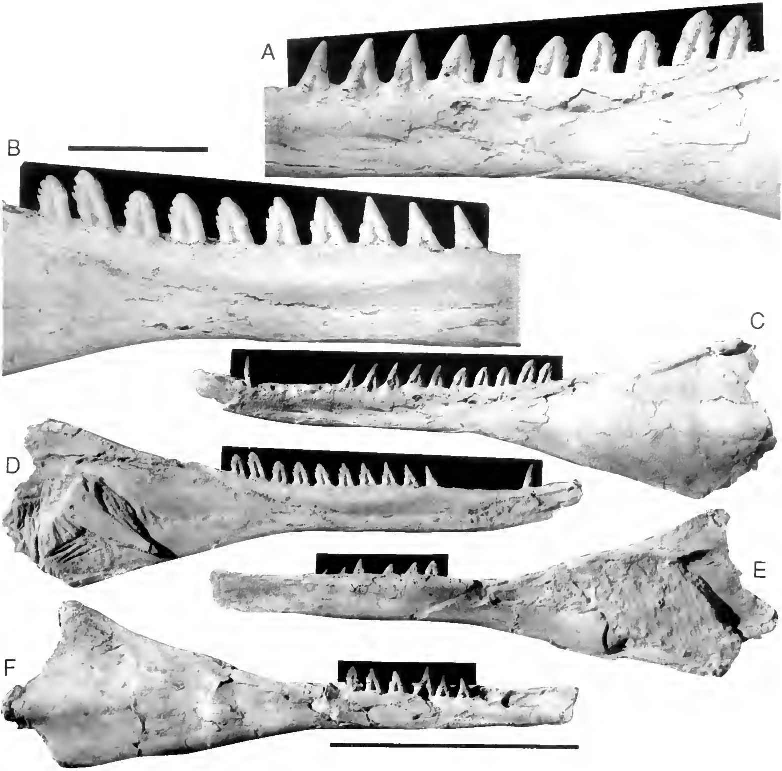

Figure 12. Mandible and teeth of *Waipatia maerewhenua*, holotype, OU 22095. All coated with sublimed ammonium chloride. A–B, detail of left cheek teeth, both at same scale; scale = 50 mm. A, buccal; B, lingual. C–F, mandibles; all at same scale; scale = 200 mm. C, lateral, left mandible; D, medial, left mandible; E, medial, right mandible; F, lateral, right mandible.

hypapophysis is small with an elongate base; this process extends 6–7 mm below and less than 5 mm behind the body. Upper and lower transverse processes are separate, not basally confluent. The eroded large upper process juts out abruptly, while the lower process has an anteroposteriorly short base. Rather small (diameter 5.5–8 mm) laterally facing transverse foramina perforate the robust neural arch. Only a poor natural cast of the anterior face of the axis is preserved to reveal a large neural canal, delicate neural arches, and a blunt odontoid process.

COMPARISONS: MORPHOLOGY, HOMOLOGY, AND FUNCTION

This section briefly reviews broader aspects of the skull of *W. maerewhenua*, emphasizing homologies with other taxa and possible functional complexes.

Face.—The soft facial tissues in the Odontoceti include the maxillo-naso-labialis muscles, the soft nasal passages, and the nasal diverticula (Mead 1975; Heyning 1989). Because these structures

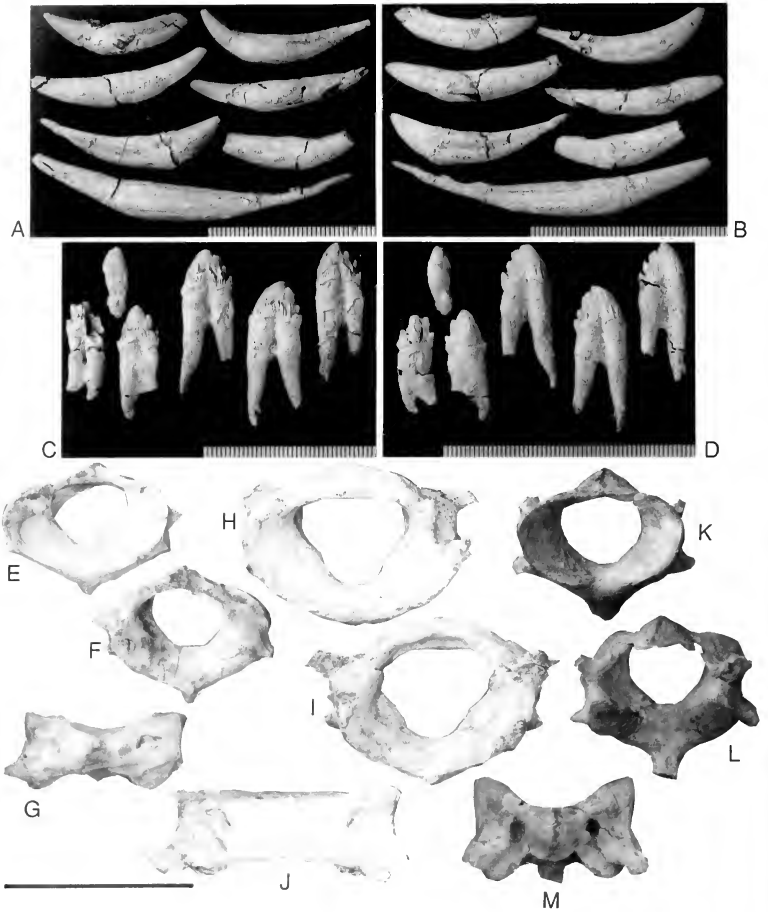

Figure 13. A–D, teeth of *Waipatia maerewhenua*, holotype, OU 22095. All coated with sublimed ammonium chloride. All life size; ruler divisions are 1 mm. A–B, upper and/or lower anterior teeth. A, lingual; B, buccal. C–D, lower cheek teeth and presumed last upper left cheek tooth. C, lingual; D, buccal. E–M, atlas vertebrae, all at same scale. Scale = 100 mm. E–G, atlas of *Waipatia maerewhenua*, holotype, OU 22095. E, anterior; F, posterior; G, dorsal. H–J, atlas of undescribed squalodontid, OU 22072. H, anterior; I, posterior; J, dorsal. K–M, atlas of *Notocetus marplesi*, holotype, C.75.27. K, anterior; L, posterior; M, dorsal.

dictate the topography of the facial bones, the structure of facial soft tissues can be inferred for fossils. Furthermore, the soft tissues of the face probably produce and transmit the high-frequency sounds used in echolocation (Mead 1975; Heyning 1989: 40–44). In terms of facial structure, *W. maerewhenua* is notably more derived than *Archaeodelphis patrius* Allen, 1921, in which the supraorbital process extends posteriorly only a little, the orbit is elevated with a prominent infraorbital process of the maxilla, the fossa for a facial muscle on the cranium is minimal, and the maxillary foramina lie roughly level with the antorbital notch. In *W. maerewhenua*, the fossa for the facial muscles is large, the roof of the orbit is depressed to lie about level with the posterior portion of the rostrum, so that rostral muscle origins and facial muscle origins are roughly on the same plane, and the maxilla does not contribute to the orbit. Well-developed premaxillary foramina and sulci are associated with a "spiracular plate" for the premaxillary sac fossa. Overall, *W. maerewhenua* has fundamentally the same facial structure as do many extant Odontoceti; it was probably capable of echolocating. In many other odontocetes (e.g., Delphinida, Ziphiidae), the face is broader, deeper, and displaced farther posteriorly relative to the orbits, so that the postorbital border of the temporal fossa is shorter, steeper, and more curved, the frontals and/or parietals are often lost from the vertex, and the supraoccipital is less obvious dorsally. Such changes probably reflect the continued expansion of the posterior parts of the maxillo-naso-labialis muscles associated with the soft diverticula of the external nares.

Like most extant Odontoceti, *W. maerewhenua* shows facial asymmetry (involving maxilla, nasals, and frontals) that presumably reflects asymmetry of the overlying facial muscles. The asymmetrical flared margin of the right maxilla (Fig. 2a) is of uncertain function; it may be homologous with the maxillary flanges of *Mesoplodon* (Ziphiidae; True 1910b), though the left maxilla lacks such a flange. Presumably, such asymmetry indicates muscle asymmetry, though it is not clear that this part of the rostrum is a significant muscle origin in extant taxa (Mead 1975; Heyning 1989). The function of the shallow depression immediately posterior to the maxillary flange is also uncertain. A similar asymmetrical profile is visible in a cast (USNM 243978) of the skull of *Microcetus sharkovi* Dubrovo, 1971 (in Dubrovo and Sharkov 1971: fig. 2), and in the skull of *Squaloziphius emlongi* Muizon (1991: fig. 1).

The function of the bifurcated posterior of the premaxilla, a feature seen in many odontocetes, is uncertain. The bifurcation perhaps marks a boundary for the facial muscles. Similarly uncertain is the function of the medial cleft in the premaxilla. Possibly homologous clefts occur near the boundary between the posterolateral plate and posteromedial splint in *Zarhachis flagellator* (figured by Kellogg 1926: pl. 2) and sporadically in the Ziphiidae. Judged from vascular patterns shown by Schenkkan (1973: fig. 5) for *Mesoplodon*, the cleft carries a vessel from the maxillary artery.

Feeding apparatus.—The long attenuated rostrum and mandibles, the relatively posterior position of the coronoid process on the mandibles, and the moderately large temporal fossae and origins for the temporal muscles suggest that *W. maerewhenua* fed by rapid snapping. The origin for the temporal muscles on the supraorbital process faces ventrally; in contrast, the temporal muscles' origin on the frontals of Archaeoceti and some Odontoceti (e.g., *Archaeodelphis* and the Physeteridae) faces roughly posteriorly. The more ventral position for this origin, widespread amongst the Odontoceti, is probably related to lever action of the mandible, but it may also be a consequence of the posterior expansion of the maxilla, in turn dictated by changes in orientation of the facial muscles.

Waipatia maerewhenua lacks a bony lateral lamina of the pterygoid sinus fossa, and there is no evidence that an ossified pterygoid contacted the falciform process. Among the Odontoceti, the presence or absence of such a bony lateral lamina (Cozzuol 1989; Fraser and Purves 1960) perhaps relates to feeding musculature. In the extant *Phocoena phocoena* (see Boenninghaus 1904: figs 3, 4; Fraser and Purves 1960: 12), which lacks a bony lamina, the medial limit of the large internal pterygoid muscle stretches from the pterygoid (and palatine?) back to the squamosal and bulla, with an extensive origin in the pterygoid ligament. Perhaps the lateral lamina is the ossified homolog of some of the pterygoid ligament, which would provide a stronger origin for the internal pterygoid muscle than would ligament alone. In terms of function, an ossified ligament could (1) compensate for enlargement of the pterygoid sinus fossa (functioning in acoustic isolation of the skull base), which could otherwise weaken the origin for the internal pterygoid, and/or (2) be dictated by an enlarged internal pterygoid muscle (functioning in feeding). More information about archaic Cetacea is needed to confirm that contact of an ossified lamina of the pterygoid with the squamosal is primitive. Furthermore, the bony lateral lamina may be constructed in different ways in platanistids, squalodelphids, pontoporiids, and eurhinodelphids (Cozzuol 1989), all of which have long, forcepslike jaws; this hints at convergence for functional reasons. It is not clear why the apparently plesiomorphic pterygoid–falciform contact might be lost.

Waipatia maerewhenua is polydont, as are most extant and fossil Odontoceti and embryonic Mysticeti. For heterodont polydont Cetacea, it is not possible to homologize the cheek teeth with those of the Archaeoceti or other eutherians (Rothausen 1968). Tooth structure in heterodont odontocetes has not been correlated with particular food preferences. The gracile procumbent incisiform teeth appear delicate, suggesting a reduced role, if any, in feeding. Perhaps they were used in display. *Notocetus marplesi*, some undescribed early platanistoids from New Zealand, and the small Miocene *Kentriodon pernix* (Kentriodontidae) have similarly procumbent teeth.

Acoustics: Ear.—Odontocete periotics are conservative elements that differ dramatically in overall topography, fossae, sulci, and foramina from periotics of other eutherians. Odontocete periotics are often diagnostic at the species level (Kasuya 1973), suggesting that interspecific differences in morphology reflect interspecific differences in acoustic abilities, but their function is understood only crudely (e.g., an inflated pars cochlearis presumably correlates with changes in cochlear structure associated with high-frequency sound reception; Fleischer 1976). The specific functions of most features seen in *W. maerewhenua*, for example, the recurved dorsally concave anteroexternal sulcus, the anterointernal sulcus, the reduced anterodorsal and anteroventral angles on and subcircular cross section of the anterior process, the profile of the pars cochlearis, the shape of the lateral tuberosity, the lateral groove on the body, the posteroexternal foramen, and the bulge on the posterior process (homologous with the articular rim), are uncertain.

The squamosal and parietal in *W. maerewhenua* are enrolled over the periotic (Fig. 8b, 9b), with the periotic detached from the braincase wall and displaced ventrolaterally relative to the cranial cavity. The formerly confluent foramen ovale and posterior lacerate foramen are separated by contact of the parietal with opposing elements along the border of the basioccipital crest. This pattern of the squamosal and parietal in the basicranium is so widespread that it is perhaps synapomorphic for the Odontoceti.

The relationship of the squamosal and periotic may be interpreted with reference to basilosaurid archaeocetes (Figs. 9a, b). In the Archaeoceti (e.g., Kellogg 1936: figs. 5, 6), the periotic has a roughly flat external wall that rises dorsally to form an elevated platelike superior process with a narrow crest. The external wall contacts the squamosal just ventral to the parietal on the subvertical wall of the braincase (Fig. 9a; Pompeckj 1922: pl. 2). Internally, the superior process descends to a depression on the dorsal surface of the periotic lateral to the internal auditory meatus. Presumably the depression is for the superior petrosal sinus dorsolaterally and the subarcuate (subfloccular) fossa ventromedially (e.g., Kellogg 1936:

figs. 5, 6). Some homologs of archaeocete structures occur in the Odontoceti. The periotic of *W. maerewhenua* lacks an elevated platelike superior process; the homologous structure is the convex external to dorsoexternal surface of the body (Figs. 11b, 9b) that rises from the hiatus epitympanicus to the dorsal crest. The dorsal crest is a persistent feature among archaic odontocetes (e.g., the platanistoids of Figs. 10, p, v, b'; *Prosqualodon australis* Lydekker, 1894, of True 1909) and is the presumed homolog of the crest on the archaeocetes' superior process. Farther internally, a variably present small groove may mark the superior petrosal sinus. Although I have seen no odontocete with a discrete bony subarcuate fossa, Burlet (1913: fig. 10) identified this fossa in an embryo of *Phocoena phocoena*. The position of the superior petrosal sulcus of Pompeckj (1922) is uncertain. The convex surface of the periotic body (Fig. 9b) parallels the overlying periotic fossa in the squamosal, while the dorsal crest of the periotic lies ventral to the parietal–squamosal suture. The cavity between the periotic and periotic fossa is probably vascular in part. In other taxa, Muizon (1987: 5) described the subcircular fossa (here identified as an enlarged foramen spinosum) in *Notocetus vanbenedeni*, while Kellogg (1926: pl. 5) figured an unidentified "foramen 1" dorsal to the periotic in *Zarhachis flagellator*.

Platanistoids vary in the posterior contact of the periotic with the squamosal and bulla. Muizon (1987) discussed and figured articulations in the Squalodelphidae and Platanistidae, and mentioned (Muizon 1991) that an articular rim or articular process occurs in the Squalodontidae. In some New Zealand Squalodontidae (OU 22072, Figs. 10r, s; OU 21798, Fig. 10y), a prominent articular process is present dorsolateral to the long rough articular groove for the spiny process. It is not clear whether this articular process is homologous or convergent with that of the Squalodelphidae. *Waipatia maerewhenua* (Waipatiidae; Figs. 10b, c) and *Notocetus marplesi* (Squalodelphidae; Figs. 10m, n) have only a bulge, rather than a process, at the site where the articular rim develops. Periotics referred to the Eurhinodelphidae (Fordyce 1983) have a process similar to that of the Squalodontidae. Muizon (1987) considered the feature in eurhinodelphids as not homologous with the articular rim or process, but the case is not clear. In *Waipatia maerewhenua* the posterior process is not fused apically or dorsally with the squamosal, but in some Squalodontidae (e.g., "*Prosqualodon*" *hamiltoni* Benham, 1937, OM C.02.8; *Squalodon calvertensis* Kellogg, USNM 23537) spongy bone along the dorsal edge of the posterior process of the periotic appears to fuse with the adjacent squamosal.

Possible functional explanations for the relationship of the periotic to adjacent elements include (1) a need for acoustic isolation from cranial circulation associated with the brain, (2) a need for acoustic separation from the braincase, thus enhancing left–right acoustic isolation to provide better directional hearing, or (3) a consequence of changes in the braincase dictated by changes in the brain itself.

Acoustics: Pterygoid sinus complex.—Waipatia maerewhenua lacks orbital extensions of the pterygoid sinuses. Such extensions in the Squalodelphidae, Platanistidae, and some Squalodontidae (Muizon 1991) perhaps help acoustically isolate the basicranium from the face. There is no fossa for a posterior sinus in *W. maerewhenua*, but a sinus may have been present, for Fraser and Purves (1960) showed that the sinus is ubiquitous among the Odontoceti while a bony fossa is only variably developed. Fraser and Purves (1960) further showed that the middle sinus of the middle ear is ubiquitous in extant Odontoceti but absent in the Mysticeti; I interpret the middle sinus as a synapomorphy for the Odontoceti. In many extant Odontoceti, the middle sinus occupies a distinct tympanosquamosal recess (Fraser and Purves 1960), but the recess is only variably developed among archaic Odontoceti; for example, it is absent in *W. maerewhenua* and sporadically present in the Squalodontidae. However, structures immediately in front of the anterior meatal crest suggest that, despite the lack of a recess, a middle sinus was present in *W. maerewhenua* and indeed in all archaic Odontoceti. In all Odontoceti, the skull lacks a postglenoid foramen and lacks the anterior transverse ridge that in the Archaeoceti (e.g., *Zygorhiza kochii*, USNM 11962) and archaic Mysticeti bounds the vestigial postglenoid foramen. The site of the postglenoid foramen corresponds to the posterior poriton of the tympanosquamosal recess in those taxa where the recess is distinct. I suggest that the site of the postglenoid foramen was probably obliterated with, first, the evolution of the middle sinus and, second, the evolution of a tympanosquamosal recess to accommodate the sinus.

CLADISTIC RELATIONSHIPS

Generalized features and traditional placement.— Waipatia maerewhenua shows many generalized features of the Odontoceti, while structures diagnostic of extant families (for example, conspicuous derived conditions of the premaxilla, premaxillary sac fossa, bony nares, and pterygoid sinus fosse) are not obvious. Generalized features include the supraorbital processes of the maxillae being relatively narrow rather than inflated, the face not being particularly voluminous, the large temporal fossae not being roofed fully by the supraoccipital, parietal, frontal, and maxilla, the remnant intertemporal constriction with the parietals exposed dorsally, the prominence of the lambdoid and nuchal crests, the palatines' being broadly exposed transversely across the palate and not invaded by pterygoids or pterygoid sinus fossae, the fossae for the pterygoid sinuses being restricted to the basicranium and not excavated dorsally to extend into the orbit, the teeth being heterodont and polydont, the periotic's having a rather elongate narrow internal auditory meatus on a slightly inflated pars cochlearis, and the periotic's retaining a dorsal crest and an attenuated apex on the posterior process. To some cetologists, such features might warrant placing *W. maerewhenua* in the Squalodontidae, along with some other small-toothed heterodont dolphins reviewed below, but cladistic analysis indicates otherwise.

Cladistic analyses of the Odontoceti.—The traditional families and higher subdivisions of the Odontoceti (e.g., Fraser and Purves 1960; Simpson 1945) have been reappraised in recent cladistic studies (Fig. 14), such as those of Barnes (1985, 1990), Heyning (1989), Heyning and Mead (1990), and Muizon (1987, 1988a, 1988b, 1991). Barnes, Heyning, and Muizon gave valuable lists of characters, many of which I have used (Appendix), but only Heyning explicitly discussed character polarities or used computer analyses to explore multiple cladograms. The published analyses show that relationships among odontocete taxa are still volatile (Fig. 14). For example, the Ziphiidae are placed with either the Physeteroidea (Muizon 1991) or extant Odontoceti other than the Physeteroidea (Heyning 1989). Barnes (1985, 1990) placed the Pontoporiidae, Iniidae, and Lipotidae (as the Lipotinae) in the Platanistoidea, while Muizon (1988b) used an infraorder Delphinida for the Delphinoidea (Kentriodontidae, Delphinidae, Monodontidae, Phocoenidae, and Albireonidae), Pontoporiidae, Iniidae, and Lipotidae (the last three taxa are "river dolphins"). Heyning (1989: 56) identified the Platanistoidea in the traditional sense as paraphyletic and, like Muizon, recognized a monotypic Platanistidae, with the Iniidae (including *Inia*, *Pontoporia*, and *Lipotes*) as a sister group to the Delphinoidea.

The following odontocete families are known well enough to be used in a cladistic analysis: the Agorophiidae, Albireonidae, Delphinidae, Dalpiazinidae, Eoplatanistidae, Eurhinodelphidae (= Rhabdosteidae of recent use), Iniidae, Kentriodontidae, Kogiidae, Lipotidae, Monodontidae, Patriocetidae, Phocoenidae, Physeteridae, Platanistidae, Pontoporiidae, Squalodontidae, Squalodelphidae, and Ziphiidae. Some of these taxa may be

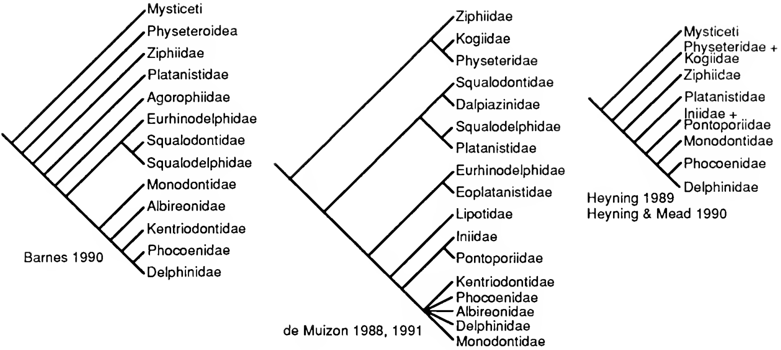

Figure 14. Alternative cladograms of broader relationships of the Odontoceti. Left, Barnes (1990); middle, Muizon (1988b, 1991); right, Heyning (1989, Heyning and Mead 1990).

given subfamily rank (e.g., the Kogiinae, Lipotinae, and Patriocetinae), and, depending on the taxonomist, others are paraphyletic (e.g., the Agorophiidae and Kentriodontidae). Other nominal families (e.g., the Acrodelphidae, Microzeuglodontidae, and Zignodelphidae) are junior synonyms or are too dubiously based to be analysed cladistically.

Cladistics: Approaches.—A cladistic analysis of the relationships of *Waipatia maerewhenua* was carried out by means of the computer program PAUP, version 3.1.1 (Swofford 1993, Swofford and Begle 1993). The final data matrix includes 20 taxa and 67 characters (Table 2, Appendix). Characters were polarized by outgroup comparison (outgroup: *Zygorhiza kochii*). Uninformative characters are omitted. Some potentially useful features discussed here were not included in the data matrix because they are not preserved or illustrated in enough taxa, or because homologies in some taxa are uncertain. Characters included were chosen with the aim of elucidating the relationships of *W. maerewhenua* rather than reappraising the relationships of all major odontocete groups. The approach is conservative; all characters are treated as unweighted and ordered.

From a spectrum of Odontoceti taxa were chosen to form a framework into which *W. maerewhenua* might be placed. Character states were determined from (1) direct study of specimens (optimal) or casts, (2) personal notes or photographs (less satisfactory), and (3) published literature, which is often inadequate for the details of the basicranium and earbones, so that many characters are coded as missing. Taxa and specimens (or principal references) included are *Zygorhiza kochii* (Archaeoceti: Basilosauridae), cast of USNM 11962, Kellogg (1936); *Archaeodelphis patrius* (Odontoceti *incertae sedis*), Allen (1921); *Physeter catodon* (Odontoceti: Physeteridae), Kasuya (1973) and many published illustrations of skulls; *Kogia breviceps* and *K. simus* (Odontoceti: Kogiidae), OM A.84.14, Kasuya (1973) and many published illustrations of skulls; *Mesoplodon grayi* (Odontoceti: Ziphiidae), OM A.64.1; *Tasmacetus shepherdi* (Ziphiidae), OM A.88.177; Eurhinodelphidae, taxa and/or characters reviewed by Muizon (1988a, 1988b, 1991); *Kentriodon pernix* (Odontoceti: Kentriodontidae), cast of USNM 10670, Kellogg (1927); *Pontoporia blainvillei* (Odontoceti: Pontoporiidae), Kasuya (1973), Barnes (1985), and many published illustrations of skulls; *Tursiops truncatus* (Odontoceti: Delphinidae), OU 21820, Barnes (1990), and many published illustrations of skulls; *Cephalorhynchus hectori* (Odontoceti: Delphinidae), OU 21819; *Prosqualodon australis* and *P. davidis* Flynn, 1923 (Odontoceti: Squalodontidae *sensu lato*), cast of a skull figured by Flynn (1948), Lydekker (1894), and True (1909); *Squalodon* spp. (*sensu lato*) (Squalodontidae), OU 21798 (Fordyce 1989: 23), Kellogg (1923a), and Rothausen (1968); "*Prosqualodon*" *hamiltoni* (Squalodontidae), OM C.02.8, Benham (1937); *Zarhachis flagellator* (Odontoceti: Platanistidae), Kellogg (1924, 1926) and Muizon (1987); *Platanista gangetica* (Platanistidae), Kellogg (1924) and many published illustrations of skulls; *Squalodelphis fabianii* Dal Piaz, 1917 (Odontoceti: Squalodelphidae), Dal Piaz (1977) and Muizon (1987); *Notocetus vanbenedeni* (Squalodelphidae), Lydekker (1894) and Muizon (1987); *Notocetus marplesi* (Squalodelphidae), OM C.75.27, Dickson (1964).

Some odontocete families were not included in the analysis because (1) their relationships seem inadequately established for the purposes of this exercise, (2) not enough is published about structures needed for a cladistic analysis, or (3) specimens were not available for study in New Zealand. The Agorophiidae *sensu stricto* and Patriocetidae were excluded. Barnes (1985, 1990), Heyning (1989), and Muizon (1991) demonstrated that the Albireonidae, Monodontidae, and Phocoenidae belong with other Delphinoidea. Furthermore, these authors suggested that the Iniidae and perhaps the Lipotidae are related closely to the Pontoporiidae and in turn to traditional Delphinoidea. Muizon (1991) suggested that the poorly known Eoplatanistidae are a sister group of the Eurhinodelphidae and placed the Dalpiazinidae [currently monotypic, including only *Dalpiazina ombonii* (Longhi)] uncertainly as a sister group of the Squalodontidae. I excluded the Dalpiazinidae from this analysis because I could not identify enough characters from the literature and because a new supposed dalpiazinid from New Zealand (Fordyce and Samson 1992) is not yet described.

Computer searches were pursued as follows: (1) an initial minimal cladogram of 121 steps was obtained by a general heuristic search, (2) 81 nonminimal cladograms of 123 or fewer steps were obtained, (3) these 81 nonminimal cladograms were input and analysed by varied methods reviewed by Swofford and Begle (1990: 32–40, 100–104).

Cladistic relationships of Waipatia maerewhenua: Results.—A single cladogram of 121 steps (consistency index 0.628) was obtained (Fig. 15). This cladogram shows *Waipatia maerewhenua* as a sister taxon to a clade consisting of the Platanistidae and Squalodelphidae and reinforces Muizon's (1991) concept of the Platanistoidea as an odontocete superfamily including the Squalodontidae, Squalodelphidae, and Platanistidae. Other clades recognized are (1) a *Kentriodon* + *Pontoporia* + *Cephalorhynchus* + *Tursiops* group, which partly represents the Delphinida of Muizon (1988b, 1991), (2) the Eurhinodelphidae as a sister taxon to the cluster of the Delphinida, a relationship also proposed by Muizon (1991: fig. 15), and (3) a Physeteroidea (Physeteridae + Kogiidae) + Ziphiidae group, also recognised by Muizon (1991: fig. 5) as his Physeterida. Of note, the Physeterida appear as a sister group to a clade consisting of the Delphinida and Eurhinodelphidae, in contrast to the position shown by Barnes (1990), Muizon (1991), and Heyning (1989) for the Physeteroidea and/or Ziphiidae (Fig. 14). Furthermore, *Prosqualodon australis* appears as the sister taxon to the Squalodontidae, in contrast to the suggestions of Cozzuol and Humbert-Lan (1989) and Muizon (1991).

The 8 cladograms at 122 steps and 81 cladograms at 123 steps show a clade consisting of *Waipatia*, the Squalodelphidae, and the Platanistidae, but the positions of other taxa vary. More study of the relationships of the Physeteroidea, Ziphiidae, and Eurhinodelphoidea is needed. For example, if extant Mysticeti are added to the current data set as outgroups, and irreversible soft-tissue (e.g., nasal diverticula; see Heyning 1989) and osteological (e.g., premaxillary sac fossa, foramen, and sulci) characters are used, the Ziphiidae are positioned as a sister group to the Platanistoidea and Delphinida, as proposed by Heyning (1989). Below I review the relationships of *Waipatia* in more detail.

Comparisons with the Agorophiidae.—The Agorophiidae may be used narrowly (e.g., Fordyce 1981), to include only *Agorophius pygmaeus*, or broadly (e.g., Barnes et al. 1985) as a paraphyletic group of archaic and presumably late Oligocene Odontoceti (e.g., *Archaeodelphis*, *Xenorophus*, *Atropatenocetus*, and *Mirocetus*). *Waipatia maerewhenua* is not an agorophiid, differing in possessing the following derived features: shorter and wider (almost square) face, shorter and wider intertemporal region, and shorter parietals. Cladistic analysis (Fig. 15) places *Archaeodelphis patrius* as a basal odontocete, but one having some derived features relative to *W. maerewhenua* (i.e., larger lacrimal and massive pterygoids that meet medially above the choanae). Cladistic relationships of *Xenorophus sloani* Kellogg, 1923, the fragmentary *Atropatenocetus posteocenicus* Aslanova, 1977, and the enigmatic *Mirocetus riabinini* Mchedlidze, 1970, are uncertain.

Comparisons with the Physeteroidea and Ziphiidae.—*Waipatia maerewhenua* lacks the key synapomorphies of sperm and beaked whales [see Fig. 15 and osteological characters discussed by Muizon (1991)]. *W. maerewhenua* resembles the ziphiid *Mesoplodon grayi* in the asymmetrical posterior apices of its premaxillae, but this is probably convergent; Heyning (1989) reported variable bone contacts on the vertex among extant Ziphiidae.

Comparisons with the Eurhinodelphoidea.—*Waipatia maerewhenua* lacks the key synapomorphies of the Eurhinodelphoidea [i.e., Eurhinodelphidae and Eoplatanistidae of Muizon (1988a, 1991); Rhabdosteidae of Barnes (1990: 20)]. Cladograms of 122

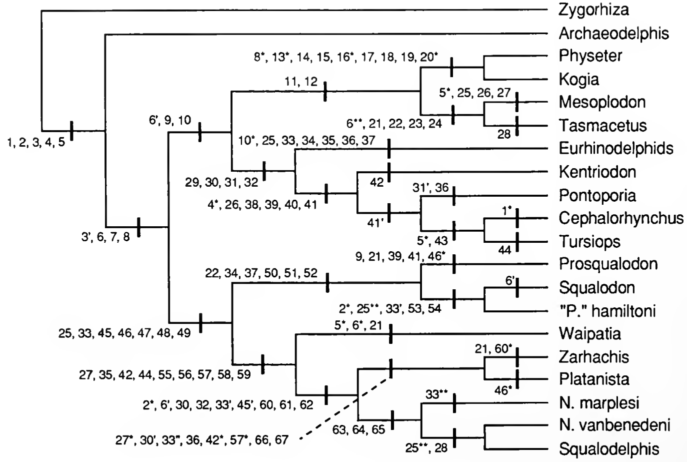

Figure 15. Cladogram of relationships of *Waipatia maerewhenua*. Numbers at each node refer to characters discussed in the text and listed in the Appendix. Symbols: ', change from state 1 to state 2; ", change from state 2 to state 3; *, reversal from state 1 to state 0; **, reversal from state 2 to state 1.

steps (one over the minimum) suggest various relationships for the Eurhinodelphoidea. Affinities with the Delphinida need more study, though comparisons are hampered by the lack of published information on eurhinodelphoid basicrania. Similarities, presumably convergent, between *W. maerewhenua* and some eurhinodelphids include nodular nasals, as in *Argyrocetus patagonicus* (Lydekker 1894: pl. V), and periotic axis (viewed dorsally) being sigmoidal, with the anterior process skewed medially and the posterior process skewed laterally.

Comparisons with the Delphinida.—Waipatia maerewhenua lacks the key synapomorphies of the Delphinida (*sensu* Muizon 1988b; see also Barnes 1990: 20, taxa under nodes 23–44 and some under node 45). The cladogram (Fig. 15) is consistent with concepts of the Delphinidae and associated taxa advanced by Muizon (1988b) and Heyning (1989: 56).

Relationships with the Platanistoidea.—Muizon (1987, 1991) abandoned the Platanistoidea *sensu* Simpson (1945) to propose a Platanistoidea encompassing the Platanistidae, Squalodelphidae, Squalodontidae, probably Dalpiazinidae, and the enigmatic *Prosqualodon*. A simplified outline of Muizon's proposed relationships appears in Fig. 14 (which lacks *Prosqualodon*). Heyning (1989) also separated the Platanistoidea from other extant river dolphins (*Lipotes*, *Pontoporia*, *Inia*), which Heyning placed in the Delphinoidea. Muizon's hypothesis of relationships is broadly supported by Fig. 15, which identifies *Waipatia* as a platanistoid related more closely to the squalodelphid–platanistid clade than to the Squalodontidae.

Apparent synapomorphies of the Platanistoidea (Fig. 15; Muizon 1987, 1991) are as follows (numbers refer to characters listed in Appendix): the profile of the anterior process of the periotic is smoothly to abruptly deflected ventrally in lateral view (25); the anterior process of the periotic is roughly cylindrical in cross section (47); the periotic has a ridge- or peglike articular process (33); the bulla has an anterior spine and an inflated anterolateral convexity (45, 46); the scapula lacks a coracoid process (49); and the acromion process lies on the anterior edge of the scapula, which lacks a supraspinous fossa (48). Of note, the last two scapular features are not seen consistently in supposed Platanistoidea. Cozzuol and Humbert-Lan (1989) stated that the squalodontid *Phoberodon arctirostris* Cabrera, 1926, has a scapula with an apparent coracoid process, a conspicuous supraspinous fossa, and an acromion not located on the anterior edge. Muizon (1987) noted that the scapula in *Sulakocetus dagestanicus* has a narrow coracoid process; *S. dagestanicus* is identified below as probably related to *W. maerewhenua* and thus to other Platanistoidea.

Future work on new or re-prepared late Oligocene and early Miocene platanistoids should further elucidate patterns of homology, including whether character transitions were reversible or irreversible). Thus the detailed pattern of platanistoid relationships shown in Fig. 15 is likely to change.

Relationships with the Squalodontidae.—Waipatia maerewhenua lacks the key synapomorphies for Squalodontidae as defined below, but shares synapomorphies of the periotic and basicranium with the Platanistidae and Squalodelphidae. The cladogram (Fig. 15) is broadly consistent with the concept of squalodontid relationships proposed by Muizon (1991). Some discussion of the Squalodontidae is needed, however, for many heterodont Cetacea, including *Waipatia*-like taxa, have been referred to this family. The following brief review incorporates some revisions made by Muizon (1987, 1991).

The Squalodontidae derive their identity in nomenclature from *Squalodon gratelupi* Pedroni (= *Squalodon typicus* Kellogg, 1923), the type species of *Squalodon* (see Rothausen 1968). The holotype of *Squalodon gratelupi* (early Miocene) is a partial rostrum (Grateloup 1840: fig. 1; Kellogg 1923a; Rothausen 1968). *Squalodon* is well known from skulls, such as those referred to *S. bariensis* (Jourdan) and *S. calvertensis*, and other specimens (e.g., *S. melitensis*, *S. kelloggi*) represented by teeth and partial jaws are reasonably assigned to *Squalodon*. Overall, *Squalodon* provides a sound typological base for diagnosing the Squalodontidae. Of note, some nominal species of *Squalodon* based on teeth probably do not represent *Squalodon*, the Squalodontidae, or even the Odontoceti; e.g., *Squalodon serratus* Davis (archaic Mysticeti?) and *Squalodon* (*Microzeuglodon*?) *wingei* Ravn (archaic Odontoceti?). Beyond *Squalodon*, concepts of the Squalodontidae vary markedly. Kellogg (1923a) stressed that many heterodont odontocetes had been placed arbitrarily in the Agorophiidae, Microzeuglodontidae, Patriocetidae, or Squalodontidae. Later, Kellogg (1928) listed *Squalodon*, *Prosqualodon*, *Microcetus* and 11 other genera as squalodontids, recognized the Agorophiidae (*Agorophius*, *Xenorophus*), and placed *Patriocetus* and *Agriocetus* (with *Archaeodelphis*) as Cetacea *incertae sedis*. Simpson (1945) proposed a superfamily Squalodontoidea, but otherwise largely followed Kellogg. Rothausen (1961) confirmed the squalodontid affinities of *Microcetus*, discussed below. Rothausen (1968) placed the Patriocetinae (*Agriocetus*, *Patriocetus*) in a grade Squalodontidae. Muizon (1987) alluded to the possible polyphyly of the Squalodontidae but later (Muizon 1991) listed synapomorphies of the Squalodontidae within the Platanistoidea. Cozzuol and Humbert-Lan (1989) excluded *Prosqualodon australis* (including *P. davidis*) from the Squalodontidae, suggesting relationships with the Delphinida. More broadly, Cozzuol and Humbert-Lan (1989) questioned the synapomorphies used by Muizon to include the Squalodontidae in the Platanistoidea.

I use the name Squalodontidae conservatively here, to include *Squalodon*, *Eosqualodon*, *Kelloggia*, and *Phoberodon* (Cabrera 1926; Muizon 1991; Rothausen 1968), and "*Prosqualodon*" *hamiltoni*. Whitmore and Sanders (1977) and Fordyce (1989: 23) mentioned skulls of new squalodontids, not yet formally described; elements of the latter (OU 21798) are figured here (Figs. 10x–c'). "*Prosqualodon*" *marplesi* is a squalodelphid; see below. *Prosqualodon australis* is discussed below. None of the other "shark-toothed dolphins" is demonstrably close to *Waipatia*. For example, *Neosqualodon* and *Patriocetus* are of uncertain relationships (cf. Rothausen 1968). *Agriocetus*, *Austrosqualodon*, *Metasqualodon*, *Microzeuglodon*, and *Tangaroasaurus* are based on fragmentary specimens I regard as Odontoceti *incertae sedis*. *Microcetus*, *Sachalinocetus*, and *Sulakocetus* are not clearly squalodontids but are perhaps related to the Squalodelphidae and *Waipatia*, as discussed below.

Waipatia maerewhenua lacks the following key synapomorphies seen in the skulls of Squalodontidae (as defined above): skull long (estimated condylobasal length >700 mm in adults); rostrum robust and long with expanded apex (Muizon 1991); rostrum proximally deep, probably a consequence of a narrow deep mesorostral groove; cheek teeth triangular, large (>20 mm long), high-crowned, denticulate, and elongate but somewhat inflated laterally; and crowns of anterior to middle cheek teeth with rather small denticles widely spaced on anterior and posterior cheek-tooth keels. Furthermore, *Waipatia maerewhenua* lacks the following key synapomorphies (numbers refer to characters listed in Appendix) seen in the tympano-periotics of squalodontids (see squalodontids OU 22072, Figs. 10r–w, and OU 21798, Figs. 10x–c'): the subcylindrical anterior process has a prominent tubercule on the apex (53); the dorsal surface of the anterior process is smoothly curved (in lateral view) so that the apex of the process lies ventrally; there is no anteroexternal sulcus for the middle meningeal artery; there is no subhorizontal anterointernal sulcus, though multiple fine vertical vascular grooves run across the internal surface of the anterior process (54); the fenestra rotunda is reniform, prolonged dorsomedially, and associated with a fissure and posterior ridge that run dorsally to the aperture for the cochlear aqueduct (22); the

TABLE 1. Measurements of *Waipatia maerewhenua*, OU 22095, holotype (mm).

Skull (± 1 mm; following Perrin 1975)	
Condylobasal length	>556
Rostrum length	>320
Rostrum width at base	147
Rostrum width at preserved mid length	59.5
Premaxillary width dorsally at level of preserved midlength of rostrum	27
Premaxillary width dorsally at level of antorbital notches	95
maximum premaxillary width dorsally, about level with mid-orbit	113.5
Distance from level of antorbital notches to most anterior border of nasals	71
Distance from level of antorbital notches to border of internal nares (pterygoids missing)	69+
Cranial length (averaged to compensate for distortion)	235
Preorbital width at level of lacrimal–frontal suture	199
Postorbital width, maximum across postorbital processes	237
Palatine length, in midline	89
Maximum width of external nares (between margins of premaxillae immediately anterior to nasals)	42.5
Width of left frontal at level of apex of premaxilla	20
Width of right frontal at level of apex of premaxilla	28
Minimum width, intertemporal constriction	115
Distance from anterior of inter-nasal suture to apex of supraoccipital	63
Maximum width across zygomatic processes	244
Point-to-point distance, apex of supraoccipital to dorsal intercondylar notch	102
Periotic (± 0.5 mm; right periotic unless specified)	
Anteroposterior length	40.0+
Width, internal margin of pars cochlearis to external margin at hiatus epitympanicus, level with fenestra ovalis	20.4
Length of pars cochlearis, from groove for tensor tympani to mid-point of stapedial muscle fossa	19.3
Length of internal auditory meatus	10.0
Length of posterior bullar facet (left)	19.0
Tympanic bulla (± 0.5 mm; after Kasuya 1973)	
Standard length, anterior apex to apex of outer posterior prominence	48.8+
Length, anterior apex to apex of inner posterior prominence	45+
Distance, outer posterior prominence to apex of sigmoid process	33.5+
Width at level of sigmoid process	33.2
Dorsoventral depth of involucrum immediately in front of posterior pedicle	18.4
Elliptical foramen	>5 (high) × >1 (wide)
Maximum point-to-point length of posterior process	25.2
Mandible (± 1 mm; following Perrin 1975)	
Length of left tooth-row, from posterior margin of most posterior alveolus to tip of mandible	278+
Maximum length of right mandible	446+
Maximum length of left mandible	458+
Maximum height of right mandible, perpendicular to maximum length	133
Atlas (± 1 mm)	
Maximum vertical diameter, parallel to anterior face	72+
Maximum vertical diameter of neural canal	c. 30
Maximum vertical diameter of neural canal	c. 40
Minimum anteroposterior diameter of centrum ventrally (just lateral to hypapophysis)	27.5

lateral face of the periotic between the internal auditory meatus and hiatus epitympanicus is wide and flat to gently convex (50) (Muizon 1991: 305); the apex of the posterior process of the periotic is attenuated (Muizon 1991: 305), narrow, and dorsoventrally deep, with a porous to spiny dorsal surface (37); and the bullar facet on the posterior process extends dorsally onto the posteromedial face of the process (51). The atlas is less compressed than in the squalodontid OU 22072 (Figs. 13h–j).

Other structures cited as characteristic of the Squalodontidae (see Kellogg 1923a; Rothausen 1968; Mchedlidze 1984; Muizon 1987, 1991; Cozzuol and Humbert-Lan 1989) are not all reliable synapomorphies. For example, large robust apical teeth also occur in the Archaeoceti. Heterodont teeth, a symmetrical cranium, and large temporal fossae are primitive features seen in archaeocetes and the odontocete *Agorophius pygmaeus*. Many odontocetes have a well-telescoped skull in which the maxillae closely approach or contact the supraoccipital, so that the parietals are not exposed in a continuous band across the vertex [but I disagree with Muizon (1991: fig. 15, character 1) in his use of a contact of the maxilla with the supraoccipital as a key synapomorphy of Odontoceti]. The frontals contact the apex of the supraoccipital, excluding the parietals from the vertex (e.g., Eurhinodelphidae, Ziphiidae, and Kentriodontidae). The apex of the pterygoid hamulus is also elongated, subconical, and not excavated by the pterygoid sinus in Eurhinodelphidae and in an undescribed "agorophiid" (USNM 256517). The lateral lamina of the pterygoid contacts the falciform process of the squamosal in *Zygorhiza*, the Balaenopteridae, and the Platanistidae, for example, and the dorsal region of the pterygoid sinus fossa primitively lies below the level of the orbit in archaeocetes and some undescribed "agorophiids."

Cozzuol and Humbert-Lan (1989) and Muizon (1991) excluded the enigmatic *Prosqualodon australis* from the Squalodontidae and placed it *incertae sedis*. Initially I followed this assignment, but the taxon emerges in the squalodontid clade of Fig. 15. The study of specimens, rather than casts, of *P. australis* may alter characters in Table 2, thus modifying the proposed relationships.

Comparisons with the Dalpiazinidae.—Muizon (1988a) proposed the new monotypic family Dalpiazinidae and new genus *Dalpiazina* for *Champsodelphis ombonii*. *Dalpiazina ombonii* is known from a partial rostrum, partial skull, and periotic, which Muizon (1988a) described and figured. Later, Muizon (1991: fig. 15) identified Dalpiazinidae as a possible sister taxon to the Squalodontidae. *Waipatia maerewhenua* lacks the presumed synapomorphies of *D. ombonii*; for example, it lacks homodont teeth, deep premaxillary sulci, an enlarged exposure of vomer on the rostrum, and a short wide vertex. *Waipatia maerewhenua* is more derived in that its mandibles have a shorter unfused symphysis and the anterior process of the periotic is relatively larger and more inflated transversely, with a blunter apex reflected more abruptly ventrally. I doubt that *Waipatia maerewhenua* is descended from or ancestral to *D. ombonii*.

Comparisons with the Squalodelphidae and Platanistidae— My results suggest that *Waipatia maerewhenua* is the sister taxon to the Platanistidae and Squalodelphidae (Fig. 15). Though *W. maerewhenua* is more primitive than Platanistidae and Squalodelphidae in many characters, I doubt that it is merely a generalized "ancestral" squalodelphid. Compared with these taxa, it is derived in some features, and it is not demonstrably descended from any known platanistid or squalodelphid.

The family Squalodelphidae Dal Piaz, 1917 (*sensu* Muizon 1987, 1988a), includes *Squalodelphis fabianii*, *Notocetus vanbenedeni*, *Notocetus marplesi*, *Phocageneus venustus* Leidy, 1869 (see Kellogg 1957), and *Medocinia tetragorinus* (Delfortrie, 1875); all are early Miocene. (*Notocetus* spp. and *S. fabianii* are included in Fig. 15, though in *S. fabianii* many sutures are uncertain). Thus delimited, squalodelphids possess several cranial features more derived than those of *Waipatia maerewhenua*, some of which are included in Fig. 15. Published comments (Barnes 1990; Dal Piaz 1917; Lydekker 1894; Moreno 1892; Muizon 1987, 1991; True 1910a) and interpretations of published figures suggest that these features include the following: the median cranial elements are more asymmetrical and more skewed to the left; the maxillae are

TABLE 2. Data matrix used with PAUP 3.1.1 in the cladistic analysis of *Waipatia maerewhenua*. Number of taxa, 20; number of characters, 67. Symbols used are 0, 1, 2, 3. Missing characters are coded *; irrelevant characters are coded –. An "equate" macro was used thus: – = *; a = (01); b = (12); c = (123); d = (23). See text for details.

	Character													
Taxon	5	10	15	20	25	30	35	40	45	50	55	60	65	
Zygorhiza	00000	00000	00***	**00*	a0000	00000	*00*0	00000	00*00	00000	00000	00000	000–0	00
Archaeodelphis	1*1**	000*0	*0***	**00*	*000*	00*00	*0*0*	***00	0**0*	*0***	*000*	***0*	00*00	0*
Physeter	*12*1	2101*	11011	01110	0000*	0-000	00000	0000*	––*0	00000	00000	00-00	00000	00
Kogia	112**	2101*	11011	01110	00000	00000	00000	0000*	–*00	00000	00000	00-00	00000	00
Mesoplodon	11210	11111	11100	10001	11111	11000	00000	00000	00000	00000	00000	00-00	00000	00
Tasmacetus	11211	11111	11100	10001	11110	00100	0*000	00000	00000	00000	00000	00-00	00000	00
Squalodon	10211	21100	00***	**00*	01001	00000	*0210	01000	00*01	11111	11110	–00**	00000	00
"P." hamiltoni	**21*	a11*0	00***	**00*	01001	00000	**2*0	010*0	0**0*	*1111	11110	00000	00000	0*
Prosqualodon	*121*	11110	00***	**00*	1*002	000*0	*0110	0*010	10***	01111	*1000	0*0*0	00*00	0*
Eurhinodelphid	11211	21110	00***	**00*	0*001	0001*	*1111	11000	0–**0	0*000	0000*	0*–00	00000	00
Waipatia	11210	011*0	00***	**00*	10002	01000	*01*1	00000	01*11	11**0	00001	11110	00000	00
Notocetus marplesi	1*21*	*11*0	00***	**00*	00002	01001	**1*1	*00*0	01*1*	*1110	00001	111*1	11111	00
N. vanbenedeni	*0211	21100	00***	**00*	00001	01101	*12*1	00000	0***2	11110	0000*	11111	11111	00
Squalodelphis	**211	*1**0	00***	**0**	000*b	0*1**	**2*1	00**0	****2	11**0	00001	**11*	1*1**	**
Zarhachis	10211	21100	00***	**00*	1000b	000*2	*1301	10000	0***2	1***0	*0001	10–10	11000	11
Platanista	10211	21100	00100	10001	0*00b	00002	01301	10000	000*2	0*110	0000*	1*–11	11000	11
Kentriodon	11201	21111	00***	**00*	00000	10011	*10*0	001*1	11*00	00000	00000	00–00	00000	00
Cephalorhynchus	01200	21111	00100	10001	00000	10011	11000	00111	20100	00000	00000	00–00	00000	00
Tursiops	11200	21111	00100	10001	00000	10011	11000	00111	20110	00000	00000	00–00	00000	00
Pontoporia	*1201	21111	00100	10001	00000	10011	21000	10111	200*0	00000	00000	0*–00	00000	00

markedly thickened to form crests above the orbits and have a "squared off" posterior profile (dorsal view) at the contact with the nuchal crest of the supraoccipital, where the parietals are eliminated from the vertex; the premaxillae overhang the mesorostral groove more; the face between the level of the antorbital notch and the nasals is more foreshortened, with a more curved premaxillary–maxillary suture concentric around the nares; the internarial suture and nasofrontal suture are deep and narrow; the palatine is not exposed broadly from side to side on the rostrum, since the apex of the pterygoid here contacts the maxilla, but is exposed laterally; the narrow pterygoid sinus fossae are excavated dorsally (as seen from below), with a continuous lateral lamina of pterygoid extending back to contact the falciform process of the squamosal; there are marked orbital fossae in thickened frontals for orbital extensions of the pterygoid sinuses; and the supraoccipital is asymmetrical, with a skewed median ridge and rather abrupt anterolateral corners. The periotics of the Squalodelphidae are more derived than those of *W. maerewhenua* in having a prominent to peglike articular process in most, a more circular pars cochlearis, a more prominent lateral groove on the periotic, so that the profile in dorsal view is more sigmoidal, a larger aperture for the cochlear aqueduct in most, a rounder internal auditory meatus, and a posterior process with a long smooth parallel-sided facet for contact with the bulla. Described squalodelphid teeth are nearly homodont. Synapomorphies listed by Muizon (1987, 1991), some of which are included in Fig. 15, adequately separate the Platanistidae from *Waipatia*.

A new family Waipatiidae.—These comparisons suggest that *Waipatia maerewhenua* warrants a new family. The species is a platanistoid more closely related to the Squalodelphidae and Platanistidae than to the Squalodontidae, but it differs from the former taxa in possessing the following derived features: the mandibles have a shorter unfused symphysis (5); the nasals are short and broad; the pterygoid sinus fossa posteromedial to the foramen ovale is larger (6) (this fossa is absent in the squalodelphid *Notocetus marplesi*); the falciform process is bifid, without clear evidence of contact with an ossified lateral lamina of the pterygoid; the anterior process of the periotic is relatively larger and more inflated transversely (21), with a blunter tip and an axis more abruptly reflected ventrally (see *Notocetus marplesi*, Fig. 10n); and the atlas lacks a long hypapophysis.

Other odontocetes superficially similar to *W. maerewhenua* are known. Of these, *Agriocetus incertus* (Brandt, 1874) (see Abel 1914: pls. 4–5) is similar in size and age to *Waipatia maerewhenua*. The holotype is part of a cranium (late Oligocene, Austria) too heavily encrusted with matrix to reveal the suture detail necessary for useful comparisons. *Agriocetus incertus* cannot be assigned to a family, and the holotype is so uninformative that the name may be a *nomen dubium*.

Rothausen (1961) reviewed the heterodont *Phoca ambigua* Meyer, 1840 (late Oligocene, Germany), which is the type species of the supposed squalodontid genus *Microcetus* Kellogg, 1923. The species is known only from cheek teeth, which are smaller than those of *Waipatia maerewhenua*. It shares with *W. maerewhenua* the (derived?) loss of anterior denticles on the cheek teeth. In *M. ambiguus*, the cheek-tooth crowns are lower and thicker, with finer apical ornament, and the roots are thicker. Characters of heterodont teeth of Cetacea are understood too poorly to enable cladistic comparison of *Microcetus* with *Waipatia*, but the stated differences probably separate these genera in terms of traditional taxonomy. *Microcetus ambiguus* is probably not a squalodontid but may be a waipatiid.

Other nominal species of *Microcetus* are not clearly congeneric with *M. ambiguus*. *Microcetus sharkovi* is based on a crushed partial skull and incomplete mandible (late Oligocene, Kazakhstan). The skull is similar in size and profiles to *W. maerewhenua*, but its sutures are indistinct. As in *W. maerewhenua*, the base of the rostrum, antorbital notches, and preorbital processes are asymmetrical, though the right process is more pronounced. These features and the small cheek teeth eliminate *M. sharkovi* as a squalodontid. The species differs from *W. maerewhenua* in that the premaxilla overhangs the mesorostral groove more, the posterolateral sulcus is deeper, and the worn mandibular cheek teeth are smaller and less emergent. This species does not clearly belong in *Microcetus*. It may be a waipatiid.

Microcetus hectori Benham, 1935, is known only from the holotype (NMNZ Ma 653), collected in the Waitaki Valley, near the type locality of *W. maerewhenua*. The holotype includes a distorted partial cranium, the described incomplete right mandible with 5 small heterodont cheek teeth in place, and loose teeth. The holotype is from about the middle of the Maerewhenua Member of the Otekaike Limestone, about lower Waitakian Stage (= earliest Miocene, about 23 Ma). Benham (1935) assigned the species to *Microcetus* because its cheek teeth lack anterior denticles. *Microcetus hectori* differs from *M. ambiguus* in that the former has cheek teeth on which the crowns are relatively higher, more inflated laterally, and smoother. Rothausen (1961) suggested that these species are probably not congeneric. Rothausen (1970: fig. 1) proposed the generic name *Uncamentodon* for *M. hectori* without further diagnosis. *Microcetus hectori* is similar in size to *W. maerewhenua*, and also has deeply rooted and presumably procumbent incisors, but *M. hectori* differs in the following features: middle to posterior mandibular cheek teeth subconical, smaller, and more inflated laterally, with reduced ornamentation; tympanosquamosal recess more pronounced and more pitted posteriorly; and foramen spinosum (an incipient subcircular fossa) markedly larger. These species are not conspecific, and are probably not congeneric. The large foramen spinosum indicates that *Microcetus hectori* is probably a squalodelphid; it is not a squalodontid (cf. Fordyce 1982; Rothausen 1961).

The New Zealand species "*Prosqualodon*" *marplesi* is known only from the holotype (OM C.75.27), which includes an incomplete skull (Figs. 16e, f), an undescribed periotic, and assorted elements listed or described by Dickson (1964). The type locality is "Trig Z," near Otiake, Waitaki Valley. The holotype is probably from the "lower shell bed" at the top of the Maerewhenua Member of the Otekaike Limestone, about middle Waitakian Stage (= earliest Miocene, about 22–23 Ma; Fordyce et al. 1985; Hornibrook et al. 1989). This is younger than *Microcetus hectori* and *Waipatia maerewhenua*. The skull of "*Prosqualodon*" *marplesi* differs markedly from that of squalodontids and *Prosqualodon* in its asymmetry and other features noted in the cladistic analysis. Despite its small size, procumbent anterior teeth, and probable heterodont dentition, "*Prosqualodon*" *marplesi* is not conspecific or congeneric with *W. maerewhenua*; rather, "*Prosqualodon*" *marplesi* resembles *Notocetus vanbenedeni* (early Miocene, Patagonia) in its deeply sutured nodular asymmetrical frontals, "squared off" posterior margin of the maxillae along the contact with the supraoccipital, asymmetrical supraoccipital, larger hypapophysis (Figs. 13k–m) on the atlas, and a range of features on the previously undescribed periotic (e.g., acute anterointernal apex, sigmoidal profile in dorsal view, prominent dorsal crest on the dorsal surface of the periotic at the junction between the body and anterior process, and long smooth parallel-sided facet on the posterior process). "*Prosqualodon*" *marplesi* is here formally transferred from the Squalodontidae to *Notocetus* (Squalodelphidae) (see Fig. 15).

Sulakocetus dagestanicus is a late Oligocene supposed squalodontid, based on a holotype from the Caucasus. The incomplete skull (Figs. 16c, d; Mchedlidze 1984: pls. 13, 14; Pilleri 1986: pls. 5–8) is small and heterodont, with a rostrum moderately wide at the base and attenuated distally. Mchedlidze (1984) outlined general features of the skull; most details of the sutures are uncertain, and the periotic is unknown. *Sulakocetus dagestanicus* is not clearly a squalodontid. In lateral view, the skull is similar in profile to that of *W. maerewhenua*. The mandibular teeth (Mchedlidze 1984: pls. 14, 15) are smaller and more gracile than those of the Squalodontidae, resembling those of *W. maerewhenua*. *Sulakocetus* perhaps belongs in the Waipatiidae but is known too poorly for cladistic analysis. *Waipatia maerewhenua* apparently differs from *S. dagestanicus* as follows: preorbital process not as thick dorsoventrally; premaxillary–maxillary suture on rostrum less pronounced; premaxillary sulci shallower; premaxilla overhangs mesorostral groove less; premaxilla has transversely flatter profile in front of nares; nasals appear more nodular; posterolateral plate has more convex profile (lateral view); vertex is not as elevated or rounded in lateral view; mandibular cheek teeth more emergent with less triangular crowns; body of mandible more robust; and pan bone of mandible less inflated ventrally. It is not clear whether the maxilla contacts the supraoccipital in *S. dagestanicus* (cf. Muizon 1987). *Sulakocetus dagestanicus* is not clearly conspecific with other described heterodont taxa.

Sachalinocetus cholmicus Dubrovo, 1971, is an early or middle Miocene supposed squalodontid from Sakhalin, northwest Pacific. The holotype skull is about 600 mm long. Dubrovo's (1971) reconstructions (Figs. 16a, b) suggest that the skull is similar in profile to *W. maerewhenua* in dorsal and ventral views, but a lateral view of the skull reveals a deeper fossa for facial muscles. On the vertex, the frontals appear to be longer and narrower than in *W. maerewhenua*. Not enough is shown of skull sutures to allow detailed comparisons. The teeth are heterodont, and the slender long incisors were probably procumbent. Posterior cheek teeth lack much ornamentation on the crowns and have reduced posterior denticles. In a traditional approach to classification, similarities between *Sachalinocetus* and *Waipatia* would probably see these genera in the same family. Contrary to Dubrovo's (1971) conclusions, *Sachalinocetus* is not clearly a squalodontid. I suspect that *Sachalinocetus* belongs in the Waipatiidae, and that the clade thus ranges into the Miocene.

CONCLUSIONS

Waipatia maerewhenua is sufficiently generalized that it might be placed in one of several odontocete clades. Dorsal structures on the cranium in *W. maerewhenua*, traditionally used in odontocete classification, indicate that cranial asymmetry arose by the late Oligocene, but otherwise suggest only that the species perhaps is not a squalodontid. What remains of the pterygoid sinus complex is also generalized, apart from the posteromedial expansion of the sinus. Features of the tympano-periotic and basicranium allow *W. maerewhenua* to be placed in the Platanistoidea and in a new family, Waipatiidae, as a sister group to the Squalodelphidae and Platanistidae. Some described Oligocene and earlier Miocene "squalodontids" may also be waipatiids, but most are too incomplete or too poorly described to be sure. The range of described *Waipatia*-like species hints at a significant diversity of the Waipatiidae later in the Oligocene. Waipatiids were perhaps the ecological equivalents of medium-sized extant delphinids with robust rostra, such as *Tursiops truncatus*. Judged from New Zealand late Oligocene specimens such as the *Squalodon*-like OU 21798 (Fordyce 1989: 23), contemporaneous squalodontids were larger predators with no clear modern analogs. Squalodelphids and a *Dalpiazina*-like small odontocete lived in New Zealand waters during the latest Oligocene or earliest Miocene (Fordyce and Samson 1992), and early Miocene representatives (Muizon 1991) are well known elsewhere. Such fossils suggest that platanistoids were globally diverse and ecologically important earlier than suspected. Later Neogene long-beaked *Zarhachis*-like taxa, which reveal little of this older history of platanistoids, foretell the origins of the fluviatile *Platanista* spp.—the near-extinct relicts of a once-diverse marine taxon.

ACKNOWLEDGMENTS

I wish to dedicate this article to Frank C. Whitmore, Jr., with grateful thanks for over a decade of wide-ranging counsel on fossil cetaceans. Through his thoughtful, supportive, and temperate comments, through ideas shared freely with many colleagues, and

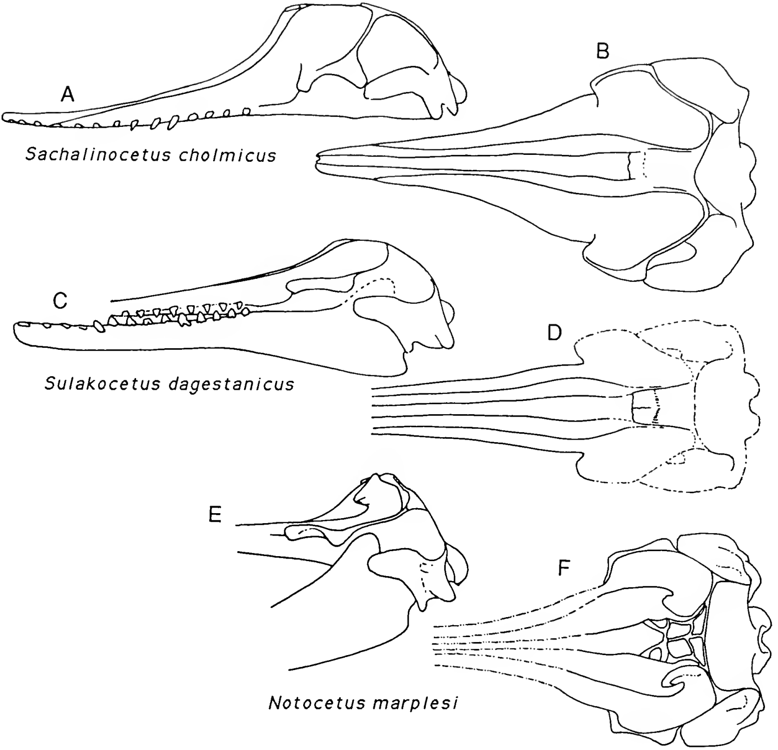

Figure 16. Reconstructions of skulls of some archaic platanistoids, not to same scale. A–B, *Sachalinocetus cholmicus*, based on Dubrovo (1971). A, lateral; B, dorsal. C–D, *Sulakocetus dagestanicus*, based on Mchedlidze (1976, 1984). C, lateral; D, dorsal. E–F, *Notocetus marplesi*, based on Dickson (1964) and on holotype. E, lateral; F, dorsal.

through an appreciation of the human element in science, Dr. Whitmore has done much to further the study of fossil Cetacea world-wide.

I also thank the following for their help. The Harvey family gave permission to work on their property. Andrew Grebneff assisted in the field, skillfully prepared the holotype of *Waipatia maerewhenua*, and helped with illustrations. Greg Ferguson helped with preparation, literature work, and photography. Bob Connell assisted with field work. Christian de Muizon and Catherine R. Samson provided very useful comment on the manuscript and/or specimens. The editors, M. Gottfried, and an anonymous referee also gave constructive comments. Lawrence G. Barnes, Mario A. Cozzuol, James G. Mead, and Frank C. Whitmore, Jr., discussed cetacean systematics. N. de B. Hornibrook and Michael A. Ayress helped with biostratigraphy. Jeffrey D. Stilwell provided translations. John T. Darby (Otago Museum), Alan N. Baker (National Museum of New Zealand), Clayton E. Ray (Smithsonian Institution), and Richard H. Tedford (American Museum of Natural History) provided access to specimens. Field work was aided by the Francis, McKenzie, Parker, Simpson, and Williamson families and others of the Duntroon district. The holotype and other specimens were collected and prepared with support from the National Geographic Society (grants 4024-88 and 4341-90; field work and preparation), the New Zealand Lottery Research Board (equipment), and the Research Committee of the University of Otago (preparation).

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APPENDIX: CHARACTERS USED IN CLADISTIC ANALYSIS OF THE RELATIONSHIPS OF *WAIPATIA MAEREWHENUA*

These characters are discussed in the text and/or by Barnes (1990), Heyning (1989), and Muizon (1987, 1988a, 1988b, 1991). 0, primitive; 1–3, derived.

1. Posterior lacerate foramen confluent with foramen ovale to form "cranial hiatus": 0, yes; 1, no, parietal and/or squamosal contact basioccipital to separate posterior lacerate foramen from foramen ovale.

2. Foramen "pseudo-ovale": 0, present; 1, absent. The foramen "pseudo-ovale" marks the exit of the mandibular branch of the trigeminal nerve from the region of the pterygoid sinus fossa. The foramen is bounded by the pterygoid and falciform processes of the squamosal and normally by the ossified outer lamina of the pterygoid. Present in Archaeoceti, Mysticeti, and those Odontoceti (e.g., *Platanista*) in which an extensive ossified outer lamina of the pterygoid contacts the falciform process. The palatine may contact the falciform process in some Delphinoidea.

3. Overlap of maxilla onto frontal in supraorbital region: 0, no overlap; 1, partial overlap; 2, supraorbital process of maxilla extends posterior to mid-orbit.

4. Form of anterior bullar facet of periotic: 0, facet flat or absent; 1, facet depressed with shallow groove; 2, facet depressed with deep groove.

5. Mandibles fused at symphysis: 0, no; 1, yes.

6. Depth of pterygoid sinus fossa in basicranium: 0, shallow or little excavated; 1, deep, excavated dorsal to level of foramen ovale; 2, deep and extended dorsally toward or into orbit. Functional reasons for apparent reversals from state 1 to 0 or 2 to 1 are uncertain; irreversibility seems likely.

7. Maxilla present in anterior wall or in floor of orbit: 0, yes; 1, no.

8. Position and orientation of origin for temporal muscle on supraorbital process of frontal: 0, origin lies on the posterior face of the supraorbital process and is directed roughly posteriorly; 1, origin lies on posteroventral face of supraorbital process and is directed roughly ventrally.

9. Ossified lateral lamina of pterygoid present and in contact with falciform process: 0, yes; 1, ossified lamina reduced or absent.

10. External auditory meatus: 0, wide; 1, narrow.

11. Contact of enlarged posterior process of bulla with paroccipital: 0, no contact; 1, sutural contact.

12. Accessory ossicle of periotic: 0, small to medium, not well fused; 1, enlarged, subspherical, and fused tightly to periotic.

13. Blowhole ligament present: 0, no; 1, yes. Not known for fossils. In extant Mysticeti, not included in this analysis, the blowhole ligament is absent; its absence in the Physeteroidea is probably primitive, rather than a result of reversal. Heyning (1989) discussed the soft anatomy of the face (e.g., characters 13–17).

14. Nasal passage—distal sac developed: 0, no; 1, yes. Derived for the Physeteroidea.

15. Nasal passage—proximal sac evolves into frontal sac: 0, no; 1, yes.

16. Nasal passage—proximal sac evolves into sac complex: 0, no; 1, yes. Regarded as derived for extant Odontoceti other than the Physeteroidea; the absence in Physeteroidea is probably primitive, rather than a result of reversal as indicated in Figure 15.

17. Spermaceti organ present: 0, no; 1, yes.

18. Supracranial basin in skull: 0, absent; 1, present.

19. Number of nasals: 0, two; 1, one or both lost.

20. Nasal passages confluent distal to bony nares: 0, no; 1, yes. In extant Mysticeti, the nasal passages are separate distal to the bony nares; separation in the Physeteroidea is probably primitive, rather than a result of reversal.

21. Anterior process of periotic: 0, not thickened tranversely; 1, thickened tranversely by expanded internal and external faces at some point beyond the base of the process.

22. Fenestra rotundum of periotic reniform, with a dorsal fissure directed toward the aperture for the cochlear aqueduct: 0, no; 1, yes.

23. Premaxilla with a transversely flattened vertical face and prominent lateral crest at the level of the nares: 0, no; 1, yes.

24. Enlarged dorsal lamina of pterygoid tightly fused with alisphenoid anterior to foramen ovale: 0, no; 1, yes.

25. Profile of anterior process of periotic ventrally deflected in lateral view: 0, no, has crudely rectangular profile; 1, smoothly deflected; 2, abruptly deflected.

26. Periotic - parabullary ridge developed laterally along ventral border of anterior process: 0, ridge absent; 1, ridge present.

27. Long posterior apex of premaxilla lies posterior to nasals wedged between elevated edge of maxilla and frontal on vertex; apices show left–right asymmetry: 0, no; 1, yes.

28. Cochlear aqueduct on periotic large with a thin edge: 0, no; 1, yes.

29. Articulation of posterior process of tympanic bulla with squamosal: 0, process contacts post-tympanic process of squamosal and posterior process of periotic; 1, bulla contacts periotic only.

30. Frontal excavated for orbital extensions of pterygoid sinus(es): 0, not excavated; 1, slightly excavated with shallow-edged depression; 2, deeply excavated.

31. Nasal passage—vestibular sac: 0, absent; 1, present; 2, hypertrophied.

32. Palatine invaded by or modified by pterygoid sinus fossa: 0, no; 1, yes. The palatine is progressively narrowed to ventral view between maxilla and pterygoid as the pterygoid sinus fossa invades the palatine.

33. Articular process on periotic: 0, process absent; 1, incipient ridge present; 2, strong ridge present; 3, peg present.

34. Apex of pterygoid hamulus solid, robust, long and subconical in ventral view: 0, no; 1, yes.

35. Lateral groove or lateral depression affects profile of periotic as viewed dorsally: 0, no obvious vertical groove dorsal to hiatus epitympanicus; 1, groove present so that overall profile of periotic is slightly to markedly sigmoid in dorsal view.

36. Rostral suture between premaxilla and maxilla deeply grooved: 0, no; 1, yes.

37. Dorsal edge of posterior process of periotic spongy and fused or tightly articulated with adjacent squamosal: 0, no; 1, yes.

38. Dorsal surface of involucrum of bulla markedly depressed or excavated anterior to the base of the posterior process, so that the involucrum has parallel dorsal and ventral profiles in medial view: 0, no; 1, yes.

39. Palatine with ossified lateral lamina directed posterolaterally from about the level of the choanae: 0, no; 1, yes.

40. Anterior bullar facet lost from periotic: 0, no; 1, yes.

41. Relationship of ascending process of premaxilla with nasal: 0, left and right processes extend posteriorly beyond anterior of nasals; 1, processes contact only front of nasal; 2, one or no process contacts nasal.

42. Incisors relatively delicate and procumbent: 0, no; 1, yes.

43. Nasal passage—posterior sac lost: 0, no; 1, yes.

44. Pterygoid sinus fossa present in alisphenoid and/or basioccipital, dorsolateral to basioccipital crest and posteromedial to foramen ovale: 0, no; 1, yes.

45. Anterior spine present on bulla: 0, no; 1, spine small to moderate; 2, spine long.

46. Bulla with inflated anterolateral convexity that may be associated with an anterolateral notch: 0, no; 1, yes.

47. Anterior process of periotic roughly cylindrical in cross section: 0, no; 1, yes.

48. Scapula—acromion process lies on anterior edge, with loss of supraspinous fossa: 0, no; 1, yes.

49. Scapula—coracoid process: 0, present; 1, absent.

50. Periotic with low, wide, and regularly convex transverse profile across dorsal surface (= across dorsal process, *sensu* Muizon): 0, no; 1, yes.

51. Bullar facet on posterior process of periotic extends dorsally onto the posteromedial face of the posterior process: 0, no; 1, yes.

52. Posterior portion of rostrum robust and deep, with open and deep mesorostral groove: 0, no; 1, yes.

53. Apex of anterior process of periotic tuberculate: 0, no; 1, prominent small tubercule present.

54. Anterior process of periotic with multiple subvertical fine fissures on the internal face: 0, no; 1, yes.

55. Anteroposterior ridge on dorsal side of anterior process and body of periotic, associated with the development of a depression adjacent to groove for tensor tympani: 0, absent; 1, present.

56. Anteroexternal sulcus profile on periotic recurved so that it is concave dorsally (seen in external view): 0, no; 1, yes.

57. Foramen spinosum enlarged to form a subcircular fossa dorsal to periotic: 0, no; 1, yes.

58. Crown of heterodont teeth: 0, long (>10 mm); 1, short (≤10 mm).

59. Bulla—ventral groove: 0, groove not marked anteriorly; 1, groove present anteriorly (shallow or deep, may include anterior spine).

60. Atlas vertebra—relative size of dorsal transverse process: 0, moderate; 1, large.

61. Pars cochlearis of periotic inflated with subrectangular profile: 0, no; 1, yes.

62. Posterior maxillary (infraorbital) foramen placed posteromedially, near the bifurcation in the posterior of the premaxilla: 0, no; 1, yes.

63. Facet for bulla on posterior process of periotic relatively narrow, long, and parallel-sided: 0, no; 1, yes.

64. Posterior margin of maxilla elevated, with "squared off" profile as viewed dorsally: 0, no; 1, yes.

65. Nodular frontals prominent on vertex, separated by a prominent medial groove: 0, no; 1, yes.

66. Ridge or crest of maxilla/frontal, pneumatized ventrally, present along lateral margin of face above orbit: 0, no; 1, yes.

67. Bulla with thin outer lip that is smoothly overarching and high relative to transverse width of bulla: 0, no; 1, yes.

A Phylogenetic Analysis of the Sirenia

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ABSTRACT.—Analysis of 62 cranial and dental characters of 36 species and subspecies of sirenians, by means of the Hennig86 computer program without character weighting, produced 60 maximally parsimonious trees (length 152, consistency index 0.55, retention index 0.83). With successive character weighting, these were reduced to six maximally parsimonious trees, of which the Nelson consensus tree is presented here (length 162, consistency index 0.76, retention index 0.91). Sample size and intrapopulational variation are insufficiently studied problems in cladistic analysis, and a statistically based method for scoring variable characters is introduced. The tree's topology is least certain in three groups of taxa: Eocene dugongids, dugongines (here including rytiodontines), and species of *Metaxytherium*. The most novel results of this study: (1) The Miosireninae are the sister group of the Trichechidae as previously defined, and are here placed in that family; a subfamily Trichechinae is formally erected for the remaining trichechids. (2) The Trichechidae in this broader sense appear to have arisen somewhat later than previously supposed (late Eocene or early Oligocene rather than middle Eocene) and are rooted well within the Dugongidae instead of being derived separately from the Protosirenidae. (3) *Dugong* lies within the clade heretofore called the Rytiodontinae, on the basis of the first strong evidence of where among the Dugongidae the living dugong's phyletic affinities lie. The name Dugonginae is extended to this entire clade in place of the junior name Rytiodontinae. Except within the Dugonginae, age rank and clade rank are highly correlated, suggesting that the fossil record provides a good picture of the history of the Sirenia. A revised provisional classification is proposed for the sirenian taxa analyzed here.

INTRODUCTION

The first formal cladogram of the order Sirenia to be published was that of Savage (1977). Since then, cladistic analyses have been presented for several subsets of the order: the Trichechidae (Domning and Hayek 1986), the Rytiodontinae (Domning 1989a,b, 1990), and the European species of *Metaxytherium* (Domning and Thomas 1987). In this paper I revise and extend this previous work to encompass all of the better-known Sirenia.

This study has been done in the context of much recent work that strongly supports the strict monophyly (= holophyly) of the order Sirenia and its membership in a supraordinal group (Tethytheria) with the Proboscidea and Desmostylia (e.g., Domning et al. 1986; Shoshani 1986; Tassy and Shoshani 1988; Novacek 1990; Thewissen and Domning 1992; and references cited therein). Although a few characters of the order gleaned from these studies are noted here, I do not review this body of work in detail or attempt to identify the sister group of the Sirenia but instead refer the reader to these sources for evidence on the relationships of sirenians to other mammals.

This paper is a preliminary report, based on a systematic revision still in progress.

MATERIALS AND METHODS

Thirty-six species and subspecies of sirenians were analyzed. Several other nominal species were excluded because they are known only from very incomplete material, because I have not examined the original specimens, and/or because I have serious doubts about their validity. For example, *Thalattosiren petersi* (Abel, 1904) was excluded because I suspect that the known skulls may represent merely immature *Metaxytherium*.

Moeritherium (Proboscidea) and *Paleoparadoxia* (Desmostylia) were used as outgroups for polarization of characters because of the evidence (cited above) that these two orders are the closest relatives of the Sirenia and because these genera are the most primitive adequately known members of their respective orders. However, both of these are apparently derived, relative to other mammals, in their imperforate lacrimals and single-rooted canines, whereas early sirenians display the primitive states (possession of a lacrimal foramen and double-rooted canines, respectively). More primitive proboscideans and desmostylians are known (anthracobunids and *Behemotops*, respectively; see Ray, Domning, and McKenna 1994, this volume) but are represented at present by little or no cranial material and cannot be scored for most of the characters used here.

This analysis is based on some 108 morphological characters of the skull, mandible, and dentition (excluding cheek-tooth cusp patterns) that I have examined in detail in almost all of the known taxa of fossil and living sirenians. Of these 108 characters, I eliminated 46 that I was unable to score consistently or that were cladistically uninformative for the taxa included here (e.g., because they vary only in taxa that were excluded). The 62 informative characters (Table 1) were analyzed with the Hennig86 computer program (Farris 1988). Three multistate characters were treated as unordered because in these cases I had significant doubts that the states formed a single transformation series. Some other significant cranial and postcranial characters not used in the analysis corroborate and supplement certain parts of it.

Two aspects of cladistic data sets that are normally ignored are explicitly addressed here: sample size and intraspecific variation. Table 1 lists for each taxon the largest number of specimens examined for which any character could be scored. For any given character, the actual number of specimens scored was often much less than this maximum; however, separate citation of a sample size for each character of each taxon [as Domning and Thomas (1987) did for a much smaller data set] would have made the table prohibitively large and cumbersome. The present compromise at least provides an approximation of the sample sizes available for this study. As for variation, since Hennig86 does not accept multiple states of a character for a given taxon, polymorphisms had to be scored unambiguously as one of two states. The following procedure was adopted.

For the available samples, confidence limits for proportions and critical values of sample fractions (X/n = frequency of a state in a sample of size n) were determined (these are given in graphic or tabular form in standard statistics tables), using a confidence coefficient of 0.95. For example, if four specimens in a sample of five display a derived state, $X/n = 4/5 = 0.8$. The probability that the frequency of occurrence of the derived state in the *sampled population* was between 0.995 and 0.284 (the 95% confidence limits) is 0.95. (I here designate the lower confidence limit, 0.284 in this example, as the LCL_{95}.)

If a state (either primitive or derived) was present in the majority of the sample and its $\mathrm{LCL}_{95} > 0.5$, the taxon was scored as having that state. If the majority state had an LCL_{95} 0.5, the scoring depended on the taxon's position relative to the character's distribution in the trees obtained from preliminary analyses: the

In A. Berta and T. A. Deméré (eds.)
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taxon was scored whichever way was more congruent with other characters (i.e., whichever way did not imply a reversal). If the sample was evenly divided, it was likewise scored as having the congruent state. If the taxon lay at the borderline of the character transformation (so that neither scoring choice would imply a reversal), it was scored as having the majority state. If it was both located at the borderline and evenly divided, it was scored as having the more primitive state (this is arbitrary; the opposite rule was tried also, but in this analysis the choice did not affect the geometry of the final tree). The rationale and implications of this procedure are discussed below (see under Comments on Methods).

CHARACTERS USED

The following 62 characters are those that have proven most informative and were used in the computer analysis, out of 108 characters (assigned numbers between 1 and 158) that I have studied in some detail. For simplicity of record-keeping, the numbers originally assigned to these characters are retained here. Numbers are not assigned to some other cranial characters whose only effect would be to define terminal taxa or strengthen nodes already adequately supported, as in the case of the hydrodamalines; these characters would therefore have no effect on the geometry of the final tree, though they would alter the tree's statistics. Likewise unnumbered are postcranial characters, because data on these are missing for many taxa. None of these unnumbered characters was included in the computer analysis, though they are listed below at the appropriate nodes. The data matrix for the 62 included characters is shown in Table 1. As usual, 0 designates the most primitive state observed among the taxa studied.

3. *Rostrum*: (0) small relative to cranium; (1) enlarged (length of premaxillary symphysis $> 0.27 \times$ condylobasal skull length) (see Fig. 1). (The ratio 0.27, like other ratios used below, was chosen because it separates what appear visually to be significantly different character states.)

6. *Nasal process of premaxilla*: (0) thin and tapering at posterior end, having lengthy overlap with frontal and/or nasal; (1) broadened and bulbous at posterior end, having more or less vertical joint surface in contact with frontal (Domning 1989a,b).

7. *Nasal process of premaxilla*: (0) long; (1) very short (see Fig. 1).

8. *External nares*: (0) not retracted; (1) retracted and enlarged, reaching to or beyond the level of the anterior margin of the orbit.

9. *Premaxilla*: (0) does not contact frontal; (1) contacts frontal.

11. *Zygomatic–orbital bridge of maxilla*: (0) nearly level with palate; (1) elevated above palate, with its ventral surface lying > 1 cm above the alveolar margin (cf. Domning 1978: fig. 8).

13. *Infraorbital foramen*: (0) small (about 15×10 mm or less); (1) large (greater than 15×10 mm).

14. *Zygomatic–orbital bridge of maxilla*: (0) long anteroposteriorly (vertical thickness $< 0.40 \times$ minimum length); (1) shortened (thickness $0.40 \times$ length; cf. Domning 1978: fig. 24); (2) shortened and transformed into transverse vertical wall (Domning 1989b).

16. *Palate*: (0) thin or incomplete at level of penultimate cheek tooth; (1) > 1 cm thick at level of penultimate tooth.

31. *Nasals*: (0) meet in midline; (1) separated in midline by frontals or an incisure, or absent.

32. *Nasals*: (0) large (length of internasal suture $0.5 \times$ length of interfrontal suture exposed dorsally); (1) smaller, or separated in midline, or absent.

36. *Supraorbital process of frontal*: (0) well developed, with prominent, dorsoventrally flattened posterolateral corner; (1) dorsoventrally thickened, with posterolateral corner variably developed; (2) reduced, rounded, lacking posterolateral corner (see Fig. 1; state 2 not illustrated). (This character was treated as inapplicable to "rytiodontines" because these follow a somewhat different transformation series, here expressed by character 43; however, it

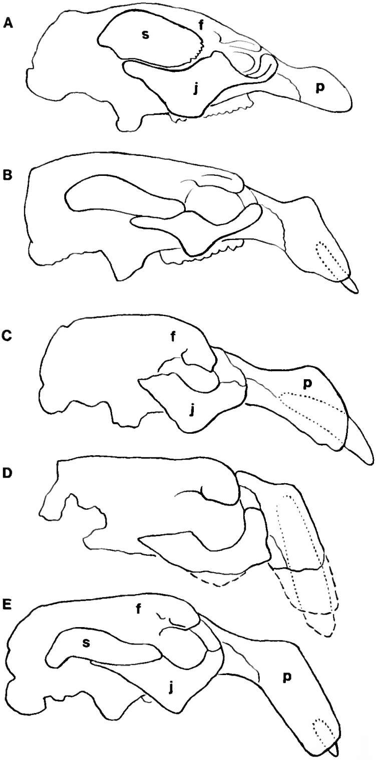

Figure 1. Skulls of sirenians in right lateral view, illustrating eight of the characters of the anterior part of the skull used in this analysis. Not drawn to same scale. See text for explanations of characters and states. Dashed lines indicate parts restored; dotted lines outline tusks within alveoli. Abbreviations: f, frontal; j, jugal; p, premaxilla; s, zygomatic process of squamosal. A, *Trichechus senegalensis*: 3(0), 7(0), 36(0), 43(0), 85(0), 89(0), 139(1), 140(0). B, *Halitherium schinzii*: 3(1), 7(0), 36(0), 43(0), 85(1), 89(0), 139(0), 140(1). C, *Dioplotherium manigaulti*: 3(1), 7(0), 36(— or 1), 43(1), 85(2), 89(1), 139(0), 140(2). D, *Rytiodus* sp.: 3(1), 7(1), 36(— or 1), 43(1), 85(2), 89(0), 139(0), 140(2). E, *Metaxytherium floridanum*: 3(1), 7(0), 36(1), 43(0), 85(2), 89(0), 139(0), 140(0).

would probably be equally correct, and would not alter the tree's topology, if all of these taxa were scored 1 for this character.)

37. *Nasal incisure* at posterior end of mesorostral fossa: (0) absent or small (does not extend posterior to the supraorbital process); (1) deep and narrow (extends posterior to the supraorbital process); (2) comparably deep but broad, with the anterior frontal margin displaying a median convexity. (Unordered character.)

38. *Lamina orbitalis of frontal*: (0) thin or absent; (1) 1 cm thick.

42. *Frontal roof*: (0) convex, or more or less flat between temporal crests (if latter present); (1) deeply concave, sloping steadily ventrad to anterior margin (cf. Domning 1990: fig. 4E).

43. *Supraorbital process of frontal*: (0) flattened in more or less horizontal plane, with dorsal surface inclined relatively gently ventrolaterad; (1) turned markedly downward, with dorsal surface inclined strongly ventrolaterad and posterolateral corner projecting posteriorly (see Fig. 1; Domning 1989a,b, 1990).

51. *Sagittal crest*: (0) present; (1) absent.

66. *Exoccipitals*: (0) meet in a suture dorsal to foramen magnum; (1) do not meet in a suture (this is a reversal to the condition found in primitive mammals; Shoshani 1986).

67. *Supracondylar fossa of exoccipital*: (0) absent; (1) distinct but shallow, directly dorsal to condyle; (2) deep and extending across entire width of occipital condyle; (3) reduced and located dorsomedial to condyle, or lost.

70. *Dorsolateral border of exoccipital*: (0) rounded and more or less smooth, not flangelike; (1) thick and overhanging posteriorly as a flange; (2) greatly thickened, forming rugose overhanging flange (Domning 1978; Domning and Hayek 1986).

73. *Posttympanic process of squamosal*: (0) absent (i.e., no facet projecting for sternomastoid muscle); (1) present; (2) enlarged and clublike.

74. *Sigmoid ridge of squamosal*: (0) present and prominent; (1) reduced or absent (cf. Domning 1978: fig. 7).

75. *External auditory meatus of squamosal*: (0) long mediolaterally (> 1 cm); (1) short (1 cm).

76. *Squamosal*: (0) does not extend to temporal crest; (1) extends to temporal crest.

77. *Processus retroversus of squamosal*: (0) absent; (1) present, moderately inflected; (2) present, not inflected (cf. Domning 1978: fig. 7). In *Dugong dugon*, it is strongly inflected (an autapomorphy). (Unordered character.)

82. *External auditory meatus of squamosal*: (0) narrow and slitlike (anteroposterior breadth less than dorsoventral); (1) about as wide anteroposteriorly as high; (2) very broad and shallow, wider anteroposteriorly than high.

84. *Zygomatic process of squamosal*: (0) medial side not swollen, appears relatively flat or concave and inclined inward dorsally; (1) medial side markedly swollen, inclined inward ventrally or forming a vertical wall (Domning and Hayek 1986).

85. *Ventral extremity of jugal*: (0) lies posterior to orbit; (1) lies approximately under posterior edge of orbit, but forward of jugal's postorbital process (if present); (2) lies ventral to orbit (see Fig. 1).

87. *Preorbital process of jugal*: (0) does not contact premaxilla; (1) contacts premaxilla.

88. *Preorbital process of jugal*: (0) relatively flat and thin (posteromedial-anterolateral breadth of portion lateral to maxillojugal suture > anteromedial-posterolateral thickness); (1) thick and robust (breadth thickness).

89. *Posterior (zygomatic) process of jugal*: (0) as long as or longer than diameter of orbit; (1) shorter than diameter of orbit (see Fig. 1).

91. *Lacrimal*: (0) with foramen (nasolacrimal canal); (1) without foramen, but still large; (2) vestigial or absent.

97. *Posterior border of palatine*: (0) not incised, merely shallowly concave; (1) incised or deeply indented; (2) very deeply incised, to as far forward as level of M^1.

99. *Palatines*: (0) extend anteriorly beyond posterior edge of zygomatic–orbital bridge; (1) do not extend so far forward.

101. *Alisphenoid canal*: (0) present; (1) absent. (Though this polarity is debatable in mammals generally, it is well supported for the Paenungulata, including the taxa considered here; Thewissen and Domning 1992.)

102. *Pterygoid fossa*: (0) absent; (1) present. (The polarity of this character is problematical, in view of the fossa's evident presence in *Prorastomus* but absence in *Paleoparadoxia* and *Protosiren*. This character is also scored 0 in *Moeritherium*, but this is apparently variable, as the fossa is present in one specimen but absent in another; J. Shoshani and J. G. M. Thewissen, pers. comm.)

103. *Foramen ovale*: (0) enclosed by bone; (1) opened to form a notch or incisure (this is a reversal to the condition found in primitive mammals; Novacek 1990).

115. *Periotic*: (0) fused to alisphenoid; (1) not fused with any other skull bone, set in closely fitting socket in squamosal.

121. *Mandibular symphysis*: (0) laterally compressed, with narrow masticating surface scarcely wider than the two rows of tooth alveoli it bears; (1) broad.

122. *Ventral border of horizontal mandibular ramus*: (0) straight or only slightly concave; (1) moderately concave, sharply downturned anteriorly; (2) moderately and evenly concave; (3) strongly concave (see Fig. 2).

123. *Accessory mental foramina*: (0) present, in addition to and usually posterior to the large principal foramen; (1) absent (see Fig. 2).

125. *Posterior border of mandible*: (0) descends ventrally or posteroventrally from condyle without marked interruption or abrupt change of direction; (1) bears a steplike process (processus angularis superior) below condyle; (2) has no distinct processus angularis superior but does have broadly convex outline beginning well below condyle (see Fig. 2).

126. *Anterior border of coronoid process*: (0) approximately vertical; (1) extends slightly anterior to base of process; (2) extends very far anterior to base (see Fig. 2).

127. *Mandibular dental capsule*: (0) completely enclosed by bone of mandible; (1) exposed posteroventrally; (2) absent.

128. *Horizontal ramus of mandible*: (0) slender (minimum dorsoventral height < 0.25 × length of mandible); (1) broad dorsoventrally (height 0.25 × length of mandible) (see Fig. 2).

129. *Ventral border of horizontal ramus of mandible*: (0) tangent to angle; (1) not tangent to angle (see Fig. 2).

136. *First upper incisor*: (0) with enamel on all sides, forming complete enamel crown; (1) with enamel mainly on lateral side.

137. *First upper incisor*: (0) enamel crown distinct from root; (1) enamel extends entire length of tusk.

138. *First upper incisor*: (0) not strongly curved; (1) strongly curved in parasagittal plane. (Polarity uncertain.)

139. *First upper incisor*: (0) present; (1) vestigial or absent (see Fig. 1).

140. *Depth of* I^1 *alveolus*: (0) much less than half the length of the premaxillary symphysis; (1) about half the length of the symphysis; (2) much greater than half the length of the symphysis (see Fig. 1).

141. *Cross section of* I^1 *crown*: (0) suboval or subelliptical; (1) lens-shaped, with sharp anterior and posterior edges; (2) lozenge-shaped (Domning 1978: fig. 3B; 1989a: fig. 4A); (3) broad and extremely flattened mediolaterally (Domning 1990: fig. 4). (Unordered character.)

142. *First upper incisor*: (0) with enamel on all sides, forming complete enamel crown; (1) with enamel mainly on medial side.

143. *Second and third upper incisors, first through third lower*

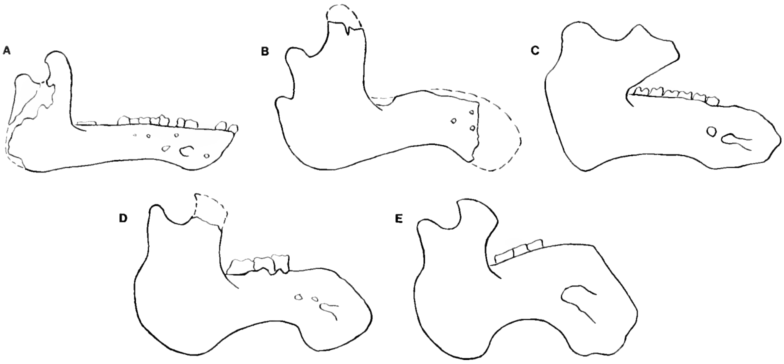

Figure 2. Right mandibles of sirenians in lateral view, illustrating six of the characters used in this analysis. Not drawn to same scale. See text for explanations of characters and states. A, *Prorastomus sirenoides*: 122(0), 123(0), 125(0), 126(0), 128(0), 129(0). B, *Prototherium veronense*: 122(2), 123(0), 125(1), 126(0), 128(0), 129(0). C, *Trichechus senegalensis*: 122(2), 123(0), 125(2), 126(2), 128(0), 129(1). D, *Halitherium schinzii*: 122(1), 123(0), 125(2), 126(1), 128(0), 129(1). E, *Metaxytherium floridanum*: 122(3), 123(1), 125(2), 126(1), 128(1), 129(1).

incisors: (0) present, at least in part; (1) all absent.

144. *Canines*: (0) double-rooted; (1) single-rooted; (2) absent.

146. *Fifth permanent premolars*: (0) present; (1) absent; i.e., no replacement occurs at P^5 and P_5 loci.

150. *Supernumerary molars*: (0) absent; (1) present and replenished indefinitely by horizontal replacement (Domning 1982).

151. *Functional cheek teeth*: (0) present in adult; (1) present in juvenile only; (2) absent (Domning 1978; Domning and Deméré 1984).

155. *Postcanine dental formula*: (0) P1–4, M1–3; (1) P1–5, M1–3, or secondarily reduced from this condition by loss of anterior premolars. [It is still unresolved whether the five premolars of early sirenians are a synapomorphy of the order, as assumed here, or a retention of a primitive placental trait. However, I still lean toward the latter opinion, as expressed in Domning et al. (1982, 1986). In any case the decision would not affect the analysis within the Sirenia since five premolars are clearly primitive for the order. See Thewissen and Domning (1992) for further discussion.]

156. *Cheek-tooth enamel*: (0) smooth; (1) wrinkled.

157. *Permanent premolars*: (0) some double- or triple-rooted; (1) all single-rooted; (2) all absent.

158. *Molars*: (0) unreduced; (1) conspicuously reduced in size relative to skull and mandible, without loss of total occlusal area [as a result of increased number of molars (Domning 1982); however, character state 150(1) also occurs in the absence of this one).

RESULTS OF CLADISTIC ANALYSIS

The analysis of the 36 sirenian taxa using the 62 unweighted characters above and the mh*;bb*; routine (which constructs trees with branch-swapping and retains all trees for each initial one found) in Hennig86 produced 60 maximally parsimonious trees, all of them 152 steps long with a consistency index of 0.55 and a retention index of 0.83. A Nelson consensus tree of these 60 revealed that the variation among them was due entirely to different combinations of variants in the topology of some Eocene dugongids (node 6 in Fig. 3) and in that of the rytiodontine–dugongine clade (nodes 20–23). The remainder of the tree was stable.

Use of Hennig86's successive-weighting option reduced the number of trees from 60 to 6 and eliminated most of the variation in the rytiodontine–dugongine clade, leaving this part of the consensus tree much better resolved (Fig. 3) and increasing the consistency and retention indices to 0.76 and 0.91, respectively, with a tree length of 162. However, as discussed below, the resolution of the rytiodontine–dugongine clade in Fig. 3 may well be incorrect. Character fits and weights for this consensus tree are given in Table 2.

Because missing data have been shown to cause problems in cladistic analysis (Platnick et al. 1991; Huelsenbeck 1991), I reran the analysis omitting the nine taxa lacking data for 20 or more characters (*Eosiren abeli*, *E. stromeri*, *Ribodon limbatus*, *Potamosiren magdalenensis*, *Anomotherium langewieschei*, *Halitherium christolii*, *Rytiodus capgrandi*, *Corystosiren varguezi*, *Xenosiren yucateca*). The mh*;bb*; routine produced two trees 140 steps long with a consistency index of 0.58 and a retention index of 0.83. Successive weighting reduced these two to a single tree that departed from the topology shown in Fig. 3 in only one respect: *Halitherium schinzii* was shifted downward two nodes, becoming the sister group of the other taxa included within node 8 of Fig. 3 (namely, of the Trichechidae, Dugonginae, *Caribosiren*, *Metaxytherium*, and Hydrodamalinae). In all other respects the tree remained stable.

The character transformations at the nodes of the tree in Fig. 3 (or in terminal taxa within these nodes) are listed below. Also listed are characters (e.g., postcranial characters) not used in the analysis but supporting various parts of this tree. The letters r and c after character-state changes denote reversals and convergences, respectively; the numbers after the letter c indicate the other nodes at which the convergence occurred (or, in the case of convergences in terminal taxa, the nodes under which the convergence is discussed

TABLE 1. Matrix of character-state data for sirenian taxa and outgroups analyzed.

	Maximum sample size[a]	Character state[b]																																																											
		3	6	7	8	9	11	13	14	16	31	32	36	37	38	42	43	51	66	67	70	73	74	75	76	77	82	84	85	87	88	89	91	97	99	101	102	103	105	121	122	123	125	126	127	128	129	136	137	138	139	140	141	142	143	144	146	150	151	155	156	157	158
Moeritherium	2	0	0	0	0	0	1	0	0	0	0	1	–	0	0	0	0	0	0	0	–	0	–	0	–	–	–	0	0	0	–	0	1	0	1	0	0	0	0	–	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Paleoparadoxia	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	–	0	0	0	0	0	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Prorastomus sirenoides	1	0	0	0	1	1	1	0	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	–	0	0	0	0	0	1	0	0	0
Protosiren fraasi	6	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	1	0	1	0	?	?	?	0	?	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0
Eotheroides aegyptiacum	4	?	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	1	1	0	0	?	0	?	?	0	0	?	1	1	1	1	1	1	1	1	1	1	0	0	?	?	?	?	?	?	?	0	1	0	0	0	1	0	1	0
Eosiren abeli	1	?	?	?	?	?	0	?	0	0	?	?	?	?	?	0	?	1	0	?	?	1	0	1	1	1	?	0	?	?	?	0	?	?	?	1	1	0	1	1	?	0	1	0	1	0	?	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0
Prototherium veronense	3	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	0	?	1	?	1	1	1	1	0	2	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0
Eosiren libyca	11	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	1	1	1	1	0	0	0	0	0	1	?	0	1	1	1	1	1	1	0	1	1	1	0	0	?	0	0	0	0	?	?	0	1	1	0	0	1	0	1	0
Eosiren stromeri	1	?	0	0	1	1	0	?	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	?	1	1	?	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?	0	1	1	0	0	1	0	?	0
Prototherium intermedium	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	?	?	?	?	?	?	?	1	?	0	0	0	0	0	?	?	?	1	1	?	?	1	1	?	2	1	1	0	0	?	0	0	0	1	?	?	0	1	?	0	0	1	0	1	0
Trichechus m. manatus	27	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	2	1	0	0	0	0	2	1	1	1	1	1	1	1	2	0	2	2	1	0	1	–	–	–	1	0	–	–	1	2	1	1	0	1	1	2	1
Trichechus m. latirostris	51	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	2	1	0	0	0	0	2	1	1	1	1	1	1	1	2	0	2	2	1	0	1	–	–	–	1	0	–	–	1	2	1	1	0	1	1	2	1
Trichechus senegalensis	30	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	2	1	0	0	0	0	2	1	1	1	1	1	1	1	2	0	2	2	1	0	1	–	–	–	1	0	–	–	1	2	1	1	0	1	0	2	1
Trichechus inunguis	45	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	1	1	1	0	1	1	0	2	0	0	0	0	0	2	1	1	1	1	1	1	1	2	0	2	2	1	0	0	–	–	–	1	0	–	–	1	2	1	1	0	1	0	2	1
Ribodon limbatus	2	?	?	?	?	?	1	1	0	1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	1	2	0	?	?	1	0	0	?	?	?	?	?	?	?	1	2	1	1	0	1	0	2	0
Potamosiren magdalenensis	1	?	?	?	?	?	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	1	2	0	?	?	1	0	0	?	?	?	?	?	?	?	1	2	1	0	0	1	0	2	0
Anomotherium langewieschei	1	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	1	0	2	0	1	0	1	1	0	2	0	?	?	?	?	?	?	?	1	1	1	1	1	1	1	2	?	1	0	0	?	?	?	?	?	?	?	1	2	1	0	0	1	0	1	0
Miosiren kocki	1	0	0	0	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	2	0	2	0	1	1	0	2	0	2	?	0	0	1	0	0	1	1	1	1	?	?	?	?	?	?	?	?	0	1	0	0	2	0	0	1	2	1	0	0	1	0	1	0
Halitherium schinzii	22	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	1	1	1	1	0	1	0	0	0	?	1	0	1	1	1	1	1	1	0	2	1	1	0	1	0	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0
Halitherium christolii	2	?	?	?	?	?	0	?	?	0	?	1	0	0	0	0	0	1	0	?	?	1	0	1	1	1	1	0	?	?	?	?	?	?	?	1	1	1	1	1	3	1	2	1	1	1	1	?	?	?	?	?	?	?	1	2	1	0	0	1	0	?	0
Rytiodus capgrandi	1	1	1	1	1	1	?	1	0	?	1	1	–	1	?	1	1	1	?	?	?	1	0	?	?	1	?	0	2	0	?	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	–	1	0	0	2	3	1	?	?	1	0	0	1	0	2	0
Corystosiren varguezi	4	1	?	1	1	1	?	?	?	?	?	1	–	2	?	1	?	1	0	1	0	1	0	?	0	?	?	0	2	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	–	1	0	0	2	3	1	1	2	1	0	0	1	0	2	0
Xenosiren yucateca	1	?	1	?	1	1	0	?	2	1	1	1	–	1	0	1	1	?	?	?	?	?	?	?	?	1	?	0	1	?	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	–	1	0	0	2	?	1	?	?	1	0	0	1	0	2	0
Dioplotherium allisoni	2	1	1	0	1	1	0	1	0	1	1	1	–	1	?	1	1	1	0	2	0	?	?	?	0	1	?	0	2	0	1	1	1	1	0	1	1	1	1	1	3	0	2	1	1	1	1	–	1	0	0	2	2	1	1	2	1	0	0	1	0	2	0
Dioplotherium manigaulti	9	1	1	0	1	1	0	1	0	0	1	1	–	1	0	1	1	1	0	2	0	?	?	?	1	?	?	?	2	0	1	1	1	2	0	1	1	1	1	?	?	?	?	?	?	?	?	0	1	0	0	2	2	0	1	2	1	0	0	1	0	2	0
Dugong dugon	65	1	0	0	1	1	0	1	1	1	1	1	1	2	0	1	0	1	1	2	0	1	0	1	1	1	1	0	2	1	1	0	1	1	1	1	1	1	1	1	3	1	2	1	1	1	1	–	1	0	0	2	0	1	1	2	1	0	0	1	0	2	0
Crenatosiren olseni	3	1	0	0	1	1	0	1	0	0	1	1	–	1	0	0	1	1	0	2	0	1	0	1	1	1	1	0	1	0	1	0	0	?	?	1	1	1	1	1	3	1	?	1	1	1	?	0	0	0	0	1	0	0	1	2	1	0	0	1	0	2	0
Caribosiren turneri	1	1	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	1	?	?	?	1	0	1	1	1	1	0	?	0	?	0	1	1	0	1	1	1	1	?	?	?	?	?	?	?	?	–	–	–	?	0	–	–	1	2	1	0	0	1	0	2	0
Metaxytherium krahuletzi	4	1	0	0	1	1	1	?	0	0	?	1	1	0	0	0	0	1	0	2	0	1	0	1	1	1	1	0	1	?	?	0	?	?	?	1	1	1	1	1	3	1	2	1	1	1	1	0	0	0	0	0	?	?	1	2	1	0	0	1	0	2	0
Metaxytherium medium	2	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	2	0	1	0	1	1	1	1	0	2	?	?	0	1	1	?	1	1	1	1	1	3	1	2	1	1	1	1	0	0	0	0	0	0	0	1	2	1	0	0	1	0	2	0
Metaxytherium calvertense	3	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	2	0	1	0	1	1	1	1	0	2	0	0	0	1	1	0	1	1	1	1	1	3	1	2	1	1	1	1	0	0	0	0	0	0	0	1	2	1	0	0	1	0	2	0
Metaxytherium floridanum	52	1	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	1	1	2	0	1	0	1	1	1	1	0	2	0	0	0	1	1	0	1	1	1	1	1	3	1	2	1	1	1	1	0	0	0	0	0	0	0	1	2	1	0	0	1	0	2	0
Metaxytherium serresii	7	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	3	0	1	0	1	1	1	1	0	2	?	?	0	1	1	1	1	1	1	1	1	3	1	2	1	1	1	1	0	0	0	0	1	0	0	1	2	1	0	0	1	0	2	0
Metaxytherium subapenninum	3	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	3	0	1	0	1	1	1	1	0	2	0	?	0	1	1	?	1	1	1	1	1	3	1	2	1	1	1	1	0	0	0	0	2	0	0	1	2	1	0	0	1	0	2	0
Dusisiren jordani	8	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	3	1	1	0	1	1	2	1	0	2	1	0	0	2	1	1	1	1	1	1	1	2	1	2	1	1	0	1	–	–	–	1	0	–	–	1	2	1	0	0	1	0	2	0
Dusisiren dewana	1	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	3	1	1	1	1	1	2	1	0	2	1	?	0	2	1	?	1	1	1	1	1	2	1	2	1	?	0	?	–	–	–	1	0	–	–	1	2	1	0	0	1	0	2	–
Hydrodamalis cuestae	5	1	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	1	1	3	1	1	1	1	1	2	1	0	2	1	0	0	2	1	1	1	1	1	1	1	2	1	2	1	1	0	1	–	–	–	1	0	–	–	1	2	1	0	1	1	?	2	–
Hydrodamalis gigas	22	1	0	0	1	1	1	1	1	0	1	1	2	0	0	0	0	1	1	3	2	1	1	1	1	0	1	0	2	1	0	0	2	1	1	1	1	1	1	1	2	1	2	0	2	0	1	–	–	–	1	0	–	–	1	2	1	0	2	1	–	2	–

[a] Maximum number of specimens of the taxon for which any character was scored

[b] A dash (–) signifies that the character is not applicable to the taxon (Hennig86 treats ? and – alike). Significant polymorphisms are noted and discussed under Results.

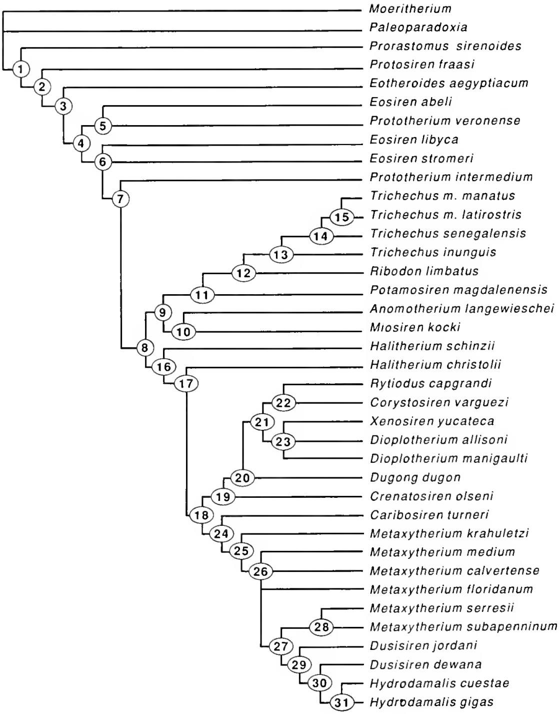

Figure 3. Nelson consensus tree of sirenian taxa and outgroups, generated by Hennig86 using 62 characters and the successive weighting option. Tree length, 162 steps; consistency index, 0.76; retention index, 0.91. Character fits and weights are given in Table 2. Note that node 27 is probably spurious (see text).

below). Autapomorphies of terminal taxa are listed if any are known. When the node at which a transformation occurred is uncertain because of missing data, the transformation is listed under the first node or terminal taxon by which it had certainly occurred, with an indication of the earlier node at which it may questionably have first occurred. Significant polymorphisms are also noted where they occur.

Places where the nodes of the tree correspond to traditionally recognized taxa are indicated. Only one new name is introduced here: inclusion of the Miosireninae within the Trichechidae necessitates the recognition of the new nominotypical subfamily Trichechinae. This and other suggested modifications to the present classification of the taxa here considered are shown in the Appendix.

Basal Radiation of the Sirenia; Prorastomidae

Node 1 (order Sirenia; one branch forms the possibly paraphyletic family Prorastomidae): 8(1), 9(1), 51(1), 155(1). Also, mastoid inflated and exposed through occipital fenestra (Novacek and Wyss 1987); ectotympanic inflated and droplike (Tassy and Shoshani 1988); pachyostosis and osteosclerosis present in skeleton (Domning and de Buffrénil 1991). The possession of five premolars, 155(1), is here provisionally treated as a synapomorphy of the Sirenia rather than a primitive retention, in view of the strong evidence placing the Sirenia well within the Ungulata, which are characterized by only four (Thewissen and Domning 1992). Although possession of double-rooted canines, 144(0), is here treated as a primitive retention in *Prorastomus*, it may be that the same reasoning should apply to this character. Autapomorphies of *P. sirenoides*: 11(1)c5,11,25, 136(1), 137(1)c10,20, 138(1), 140(1)c7,28; also, extension of premaxilla–maxilla suture forward of rear end of premaxillary symphysis; enlargement of P_1. Scoring of this species was based on a redescription of the holotype and examination of fragmentary new material (including a tusk) from Jamaica by Savage et al. (in press).

Protosirenidae and Early Dugongidae

Node 2 (one branch forms the possibly paraphyletic family Protosirenidae): 32(1), 67(1), 103(1), 115(1), 122(1), 144(1), 157(1). Also, increase in rostral deflection; reduction of wing of atlas; loss of costal groove on ribs. Autapomorphies of *Protosiren fraasi*: 3(1)c6?, 102(0)r; however, 3(1) here may be spurious, due to distortion (Andrews 1906: 204).

Node 3 (paraphyletic family Dugongidae; paraphyletic subfamily Halitheriinae): 73(1), 75(1), 76(1), 77(1), 101(1), 102(1) (node 1?), 121(1), 125(1) (node 2?), 127(1) (node 2?). Autapomorphy of *Eotheroides aegyptiacum*: 123(1)c10,17. Characters 13 and 82 are derived in exactly half the sample of *E. aegyptiacum* (actual frequencies 1/2 and 2/4, respectively); they were arbitrarily scored here as primitive for this species, which appears to be genuinely transitional in regard to these two characters. Other polymorphisms and frequencies observed in this species: 32(0), 1/3; 67(2), 1/3; and possibly 103(0), 1/3. A fourth specimen, definitely displaying 103(0) according to Abel (1913), was made the type of *Eosiren abeli* by Sickenberg (1934).

Node 4: 13(1), 82(1), 97(1), 146(1) (node 3?). Also, reduction of pubis and probable loss of terrestrial locomotor ability (node 3?).

Node 5: 141(1). Autapomorphies of *Prototherium veronense*: 11(1)c1,11,25, 32(0)rc10, 67(0)rc14, 121(0)r, 122(2)c11,29; also, pronounced narrowing of skull roof. Polymorphism and frequency observed: 76(0), 1/2. I scored the processus retroversus as present, 77(1), in *P. veronense*, contrary to Sickenberg (1934). The holotype of *Eosiren abeli* was destroyed in World War II; scoring of this species is based on the description by Sickenberg (1934) and on unpublished new material provisionally referred to this species.

Node 6: 3(1)c2?, 67(2), 91(1) (node 4?), 126(1) (node 2?). Also, broadening of supraspinous fossa of scapula; loss of symphyseal contact between pubic bones. Polymorphisms and frequencies observed in *Eosiren libyca*: 32(0), 1/11; 43(1), 1/8; 122(2), 1/4. Autapomorphies of *E. stromeri*: frontals much longer than parietals in midline; M^3 smaller than M^2.

Node 7: 125(2), 140(1)c1,28.

Node 8: 143(1), 144(2).

Trichechidae

Node 9 (family Trichechidae): 3(0)r, 77(0)rc31, 82(2); also, reduction of neural spines; possible tendency to enlargement and (at least in *Trichechus*) anteroposterior elongation of thoracic centra.

Node 10 (subfamily Miosireninae): 32(0)rc5, 38(1). Possible autapomorphy of *Anomotherium langewieschei*: 123(1)c3,17 (node 10?). Autapomorphies of *Miosiren kocki*: 16(1)c12,20 (node 10?), 36(1)c18, 73(2), 85(2)c20,26 (node 10?), 97(0)r (node 10?), 137(1)c1,20 (node 9?), 140(2)c20,28 (node 10?); also, reduction and simplification of M^3.

Node 11 (subfamily Trichechinae): 11(1)c1,5,25, 99(1)c27, 122(2)c5,29, 157(2)c18; also, thickening of molar enamel (node 9?) (Domning, in press). *Potamosiren magdalenensis* is here taken to include *Metaxytherium ortegense* (Domning, in press).

Node 12: 16(1)c10,20, 150(1); also, thinning of molar enamel (reversal; Domning, in press). *Ribodon limbatus* is here taken to include the maxilla (U.S. National Museum 167655) referred to *Ribodon* sp. by Domning (1982).

TABLE 2. Character fits and weights for the tree in Figure 3.

Character	Steps[a]	Consistency index	Retention index	Weight[b]
3	3	33	77	2
6	1	100	100	10
7	1	100	100	10
8	1	100	100	10
9	1	100	100	10
11	5	20	75	1
13	1	100	100	10
14	5	40	25	1
16	4	25	62	1
31	2	50	91	4
32	4	25	40	1
36	3	66	91	6
37[c]	3	66	80	5
38	1	100	100	10
42	1	100	100	10
43	2	50	75	3
51	1	100	100	10
66	2	50	88	4
67	7	42	82	3
70	3	66	75	5
73	2	100	100	10
74	1	100	100	10
75	1	100	100	10
76	3	33	60	2
77[c]	4	50	83	4
82	2	100	100	10
84	1	100	100	10
85	6	33	84	2
87	2	50	75	3
88	1	100	100	10
89	1	100	100	10
91	5	40	70	2
97	3	66	83	5
99	4	25	72	1
101	1	100	100	10
102	2	50	66	3
103	2	50	75	3
115	1	100	100	10
121	2	50	66	3
122	6	50	85	4
123	4	25	78	2
125	2	100	100	10
126	5	40	62	2
127	2	100	100	10
128	2	50	88	4
129	2	50	90	4
136	1	100	100	10
137	3	33	71	2
138	1	100	100	10
139	2	50	85	4
140	8	25	68	1
141[c]	3	100	100	10
142	2	50	75	3
143	1	100	100	10
144	3	66	90	5
146	1	100	100	10
150	1	100	100	10
151	2	100	100	10
155	1	100	100	10
156	1	100	100	10
157	3	66	93	6
158	1	100	100	10

[a] Number of transformations undergone by the character on this tree.

[b] Calculated by the successive weighting option of Hennig86.

[c] Unordered character.

Node 13 (genus *Trichechus*): 31(1)c18 (node 11?), 67(1)rc22 (node 11?), 91(2)c29 (node 11?), 126(2) (node 9?), 139(1)c29 (node 11?), 140(0)rc24 (node 11?), 158(1). Also, reduction of cervical vertebrae to six (node 11?); elongation of acromion process of scapula (node 9?); reduction of bicipital groove of humerus (node 11?); reduction of ilium (node 11?). Polymorphisms include 11(0) in all species, 67(0), 84(1), 99(0), 129(1), and 156(1) in *T. inunguis*, 156(0) in *T. manatus*, 156(1) in *T. senegalensis*, and 67(1), 84(0), 122(1), and 129(0) in both *T. manatus* and *T. senegalensis*; the frequencies of these states have not been determined in all cases. Autapomorphies of *T. inunguis*: 70(1)c29; also, division of foramen incisivum; lateral projection of temporal crests with postorbital apophyses on frontal frequent; inflation of supraoccipital; elongation of mandibular symphysis; increase in number of accessory mental foramina; reduction of DP^3 and DP$_3$; increase in complexity and further decrease in size of molars; reduction of thoracic vertebrae to 14–16; elongation of forelimb; loss of nails. See Domning and Hayek (1986) for details regarding *Trichechus*.

Node 14: 67(0)rc5, 84(1), 129(1)c16. Also, loss of bicipital groove of humerus. Autapomorphies of *Trichechus senegalensis*: shortening of rostrum; decrease in rostral deflection; more transverse orientation of posterolateral sides and constriction of bases of supraorbital processes; presence of longitudinal crests on floor of mesorostral fossa; broadening of zygomatic arch and coronoid process.

Node 15 (*Trichechus manatus*): 156(1). Also, elongation of vomer; more transverse orientation of median portion of frontoparietal suture; broadening of ribs. Autapomorphies of *T. m. latirostris*: widening of foramen magnum and straightening of its dorsal border; increase in rostral deflection; increase in height of mandibular symphysis.

Later Dugongidae

Node 16 (paraphyletic genus *Halitherium*): 85(1) (node 8?), 129(1)c14. Also, development of cetaceanlike triangular flukes in place of a rounded caudal fin. Polymorphism and frequency observed in *H. schinzii*: 13(0), 4/6; though in the majority, this state has an LCL$_{95}$ of only 0.223, and is also incongruent.

Node 17: 122(3), 123(1)c3,10, 128(1).

Node 18: 31(1)c13 (node 17?), 36(1)c10, 157(2)c11 (node 17?).

Dugonginae, Including Rytiodontinae

Node 19 (subfamily Dugonginae, formerly Rytiodontinae): 37(1), 43(1), 88(1). Autapomorphies of *Crenatosiren olseni*: fusion of nasals with frontals; elongation of bases of supraorbital processes; deepening of nasal incisure.

Node 20: 16(1)c10,12, 42(1), 85(2)c10,26, 137(1)c1,10, 140(2)c10,28, 142(1). Autapomorphies of *Dugong dugon*: 14(1)c26,31, 37(2)c22, 43(0)r, 66(1)c26; also, strong inflection of processus retroversus of squamosal; constant presence in juveniles of deciduous I^1, and frequent presence in adults of vestigial lower incisors (these are atavisms, seemingly due to neoteny); sexual dimorphism in size and eruption of permanent I^1 tusks; functional loss of enamel crowns of cheek teeth; persistently open roots of M$^{2-3}$ and M$_{2-3}$. Although the zygomatic process of the jugal of the adult *Dugong* is long, 89(0), the process is much shorter in fetuses and neonates, suggesting that the ancestors of *Dugong* may have had the derived state 89(1), like *Dioplotherium* and *Xenosiren* (below). *Trichechus*, in contrast, has a long process in both fetuses and adults, so a short process is not simply a condition of early ontogeny.

Node 21: 6(1), 141(2).

Node 22: 7(1), 141(3). Autapomorphies of *Corystosiren varguezi*: 37(2)c20, 67(1)rc13 (node 22?), 76(0)rc23. Separation of the squamosal from the temporal crest, 76(0), may reflect the great and uniquely derived thickening of the parietals characteristic of *Corystosiren*.

Node 23: 89(1). Also, incipient blockage of infraorbital canal by a transverse wall; apparent fusion of nasals with frontals. Autapomorphies of *Dioplotherium manigaulti*: 16(1)r?, 97(2), 142(0)r?; these "reversals" more likely indicate that this entire clade should be rooted farther down in the tree. Possible autapomorphies of *D. allisoni*: 76(0)rc22 (condition unknown in its possible descendant *Xenosiren*); 123(0)r (node 21?). *D. allisoni* here includes referred specimens from Brazil (Toledo and Domning 1991). Autapomorphies of *X. yucateca*: 14(2), 85(1)r; also, accentuation of concavity of frontal roof; thinning and medial concavity of preorbital process of jugal.

Caribosiren and *Metaxytherium*

Node 24: 140(0)rc13. It is uncertain whether the tusks of *Caribosiren* were really absent (an autapomorphy) or merely small.

Node 25 (paraphyletic genus *Metaxytherium*): 11(1)c1,5,11. See Domning and Thomas (1987) and Domning (1988) for details. Polymorphism and frequency observed in *M. krahuletzi*: 66(1), 1/2; evidently a genuinely transitional condition, scored arbitrarily as primitive.

Node 26: 66(1)c20, 85(2)c10,20. Autapomorphy of *Metaxytherium floridanum*: 14(1)c20,31. Polymorphisms and frequencies observed in *M. floridanum*: 11(0), 8/26, 14(0), 1/3; 67(1), 15/26; 85(1), 12/20. The latter two majority states have LCL$_{95}$s of only 0.369 and 0.361, respectively, and are both incongruent.

Node 27: 67(3), 99(1)c11. I believe that this node is spurious and that these changes were actually evolved in parallel by European Pliocene *Metaxytherium* and North Pacific hydrodamalines (i.e., at nodes 28 and 29 of this tree, respectively).

Node 28: 140(1)rc1,7; this increase in tusk length was interpreted by the program as a re-reversal of the reduction at node 24. The body of *M. serresii* is smaller than that of the European Miocene *Metaxytherium*; I interpret this as ecophenotypic dwarfism that was reversed in *M. subapenninum* (Domning and Thomas 1987). Polymorphisms and frequencies observed: in *M. serresii*, 31(0), 2/3; in *M. subapenninum*, 66(0), 2/3. In each case, the majority state has an LCL$_{95}$ of only 0.094 and is incongruent. Autapomorphy of *M. subapenninum*: 140(2)c10,20. This name is accepted by Pilleri (1988) as a valid senior synonym of *M. forestii*.

Hydrodamalinae

Node 29 (subfamily Hydrodamalinae; paraphyletic genus *Dusisiren*): 70(1)c13, 77(2), 87(1), 91(2)c13, 122(2)rc5,11, 128(0)r, 139(1)c13. Also, decreased rostral deflection; increased body size (to about 4.5 m in *D. jordani*). See Domning (1978) for details. Polymorphisms and frequencies observed in *D. jordani*: 66(0), 2/6; 67(1), 1/5. A peculiarity of the available specimens of *D. jordani* is separation of the palatines in the midline, a condition seen in no other sirenian. Although the palatal incisure is consequently very deep, because of the different anatomical basis of this condition (compared to *Dioplotherium manigaulti*, where the incisure is deep despite the median juncture of the palatines), character 97 was here scored 1 rather than 2. Whether this separation of the palatines is a true autapomorphy that rules *D. jordani* out of the ancestry of later species, or whether this condition was later reversed or occurred here only as an individual variation, needs to be addressed by future work.

Node 30: 74(1). Also, reduction in complexity of molars; broadening of manubrium; development of keel on xiphisternum; narrowing of supraspinous fossa of scapula; increased circularity of humeral head; reduction of deltoid crest; medial bowing of radius–

ulna; extensive modifications of carpals; reduction of metacarpals and phalanges. See Takahashi et al. (1986) for details.

Node 31 (genus *Hydrodamalis*): 14(1)c20,26, 151(1). Also, presence of dentiform process on premaxilla; more nearly rectangular shape of rostral masticating surface; broadening of lateral side of pterygoid process; concealment of infraorbital foramen in ventral view; reduced indentation of squamosal at mastoid foramen; inflation of pars temporalis of periotic; reduced curvature of coronoid process of mandible; upward extension of a vertical anteromedial ridge almost or quite into coronoid process; extension of ligamentary notch to center of humeral trochlea (node 30?); increased proximal curvature of anterior ribs; increased body size (to 7–10 m). Polymorphism and frequency observed in *H. cuestae*: 77(0), 2/5; this is a genuinely transitional condition. Autapomorphies of *H. gigas*: 36(2), 70(2), 77(0)rc9, 126(0)r, 127(2), 151(2); also, subrectangular shape of rostral masticating surface; sharp anterior demarcation of foramen incisivum; loss of tentorium ossium and bony falx cerebri; presence of deep pits in anterodorsal roof of braincase; shorter and higher shape of cranial cavity, and elevation of roof well above crista galli; rounding of cranial vault (reduction of temporal crests); more ventral placement of optic foramina relative to sphenorbital fissures; broadening of posterior end of squamosal zygomatic process and rounding of its outline; rugosity of surface of periotic; reduction or loss of coronoid canal of mandible; more posterior placement of mental foramen; square rather than rhomboid sagittal sections of thoracic vertebrae 1 and 2; straight or irregularly concave anterior border of scapula; reduction of acromion and its elevation well above glenoid fossa of scapula; restriction of ligamentary attachment to center of humeral trochlea; opening of notch for this ligament on radius–ulna toward medial rather than lateral side. Polymorphisms and frequencies observed in *H. gigas*: 14(0), 1/18; 66(0), 1/17. See Domning (1978) and Domning and Deméré (1984) for details.

DISCUSSION

Age and Clade Ranks.—A gratifying aspect of this analysis is the close correspondence between the geological ages of the taxa and their positions on the tree. The earliest known sirenian, *Prorastomus* (early and middle Eocene; Donovan et al. 1990), also stands at the base morphologically, and is followed by the other middle Eocene forms (*Protosiren*, *Eotheroides*, *Eosiren abeli*). *Prototherium* and the other *Eosiren* species are late Eocene. Node 8 comprises exclusively post-Eocene taxa; the clean Eocene–Oligocene separation on the tree is probably due in part to the lack of any named early Oligocene sirenians in the fossil record. Node 9 defines a clade including one late Oligocene form (*Anomotherium*) and seven Neogene ones; *Potamosiren*, *Ribodon*, and *Trichechus* are arrayed in known stratigraphic order. *Halitherium schinzii* and *Caribosiren* are middle Oligocene; *H. christolii*, *Crenatosiren*, and *Dioplotherium manigaulti* are late Oligocene. *D. allisoni* and *Rytiodus* appeared in the early Miocene, *Corystosiren varguezi* and *Xenosiren yucateca* in the late Miocene or Pliocene, while the Recent *Dugong* doubtless had a long but still unknown fossil record. The species of *Metaxytherium* are in known stratigraphic order from the early Miocene *M. krahuletzi* through the three middle Miocene species to the Pliocene *M. serresii* and *M. subapenninum*. Finally, *Dusisiren* diverged from *Metaxytherium* before the late Miocene and gave rise to *Hydrodamalis* by the end of the Miocene. Hence this tree could be converted into a plausible phylogram with only minor adjustments.

Norell and Novacek (1992) presented an improved method for quantifying the fit between age and clade rank, and Fig. 4 displays the data above graphically for comparison with the taxa Norell and Novacek used as examples. The correlations are highly significant for the Sirenia shorn of the major side branches Trichechidae and Dugonginae, and for the Trichechidae considered separately. Not surprisingly, the correlation for the Dugonginae is nonsignificant, largely because *Dugong dugon*, the second-earliest member of the group in terms of clade rank, is a Recent species with no fossil record. (For the purposes of this analysis, the family Trichechidae includes *Anomotherium* from the miosirenine side branch because it is the earliest taxon assigned to the family but excludes *Miosiren* in order to simplify the topology of the portion of the tree being analyzed. *Anomotherium* was also included in the "Most Sirenia" analysis together with *Crenatosiren*; *Eosiren abeli* and *Metaxytherium subapenninum* were omitted to simplify the topology.

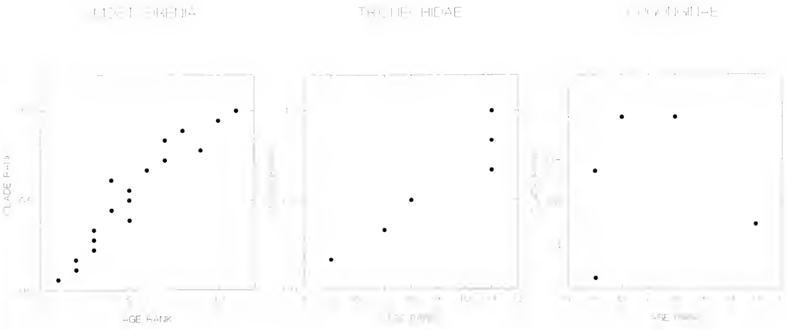

Figure 4. Plots of age ranks as a function of clade ranks for subsets of the Sirenia (see text for taxa included). Clade ranks are rescaled from 0 to 1. Correlations are statistically significant (*S*, Spearman rank correlation coefficient) for "Most Sirenia" exclusive of most Trichechidae and Dugonginae ($S = 0.974$, $P < 0.0001$) and for the Trichechidae ($S = 0.915$, $P < 0.002$), but not significant for the Dugonginae ($S = 0.263$).

The "Dugonginae" analysis included *Crenatosiren*, *Dugong*, *Dioplotherium manigaulti*, *Rytiodus*, and *Corystosiren*. Some data points on the scatter diagrams coincide.)

The highly significant correlations obtained in the two most inclusive of these analyses confirm the generally impressive effectiveness and reliability of the sirenian fossil record in recovering the sequence of phylogenetic divergences. These results are comparable to those presented by Norell and Novacek (1992) for most subdivisions of the Perissodactyla, a group thought to have a relatively complete and well-understood fossil record. With the obvious and important exception of the Dugonginae, then, it appears that the sirenian fossil record is not grossly deficient in the picture it provides of this group's history.

Comments on individual nodes.—The characters uniting all sirenians at node 1 have been discussed above. *Prorastomus* is traditionally, and justifiably, regarded as close to the ancestry of all other sirenians and placed in its own monotypic and probably paraphyletic family. It appears to possess several derived features that exclude it from the direct ancestry of other taxa. However, these characters are not well understood and some of them are based on a referred tusk (Savage et al., in press) whose identification might be questioned, so it remains to be seen just how close *Prorastomus* actually is to the base of the sirenian radiation. Meanwhile, it is by far the closest thing we have to a structural ancestor for other sirenians, and it should be used wherever possible to represent the Sirenia in interordinal comparisons.

Protosiren, at node 2, has likewise been accorded its own, probably paraphyletic family, and with at least two undescribed genera it seems to represent a grade of evolution intermediate between *Prorastomus* and other sirenians. Its possession of at least one character state seemingly more primitive than seen in *Prorastomus* [absence of a pterygoid fossa, 102(0)] is puzzling, and there may be some problem in definition or interpretation of this character.

The position of *Eotheroides* (node 3) was very stable throughout the analysis; it has generally been considered the most primitive dugongid. In the past the name *Eotheroides* has sometimes been applied instead (by myself as well as others) to all the species here placed in *Eosiren*; here *E. aegyptiacum* is provisionally maintained in its own genus, pending better knowledge of this and related forms and a thorough revision of Eocene taxa.

Nodes 4–7 are rather unstable, and this part of the tree should be considered provisional; the Eocene dugongids are badly in need of thorough revision. Node 5 is supported by only one character, which is weakly attested by specimens. The position of *Prototherium veronense* is especially problematical because this species displays several very primitive states, here interpreted as reversals. *Prototherium intermedium* (node 7) was consistently separated from *P. veronense* and should not be considered congeneric with it; the monophyly of *Eosiren* is also open to question. Better knowledge of all Eocene sirenians (of which many poorly known nominal taxa were excluded from this study) will probably change this part of the tree drastically.

Node 8, as noted above, includes all the post-Eocene sirenians and seems to mark the point at which the manatees separated from the dugongs. This separation has long been dated to the Eocene, but this analysis implies a later rather than earlier Eocene (and conceivably even an early Oligocene) divergence. The hypothesis (e.g., Domning 1982) of a protosirenid origin for manatees separate from that of the dugongids is decisively refuted by this analysis: the trichechid clade is stably rooted well within the Dugongidae as traditionally defined.

On the other hand, my suggestion (in Barnes et al. 1985) that *Anomotherium* and *Miosiren* (node 10) are closer to manatees than to other sirenians is supported by these results (node 9), as is my previous interpretation of manatee phylogeny (nodes 11–15; Domning 1982; Domning and Hayek 1986). It seems opportune to include the Miosireninae formally within the Trichechidae, necessitating the introduction here of the name Trichechinae for the contents of the Trichechidae as previously understood.

The well-known European mid-Oligocene species *Halitherium schinzii* appears to be the sister group of all later dugongids (node 16). *H. christolii* occupies a similarly significant position one rung higher (node 17), so it is particularly unfortunate that this species from the late Oligocene of Austria is so poorly known. *H. christolii* could be interpreted as a structural ancestor of the rytiodontine–dugongine clade as well as of *Metaxytherium* and the hydrodamalines (node 18), but in fact many of its character states are unknown and judgment on this point should be reserved.

The subfamily Rytiodontinae (node 19), whose validity I questioned as recently as 1985 (Barnes et al. 1985), has since proven to represent a major adaptive radiation beginning in the late Oligocene and apparently centered in the Caribbean and western Atlantic (Domning 1989a,b, 1990, 1991). Perhaps the most significant finding of this study is that *Dugong* is stably located within the rytiodontine clade (node 20). This conclusion needs to be corroborated by more fossils from the Indo-Pacific region where *Dugong* presumably evolved. However, it is the first strong indication of where in sirenian phylogeny the affinities of the modern dugong might lie, and it justifies combining the Rytiodontinae and the previously monotypic Dugonginae into a single subfamily, which must under the principle of priority take the latter name.

Although the consensus tree derived from the Hennig86 successive weighting routine resolved the remainder of the rytiodontine clade (nodes 21–23) in a way generally supportive of my previous conclusions (Domning 1989a,b, 1990), this is the least stable part of the entire tree, and any of the possible most-parsimonious arrangements involve several parallelisms and/or reversals. The reason for this instability lies in the fact that study of this group of sirenians is just beginning; several key specimens and new taxa have yet to be described, and several of the named taxa are scored on the basis of unique, fragmentary, and/or doubtfully referred specimens. As with the Eocene dugongids, greater clarity can be expected to emerge over the next few years.

The position of *Caribosiren* (node 24) was one of the least stable through the preliminary analyses; the genus is represented by only a single well-preserved but incomplete skull for which several characters cannot be scored. Its apparent middle Oligocene age also tends to cast doubt on its present position in the tree. Conversely, its horizon may actually be late Oligocene, which would improve the correlation between its age and clade ranks.

Node 25 defines the well-known and widely distributed genus *Metaxytherium*, and nodes 26 and 28 corroborate my earlier interpretation of *M. krahuletzi–M. medium–M. serresii–M. subapenninum* as an Old World phyletic series (Domning and Thomas 1987). New evidence, however, casts doubt on the origin of the genus from European *Halitherium christolii*, and the New World *Metaxytherium* species themselves are far from satisfactorily understood. Supporting a New World origin for the genus is its nearest sister taxa (*Caribosiren*, *Crenatosiren*) being New World forms, and the next sister taxon (*H. christolii*) may also be represented in North America. Furthermore, the oldest specimens of *Metaxytherium* itself now appear to be ones from the late Oligocene of the southeastern U.S. However, their small size is incongruent with the larger size of most of their likely ancestors and descendants. There are also problems of species definition as well as synonymy involving the middle Miocene *M. calvertense*, and this species and the somewhat later *M. floridanum* are difficult to separate from near-contemporary European and eastern Pacific forms (cf. Domning 1988; Aranda-Manteca, Domning, and Barnes 1994, this volume). This is another part of the tree urgently needing attention. *M. calvertense* has been proposed as the sister group and ancestor of *Dusisiren* (Muizon and Domning 1985; Aranda-Manteca, Domning, and Barnes 1994, this volume).

Node 27, which unites the Pliocene *Metaxytherium* of Europe with the late Miocene and later hydrodamalines of the North Pacific, I consider spurious on zoogeographic grounds. I believe that if node 26 were properly resolved, some sort of division between Old and New World species would appear there, and the minor characters [loss of supracondylar fossa, 67(3); shortening of palatines, 99(1)] that support node 27 would be revealed as having evolved in parallel in the Mediterranean and North Pacific. The species of *Metaxytherium* are a particular focus of my continuing research.

Node 29 defines the Hydrodamalinae, whose successive evolutionary stages leading to the recently extinct Steller's sea cow (*Hydrodamalis gigas*) are supported by numerous character transformations (nodes 30–31).

Molecular vs. morphological phylogeny.—Finally, mention should be made of the sole attempt so far at a sirenian phylogeny based on molecular data (Rainey et al. 1984). These authors conducted immunological comparisons using antisera to bone extracts of *Hydrodamalis gigas* and all four living sirenian species, as well as antisera to serum albumins of the dugong, the Florida manatee, and the Indian and African elephants.

Although their phylogeny of the Recent species agrees topologically with the paleontological consensus, their inferred ages for the most important branch points are inconsistent with the fossil data. They dated the dugongid–trichechid divergence to 17–20 Ma (early Miocene), as opposed to the 30–40 Ma (late Eocene or early Oligocene) date inferred here. They also dated the *Dugong–Hydrodamalis* divergence to 4–8 Ma (late Miocene or early Pliocene), whereas the present (and previous) results suggest a divergence not later than late Oligocene (> 25 Ma).

Rainey et al. (1984) downplayed the seriousness of these contradictions, stating that "none of this is in conflict with the actual fossil record." In reality, they misconstrued several details of the fossil record, most notably in stating that "the first good hydrodamaline (*Hydrodamalis cuestae*) occurs in the 4–8 Ma range." Apart from ignoring *Dusisiren* spp. being cladistically "good" (and much older) hydrodamalines, their reasoning implies that *Dugong* could have been derived from a hydrodamaline only 4–8 Ma old (i.e., from *H. cuestae*). As is clear from the data presented here, this is unparsimonious to an absurd degree. Rainey et al. concluded that their data "should provide a useful framework for further interpretation of the sirenian fossil record." This bold prediction has not come true.

COMMENTS ON METHODS

A peculiar, and surprisingly primitive, feature of contemporary phylogenetic systematics is its extreme typology. Most published cladistic analyses do not state how many specimens of each taxon were examined; in very many cases (especially in studies of fossil vertebrates) the sample size is probably one. Neither do most authors take any particular notice of individual variation, if indeed they have observed it in their samples. [The study by Hulbert and MacFadden (1991) was exceptional in that these authors at least acknowledged variation and stated how they dealt with it, by reporting the state observed in the majority of a sample.] The problem of polymorphism in supraspecific terminal taxa has been addressed theoretically by Nixon and Davis (1991) and a few other recent authors whom they cited, but they specifically excluded from consideration the more fundamental problem of within-population polymorphisms. Smouse et al. (1991) have shown that intraspecific variation in DNA can have significant effects on phylogenetic analyses, but there has as yet been no attempt to relate the scoring of characters to any statistical measures of intrapopulational variability, or to attach confidence limits, based on sample size, to the scorings used in an analysis, let alone to the results of the analysis as a whole. In any other branch of modern biology or systematics, particularly evolutionary systematics, this habitual disregard of quantitative methods and lack of population-based thinking would be unacceptable.

For some years I have tried to improve on this approach, at a minimum by reporting sample sizes and patterns of intrapopulational variation in the taxa being analyzed (Domning and Hayek 1986; Domning and Thomas 1987). Here I have proposed an objective method for using such data to make scoring decisions in ambiguous cases. I do not expect that this particular method will prove to be more than a first approximation to what is needed; however, I do hope that its proposal will at least call attention to the need and prompt some discussion of the problems.

The first and most fundamental problem requiring discussion is the frequency that a derived character state should attain in a population before the population as a whole is deemed to be derived: 1%? 51%? 99%? 100%? There is no consensus at present on what choice would be most biologically meaningful, let alone practical. I have arbitrarily chosen "more than 50%."

A second and distinct problem: how confident do we need to be (on the basis of *available sample* size) that the frequency in the *original population* was in fact more than 50% (or whatever frequency we prefer)? I have chosen a 95% confidence level because this is customary in much scientific work and because a higher standard is more difficult to attain; e.g., a 99% confidence level requires a minimum sample size of eight (a 95% confidence level six), even for a completely monomorphic sample. That is, 6/6 is the smallest value of X/n whose LCL_{95} is greater than 0.50 (specifically, about 0.54); a sample of only five, with *no* variation ($X/n = 5/5$), has an LCL_{95} of only about 0.48. This means that for any sample smaller than six, we cannot be 95% certain that any particular state, even one that is constant in the sample, was found in a majority of the original population. (For sample sizes up to 20, the minimum frequencies having an LCL_{95} 0.50 are as follows: 6/6, 7/7, 8/8, 8/9, 9/10, 10/11, 10/12, 11/13, 12/14, 12/15, 13/16, 13/17, 14/18, 15/19, 15/20.)

It should be emphasized that since the justification for this procedure derives from the phenomenon of intrapopulational variation, the procedure is not applicable to terminal taxa that are supraspecific. However, when the terminal taxa in an analysis are supraspecific ones, it is obviously all the more imperative that their diversity be sampled by the examination of more than one specimen each. Future work will have to determine whether statistics of this sort are of real value in deciding character scorings in borderline cases and whether they can eventually provide a means of placing numerical confidence limits on entire cladograms. The latter task, at least, I leave to others more mathematically skilled than myself. However, I cannot believe that quantitative measures of sample size and of variation—the raw material of evolution—have no relevance to phylogenetic analysis.

CLASSIFICATION

The revised classification of sirenians (see Appendix) should be regarded as merely provisional. In the interest of taxonomic conservatism, it incorporates as few as possible of the changes that could be inferred from this preliminary cladistic analysis, namely, the formal assignment of the Miosireninae to the Trichechidae and the union of the Rytiodontinae with the Dugonginae. In other respects the suprageneric classification of Simpson (1945) is unchanged. As a result, the Dugongidae and Halitheriinae are conspicuously paraphyletic, and I regard the Prorastomidae and Protosirenidae as probably paraphyletic also, not to mention several of the genera.

While I have no philosophical objection to paraphyletic taxa, I would agree that this classification is unsatisfactory. Any further rearrangements or redefinitions of suprageneric taxa, however, should await further advances in our knowledge, specifically in two of the problematic areas pointed out above: the Eocene dugongids (and Eocene sirenians in general), and the species and relationships of *Metaxytherium*. These, as well as the still incompletely resolved dugongine clade, are topics on which I am actively working, and I fully expect that these parts of the present tree will change in topology in the relatively near future. For this reason I refrain from formalizing the present tree topology in a cladistic classification by use of any of the conventions that have been proposed (sequencing, plesions, etc.), since such a classification would almost inevitably be highly unstable. Users of the present classification who wish to retrieve its cladistic content are referred to Fig. 3.

ACKNOWLEDGMENTS

I thank Diana Lipscomb for teaching me how to use Hennig86, and Dan Chaney for preparing Fig. 3. I thank Dave Bohaska, Mike Gottfried, Fred Leone, Diana Lipscomb, Clayton Ray, Hezy Shoshani, and Hans Thewissen for helpful and stimulating discussions and miscellaneous information. Mike Novacek and Lee-Ann Hayek helped me with the analyses of age and clade ranks and their illustration in Fig. 4. Ray Bernor, Annalisa Berta, Tom Deméré, Lee-Ann Hayek, Mike Novacek, and an anonymous referee reviewed the manuscript in whole or in part and helped to improve it. The data on which this analysis is based were collected with the support of my parents, Mr. and Mrs. E. F. Domning, and National Science Foundation grants DEB-8020265, BSR-8416540, and BSR-8603258.

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APPENDIX: SIRENIAN CLASSIFICATION

The following provisional classification includes the currently correct names for all the genera, species, and subspecies included in this analysis, together with the higher taxa to which they are traditionally or newly assigned. For the original sources of the names of fossil taxa, the reader is referred to the *Bibliography of Fossil Vertebrates*.

- ORDER SIRENIA Illiger, 1811
  - FAMILY PRORASTOMIDAE Cope, 1889 [paraphyletic?]
    - *Prorastomus* Owen, 1855
      - *P. sirenoides* Owen, 1855
  - FAMILY PROTOSIRENIDAE Sickenberg, 1934 [paraphyletic?]
    - *Protosiren* Abel, 1907
      - *P. fraasi* Abel, 1907
  - FAMILY TRICHECHIDAE Gill, 1872 (1821)
    - Subfamily Miosireninae Abel, 1919
      - *Anomotherium* Siegfried, 1965
        - *A. langewieschei* Siegfried, 1965
      - *Miosiren* Dollo, 1889
        - *M. kocki* Dollo, 1889
    - Subfamily Trichechinae Gill, 1872 (1821) [new rank]
      - *Potamosiren* Reinhart, 1951
        - *P. magdalenensis* Reinhart, 1951 [here includes *Metaxytherium ortegense* Kellogg, 1966]
      - *Ribodon* Ameghino, 1883
        - *R. limbatus* Ameghino, 1883
      - *Trichechus* Linnaeus, 1758
        - *T. inunguis* (Natterer in von Pelzeln, 1883)
        - *T. manatus* Linnaeus, 1758
          - *T. m. manatus* Linnaeus, 1758
          - *T. m. latirostris* (Harlan, 1824)
        - *T. senegalensis* Link, 1795
  - FAMILY DUGONGIDAE Gray, 1821 [paraphyletic]
    - Subfamily Halitheriinae Carus, 1868 [paraphyletic]
      - *Eotheroides* Palmer, 1899
        - *E. aegyptiacum* (Owen, 1875)
      - *Protothenium* de Zigno, 1887
        - *P. veronense* (de Zigno, 1875)
        - "*P.*" *intermedium* Bizzotto, 1983 [should probably not be included in this genus]
      - *Eosiren* Andrews, 1902
        - *E. abeli* Sickenberg, 1934
        - *E. libyca* Andrews, 1902
        - *E. stromeri* (Sickenberg, 1934)
      - *Halitherium* Kaup, 1838
        - *H. schinzii* (Kaup, 1838)
        - *H. christolii* Fitzinger, 1842 [here includes *H. abeli* Spillmann, 1959, and *H. pergense* (Toula, 1899)]
      - *Caribosiren* Reinhart, 1959
        - *C. turneri* Reinhart, 1959
      - *Metaxytherium* de Christol, 1840
        - *M. krahuletzi* Depéret, 1895
        - *M. medium* (Desmarest, 1822)
        - *M. serresii* (Gervais, 1847)
        - *M. subapenninum* (Bruno, 1839) [here includes *M. forestii* (Capellini, 1872)]
        - *M. calvertense* Kellogg, 1966
        - *M. floridanum* Hay, 1922
    - Subfamily Dugonginae Gray, 1821 [here includes Rytiodontinae Abel, 1914]
      - *Crenatosiren* Domning, 1991
        - *C. olseni* (Reinhart, 1976)
      - *Dugong* Lacépède, 1799
        - *D. dugon* (Müller, 1776)
      - *Dioplotherium* Cope, 1883
        - *D. manigaulti* Cope, 1883
        - *D. allisoni* (Kilmer, 1965)
      - *Xenosiren* Domning, 1989
        - *X. yucateca* Domning, 1989
      - *Corystosiren* Domning, 1990
        - *C. varguezi* Domning, 1990
      - *Rytiodus* Lartet, 1866
        - *R. capgrandi* Lartet, 1866
    - Subfamily Hydrodamalinae Palmer, 1895 (1833)
      - *Dusisiren* Domning, 1978
        - *D. jordani* (Kellogg, 1925)
        - *D. dewana* Takahashi, Domning, and Saito, 1986
      - *Hydrodamalis* Retzius, 1794
        - *H. cuestae* Domning, 1978 [here includes *H. spissa* Furusawa, 1988]
        - *H. gigas* (Zimmermann, 1780)

A New Middle Miocene Sirenian of the Genus *Metaxytherium* from Baja California and California: Relationships and Paleobiogeographic Implications

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ABSTRACT.—New middle Miocene sirenian fossils assignable to the extinct halitheriine dugongid genus *Metaxytherium* de Christol, 1840, have been discovered in the Rosarito Beach Formation, Baja California, México, and the "Topanga Formation," Orange County, California. Species of *Metaxytherium* (or "*Halianassa*" von Meyer, 1838) previously reported from both California and Baja California have subsequently been referred to other genera and subfamilies (the hydrodamaline *Dusisiren* Domning, 1978, or the dugongine *Dioplotherium* Cope, 1883). Our new discoveries constitute the first valid records of *Metaxytherium* in the eastern North Pacific. They demonstrate a range extension of the genus and document a greater diversity of sirenians in this region during middle Miocene time than was previously known. The new fossils, *Metaxytherium arctodites* sp. nov., may represent a population structurally ancestral to *Dusisiren* and ultimately to the recently exterminated Steller's sea cow (*Hydrodamalis* Retzius, 1794). The new taxon is the sister group of the Hydrodamalinae. The new records of *Metaxytherium* indicate that at least three lineages of sirenians occupied the marginal eastern North Pacific during middle Miocene time: one represented by *Dioplotherium*, probably a bottom-feeder specializing on large seagrass rhizomes, another by *Metaxytherium*, probably a more generalized seagrass eater, and another by the *Dusisiren–Hydrodamalis* lineage, which reduced and then lost their teeth and became specialized to feed on kelp.

The following nomenclatural changes are also made: *Hesperosiren* is placed in the synonymy of *Metaxytherium*, and *M. calvertense* in that of *M. crataegense* (new combination).

RESUMEN.—Nuevos sirenios fósiles del Mioceno medio asignables al extinto género *Metaxytherium* de Christol, 1840 (Halitheriinae, Dugongidae) han sido descubiertos en La Misión, Baja California, México, en la formación Playa Rosarito, y en el Condado de Orange, California, en la "formación Topanga." Especimenes de *Metaxytherium* (o *Halianassa* von Meyer, 1838) previamente reportados de California y Baja California han sido desde entonces referidos a otros géneros y subfamilias (Hydrodamalinae: *Dusisiren* Domning, 1978; Dugonginae: *Dioplotherium* Cope, 1883). Nuestros nuevos descubrimientos constituyen los primeros registros válidos de *Metaxytherium* en el Pacífico nororiental. Ellos demuestran una distribución mayor del género y una mayor diversidad de sirenios en ésta región durante el Mioceno medio que la que se conocía anteriormente. Los nuevos ejemplares fósiles, *Metaxytherium arctodites* sp. nov., pueden representar una población estructuralmente ancestral de *Dusisiren* y de la recientemente extinta vaca marina de Steller (*Hydrodamalis* Retzius, 1794). La nueva especie es el grupo mas cercano a los Hydrodamalinae. Los nuevos registros de *Metaxytherium* también indican que por lo menos tres linajes de sirenios habiteron la margen oeste de América del Norte durante el Mioceno medio: una representada por *Dioplotherium*, que probablemente fué comedor de fondo, especializado en rizomas de grandes pastos marinos; otra por *Metaxytherium*, que fué posiblemente consumidor más general de pastos marinos; y la última por el linaje *Dusisiren–Hydrodamalis* que primero redujeron y posteriormente perdieron sus dientes, especializándose así en la alimentación de algas.

Los siguientes cambios nomenclatoriales también son hechos: *Hesperosiren* es sinónimizada con *Metaxytherium*, y *M. calvertense* con *M. crataegense* (nueva combinación).

INTRODUCTION

Sirenian fossils are moderately common in Cenozoic marine deposits of North America. At least some sirenian specimens are known from most lower Miocene through Pleistocene marine deposits along the Pacific margin, and several new and interesting specimens have been discovered here in the past several years. There is now a fairly continuous record of sirenians through late Cenozoic time in the eastern North Pacific, based on fossils from México, California, and Oregon (Domning 1978; Domning and Deméré 1984; Domning and Ray 1986). All of the eastern North Pacific sirenians described to date are members of the family Dugongidae. Those previously assigned to the subfamily Halitheriinae are (with one exception) now classified in the subfamilies Dugonginae and Hydrodamalinae (Domning 1994, this volume). The new specimens we report here, however, undoubtedly belong to the Halitheriinae.

Much of the documentation of North Pacific sirenian evolution so far presented involves the hydrodamaline lineage, which culminated in the large, aberrant, toothless, and recently extinct Steller's sea cow, *Hydrodamalis gigas* (Zimmermann, 1780). Many fossil hydrodamaline specimens from California belong to the genus *Dusisiren* Domning, 1978. The type species of this genus, *Dusisiren jordani* (Kellogg, 1925), was originally assigned to the halitheriine genus *Metaxytherium* de Christol, 1840. Some later writers also applied to this species the generic name *Halianassa* von Meyer, 1838, believing it to be a senior synonym of *Metaxytherium*. The names *Metaxytherium* and *Halianassa* were also formerly applied to the species now known as *Dioplotherium allisoni* (Kilmer, 1965), presently regarded as dugongine (see Domning 1978, and this volume). The removal of both of these species from *Metaxytherium* has left the latter genus unrepresented in the North Pacific, until now.

New middle Miocene specimens assignable to *Metaxytherium* (including possibly the best-preserved fossil sirenian skull yet found) have been discovered at La Misión, Baja California, México, in the Rosarito Beach Formation, and in Orange County, California, in the "Topanga Formation" (Aranda-Manteca 1987; Aranda-Manteca and Barnes 1991a, b; Aranda-Manteca and Domning 1987; Aranda-Manteca et al. 1991). Both formations have yielded rich marine vertebrate and invertebrate assemblages that aid in correlations and provide data on paleoecology (Aranda-Manteca 1990;

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
Proc. San Diego Soc. Nat. Hist. 29:191–204, 1994

Minch 1967; Deméré et al. 1984; Gascon-Romero et al. 1991a,b; Aranda-Manteca and Barnes 1992). Our new discoveries, representing the only valid records of *Metaxytherium* in the eastern North Pacific, document a range extension of the genus and add to the known diversity of sirenians in this region during middle Miocene time.

The purpose of the present paper is to document the cranial anatomy of, and to describe as a new species, three new specimens (two from Baja California and one from California), to comment on the classification and the evolutionary and biogeographic significance of these animals, and to determine the relationships of this North Pacific *Metaxytherium* to those of the eastern South Pacific, the Caribbean and western Atlantic, and Europe, and to the hydrodamaline dugongids of the North Pacific, which were derived from some species of *Metaxytherium*.

METHODS AND MATERIALS

Geologic ages cited herein are modified according to the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout (1981). The skull measurements follow those used by Domning (1978, 1988). The acronyms for institutions cited in the text are as follows: FCM, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, Baja California, México; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; UCMP, University of California Museum of Paleontology, Berkeley, California; UABC, Universidad Autónoma de Baja California, Ensenada, Baja California, México; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Sirenia Illiger, 1811

Family Dugongidae Gray, 1821

Included subfamilies.—Halitheriinae, Dugonginae (now including the Rytiodontinae; see Domning 1994, this volume), and Hydrodamalinae.

Subfamily Halitheriinae (Carus, 1868) Abel, 1913

Genus *Metaxytherium* de Christol, 1840

Hesperosiren Simpson, 1932; new synonymy.

Emended diagnosis of genus.—Halitheriine dugongids in which the supraorbital process of the frontal is reduced and dorsoventrally thickened, the zygomatic–orbital bridge of the maxilla is elevated >1 cm above the alveolar margin, all permanent premolars are lost, the nasals are usually separated in the midline, the exoccipitals usually do not meet dorsal to the foramen magnum, and the following primitive characters are retained: upper incisor tusks, an unflangelike dorsolateral border of the exoccipital, a moderately inflected processus retroversus of the squamosal, and the horizontal ramus of the mandible being dorsoventrally broad with a strongly concave ventral border (see Domning 1994, this volume, for further details and character distributions).

Type species.—Metaxytherium medium (Desmarest, 1822).

Included species.—M. arctodites, sp. nov.; *M. crataegense* (Simpson, 1932) (new combination; = *M. calvertense* Kellogg, 1966: new synonymy); *M. floridanum* Hay, 1922; *M. krahuletzi* Depéret, 1895; *M. medium* (Desmarest, 1822); *M. serresii* (Gervais, 1849); *M. subapenninum* (Bruno, 1839) [includes *M. forestii* (Capellini, 1872)].

Nomenclatural note.—We introduce the new combination *Metaxytherium crataegense* as a senior synonym of *M. calvertense*; evidence supporting this action will be presented in a future report. The nomenclatural changes are made here in order to streamline the discussion and eliminate the need for the awkward and soon-to-be-obsolete circumlocution "*Hesperosiren*" *crataegensis*.

In brief, *Hesperosiren* Simpson, 1932 is not distinguishable morphologically from *Metaxytherium*, although this is not apparent from the original description, in which some features of the former were misinterpreted. Direct comparison of the holotypes of *M. crataegense* and *M. calvertense* shows that the only morphological distinction between these nominal species is the very slightly smaller size of the former. Given that the stratigraphic horizons of these two specimens from the southeastern United States are now considered to be close if not identical in age (late Hemingfordian or early Barstovian and early Barstovian, respectively; Bryant 1991; Gibson 1983), we do not think a specific distinction can be defended.

Metaxytherium arctodites, sp. nov.

Tables 1–3, Figures 4–9

Metaxytherium cf. *M. calvertense.* Aranda-Manteca (1987, 1990); Aranda-Manteca and Domning (1987).

Halitheriine Sirenia. Aranda-Manteca and Barnes (1991a,b).

Metaxytherium. Aranda-Manteca et al. (1991).

Holotype.—FCM 3693, associated skeleton, collected in October 1989 by F. J. Aranda-Manteca, Gerardo Gonzalez-Barba, Rolando Petterson, and students of UABC paleontology courses 89-2, 90-1, 90-2, and 91-1. This skeleton includes an exceptionally complete and undistorted cranium with mandible (perhaps the best-preserved fossil sirenian skull known); incisor tusks, DP$^{4-5}$, M$^{1-3}$, DP$_5$, and M$_{1-3}$ are preserved. Both upper and lower M3's are unworn and not yet fully erupted, and the basioccipital–basisphenoid suture remains unfused, indicating immaturity. The postcranial elements are still being prepared and will be reported on separately.

Type locality.—Mesa La Misión, FCM locality LM-1, 32° 04' N, 116° 49' 30" W, south of La Misión de San Miguel Arcangel de la Frontera, canyon no. 1 (Fig. 1).

Stratum.—Rosarito Beach Formation, Los Indios Member, bed "D" of Aranda-Manteca (1990) (Fig. 2), middle Miocene, Barstovian-correlative, 14–15 Ma.

The name Rosarito Beach Formation is used for middle Miocene marine sediments in the Tijuana, Rosarito, and La Misión areas. This sequence of basalts and reworked pyroclastic sediments represents both marine and continental environments (Minch et al. 1984). In the La Misión area the formation is represented by the Los Indios Member, a middle Miocene marine, near-shore, shallow-water deposit that overlies a basalt dated at 16.1 + 2.1 Ma (Gastil et al. 1975). The Los Indios Member is about 14 to 15 million years old and is correlative with the Luisian Foraminiferal Stage (Deméré et al. 1984), the "Temblor Fauna" of California (Minch 1967), the Barstovian North American Land Mammal Age (Gascon-Romero et al. 1993; note that this is a change from the Hemingfordian correlation proposed by Minch et al. 1970), the Topanga Formation and the Round Mountain Silt (Sharktooth Hill Bonebed) on the west coast (Gonzalez-Barba 1990) and the Calvert Formation on the east coast of the USA.

The Los Indios Member has a very important fauna of siliceous microfossils, mollusks, sharks, bony fishes (Stewart and Aranda-Manteca 1993), turtles, birds, and mammals. The shark assemblage

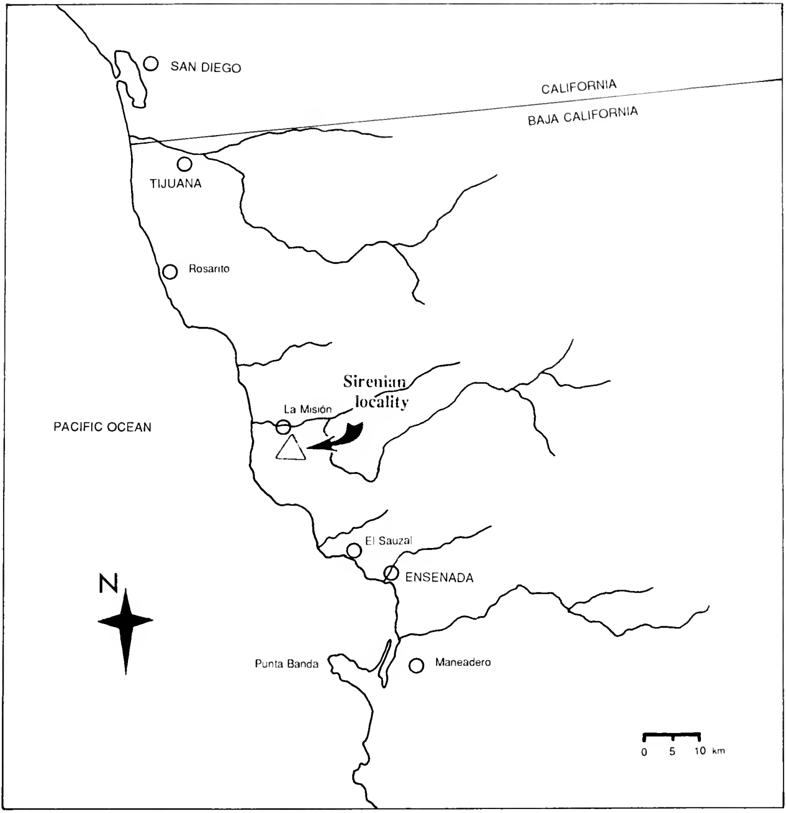

Figure 1. Discovery localities of *Metaxytherium arctodites*, n. sp., in the Rosarito Beach Formation on Mesa La Misión near La Misión, Baja California, Mexico.

has a high percentage of generic similarity with that of the middle Miocene (Barstovian-correlative) Sharktooth Hill Bonebed in California (Gonzalez-Barba 1990). The marine mammals include a species of *Paleoparadoxia* (Aranda-Manteca and Barnes 1993), a typical middle Miocene cetothere (Gascon-Romero 1991; Gascon-Romero et al. 1991a,b), other cetaceans (Gascon-Romero et al. 1993), and a typical middle Miocene allodesmine pinniped (Aranda-Manteca and Barnes 1992; Barradas and Stewart 1993). The sedimentary deposits, predominantly lapilli tuffs, were reworked in a coastal zone and deposited in a near-shore submarine canyon on the continental borderland. The stratigraphic sequence suggests a eustatic change in sea level. All the sirenian material has been collected from bed "D" (of Aranda-Manteca 1990) in the sequence exposed at Mesa La Misión (Fig. 2). This bed is a gray lapilli tuff, 8 m thick, and represents a low-energy near-shore deposit. It contains sharks, rays, and the mollusks *Turritella ocoyana* and *Tagelus* sp. The siliceous nature of the sediments preserves vertebrates well. The discovery of articulated specimens

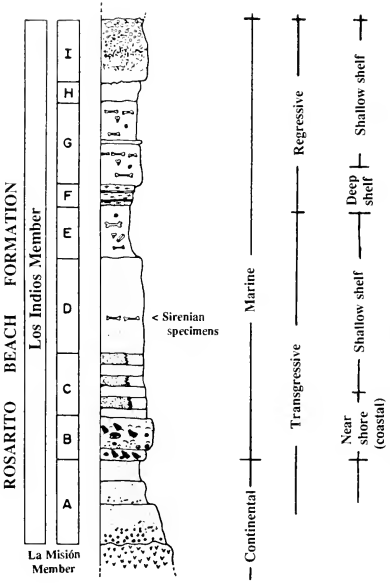

Figure 2. Stratigraphic section of the middle Miocene Los Indios Member of the Rosarito Beach Formation, Baja California; after Aranda-Manteca (1990: fig. 5). See Aranda-Manteca (1990) for descriptions of beds A–I and explanations of the transgressive–regressive cycles. The specimens of *Metaxytherium arctodites*, n. sp., described here came from bed "D," as indicated by the arrow.

with little evidence of transport suggests a low-energy depositional environment.

Referred specimen from La Misión, Baja California.—FCM 3100, associated skeleton, collected in February 1987 by F. J. Aranda-Manteca and students of UABC paleontology course 87-1. The skeleton includes an incomplete cranium with supraoccipital, exoccipital, basioccipital, parietal, frontal, squamosal, periotics, tympanics, ear ossicles, pterygoid process, and parts of the jugal and maxilla with DP^5 and M^{1-3}. DP^5 and M^1 are heavily worn, M^3 is slightly worn, and the basioccipital–basisphenoid suture is fused, indicating adulthood.

Referred specimen from the "Topanga Formation," California.—LACM 127720, posterior portion of a cranium with part of the right M^1 and the right M^{2-3}, collected in August 1986 by Raymond L. Price. The preserved elements include the supraoccipital, exoccipital, basioccipital, parietal, squamosal, pterygoid process, and part of the maxilla. The cranium, including the cheek dentition, was apparently complete until it was hit by earth-moving machinery and cut obliquely across the interorbital area at the level of the left M^3 and the right M^1. The specimen is cracked into many small pieces, partly by compaction after burial and partly by subsequent weathering and encroachment by roots of plants, and was also slightly distorted by the impact of the machinery. The specimen represents a subadult because M^3 was not yet fully erupted and M^2 is worn only on the anterior cusps, although it is as large as the specimens from Mesa La Misión.

Locality of referred specimen.—LACM locality 5511, Cook's Corner, north of El Toro, in foothills of the Santa Ana Mountains near Oso Creek, Orange County, California, USA (Fig. 3).

Stratum of referred specimen.—"Topanga Formation," middle Miocene, Barstovian-correlative, approximately 15 Ma.

The middle Miocene marine rocks that yielded this specimen are mapped as the Topanga Formation on existing geologic maps (e.g., Morton et al. 1973). The name Topanga Formation, however, is no longer used in its type area, approximately 100 km to the north in the Santa Monica Mountains, Los Angeles County. Here the Topanga has been elevated to the status of a group (Yerkes and Campbell 1979). Therefore the name Topanga Formation now has no basis, and a new name for the rocks in Orange County formerly called the Topanga Formation has not been proposed. We use the name "Topanga Formation" in quotes to indicate an informal usage of the name for the rocks so mapped in Orange County until a new name is proposed (see Howard and Barnes 1987).

LACM 127720 was discovered after being exposed in artificial cuts made during housing construction in an unconsolidated gray feldspathic sandstone. LACM locality 5511 is geographically close to and lithologically similar to a sandstone exposed nearby along the course of Oso Creek near Upper Oso Dam that yielded middle Miocene birds (Howard and Barnes 1987). The stratigraphic section at Upper Oso Dam is better exposed than at LACM 5511, and the Monterey and Vaqueros formations that, respectively, overlie and underlie the "Topanga Formation" there have been investigated and mapped (Raschke 1984).

Diagnosis of species.—A species of *Metaxytherium* sharing the following derived characters with all but the most primitive *Metaxytherium* (*M. krahuletzi*): exoccipitals separated dorsal to the foramen magnum and ventral extremity of the jugal lying below the posterior half of the orbit. Derived states, possibly shared with *M. floridanum* or independently evolved, include median incisure in the frontals extending abaft the supraorbital processes and palatine incisure extending anteriorly almost to the posterior edge of the zygomatic–orbital bridge of the maxilla. The new species differs from *M. floridanum* in that the anteroposterior length of the zygomatic–orbital bridge is not reduced. It differs from all other species of *Metaxytherium*, and resembles hydrodamalines, in that the premaxilla and jugal are in contact and the lacrimal is reduced. Symplesiomorphies retained include functional tusks present, but with alveoli extending less than half the length of the premaxillary symphysis, and supracondylar fossa deep.

Etymology.—Greek *arktos*, north, *hodites*, traveler, in allusion to the northward dispersal of the genus into the North Pacific that this species represents. In the combination with the name *Metaxytherium* ("intermediate beast"), there is also an allusion to this species' phyletic position connecting the Halitheriinae and Hydrodamalinae.

Description of skulls.—The characters noted in the following description of the three skulls are mainly those in which *M. arctodites* differs from the conditions typical of *M. floridanum* as described by Domning (1988) from the Bone Valley Formation of Florida (middle Miocene, Clarendonian). This taxon was used because it is the *Metaxytherium* whose cranial osteology is presently the best documented.

Premaxilla: The dorsal keel is relatively thin (about 1 cm) in FCM 3693, and the nasopalatine canal is not dorsoventrally flattened. The nasal process is in contact with the jugal for a distance of approximately 1–2 cm. The rostral deflection is about 71°.

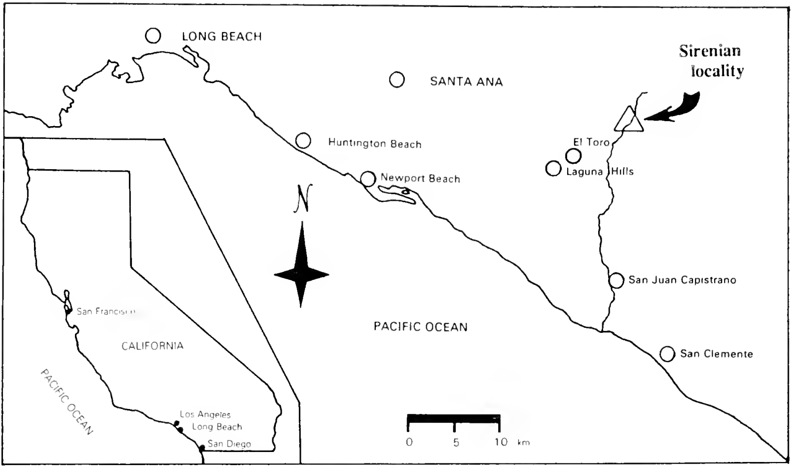

Figure 3. Discovery locality (arrow) of referred cranium, LACM 127720, of *Metaxytherium arctodites*, n. sp., in the "Topanga Formation" near Cook's Corner, Orange County, California.

Nasal: The dorsal exposure is irregular in shape in both Mexican specimens. At the rear of the mesorostral fossa the nasals are separated by 21 mm (FCM 3100) and 23 mm (FCM 3693).

Ethmoidal region: In both Mexican specimens, the perpendicular plate extends 2.0–2.5 cm below the roof of the narial passage at the level of the front of the roof. In FCM 3100, the "second" conchae form plates 5 mm thick appressed to the medial sides of the nasals.

Lacrimal: In FCM 3693, the lacrimal is more reduced than in *M. floridanum*. It measures 4.0–4.5 cm in length and about 2 cm in anteroposterior width. It fits in a socket on the dorsolateral surface of the jugal and is convex laterally though without any very distinct ridge or protuberance. Its sutures are unclear, but it seems to have a triangular outline with a corner directed forward.

Frontal: The supraorbital process is relatively blunt and knoblike in FCM 3693 (Fig. 4) but is anteriorly pointed and has a distinct posterolateral corner in FCM 3100. Orbicular apophyses are absent in the former; a very small one is present in the latter. A lamina orbitalis is present, forming the recessed lower part of the temporal surface; the upper boundary of the recessed area is not marked by a crista orbitotemporalis. The frontal roof bears a distinct median boss in FCM 3100, and the median incisure in the roof extends only to the posterior edges of the nasals; in FCM 3693 the incisure extends 1.0-1.5 cm farther posteriorly. Endocranially, the frontals are separated by a deep median groove and form a surface extending about 2.5 cm from the crista galli to the frontoparietal suture; this surface is noticeably inclined with respect to the parietal portion of the braincase roof.

Parietal: In both Mexican specimens the temporal crests are smoothly rounded and separated by about 2 cm (type C of Domning 1988); the lateral edges of the crests are sharp in FCM 3100. In this specimen the bony falx also remains sharp as far as the frontoparietal suture, the internal occipital protuberance is sharply pointed, and the tentorium is indistinct. A small median bump lies in front of the external occipital protuberance in FCM 3693.

Supraoccipital: The supraoccipital forms an angle with the parietal roof of 109° in LACM 127720, 122° in FCM 3100, and 116° in FCM 3693. The nuchal ridge reaches the squamosals in FCM 3100. The semispinalis insertions are concave in all three specimens. The sutural surfaces for the exoccipitals are separated by a notch in FCM 3693.

Exoccipital: The exoccipitals are separated dorsally, but FCM 3100 is unusual in having the supraoccipital–exoccipital sutures fused. The supracondylar fossa is deep in all three skulls. The condylar articular surface subtends angles of about 125° (LACM 127720), 126° (FCM 3100), and 119° (FCM 3693).

Basisphenoid: The sella turcica is fairly deep in FCM 3100.

Alisphenoid: A large foramen at the alisphenoid–squamosal suture seen in *M. floridanum* is lacking in FCM 3100 and 3693, but a pit (deep on the left side, shallow on the right) is present at this location in the latter skull.

Pterygoid: The edges of the pterygoid fossa join in a sharp angle near the level of the dorsal surface of the basisphenoid in LACM 127720 and FCM 3100, and about 1 cm lower in FCM 3693. In LACM 127720 and FCM 3100, the lateral and medial flanges at the tip of the pterygoid process are equally strong, and together form a distinct C-shape to which the lateral side of the alisphenoid is tangent. In FCM 3693 (and in *Dusisiren jordani*), the lateral limb of this "C" is weaker than the medial.

Palatine: In FCM 3100 the anterior parts of the palatines are not preserved, but they extended forward of the rear edge of the zygomatic-orbital bridge to about the level of the posterior side of DP^5, which is where the intermaxillary suture begins. In FCM 3693 the palatines join for a distance of about 2 cm at the level of DP^5 (i.e.,

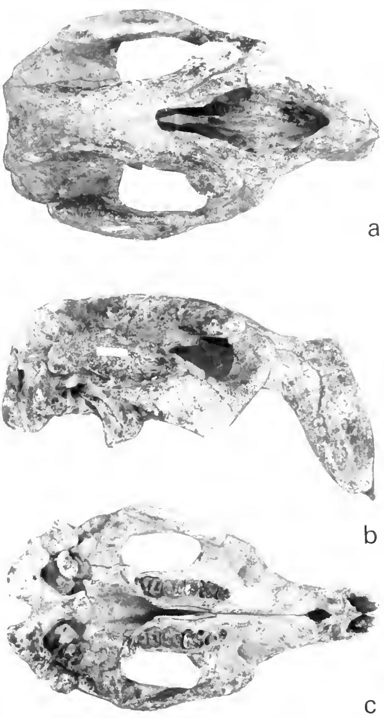

Figure 4. *Metaxytherium arctodites*, n. sp., holotype cranium, FCM 3693, from La Misión, Baja California; a, dorsal view; b, lateral view, c, ventral view.

beginning just behind the posterior edge of the zygomatic–orbital bridge), and the narrow palatine incisure reaches to the front of M^1. In this young specimen, however, mesial drift was still in progress and the teeth would have lain more anteriorly at maturity.

Maxilla: In FCM 3693 the minimum width of the palate is only about 1.5 cm, the posterior opening of the maxillo–premaxillary canal lies 1.5 cm behind the front edge of the jugal, and the zygomatic–orbital bridge is elevated less than 1 cm above the palate. FCM 3100 is unusual for *Metaxytherium* in that the posterior edge of the bridge is only 7 mm thick; however, it is still rounded rather than sharp as in *D. jordani*.

Squamosal: The dorsal shoulder of the sigmoid ridge is not strongly bent in LACM 127720, but it is in FCM 3100 and 3693 (Fig. 4). The cranial portion of the squamosal does not bulge markedly dorsal to the zygomatic root. The processus retroversus is turned inward ventrally and has more or less distinct dorsal and ventral terminations in all three specimens, and in FCM 3693 it very nearly touches the sigmoid ridge. In this specimen there is also a second diagonal ridge dorsal and parallel to the sigmoid ridge. The posterodorsal edge of the zygomatic process is concave in outline only in LACM 127720; in the others it is straight or convex.

Jugal: The ventralmost point lies below the posterior half of the orbit, at least in FCM 3693 and probably in FCM 3100. In FCM 3693 the preorbital process is about 1.5 cm thick mediolaterally.

Ear bones: In FCM 3693 the pars petrosa of the periotic has a blunt, right-angled medial corner. The posterior bulge on the medial side of the tympanic is indistinct. The stapes is approximately 10 mm long.

Mandible: In FCM 3693 the ventral edge of the horizontal ramus is sharp posteriorly (Figs. 5, 6). The masticating surface is deflected about 76° and bears four pairs of distinct vestigial alveoli, which (as in most modern *Dugong*) did not contain teeth. The ventral side of the symphysis is biconvex transversely, and the symphysis appears to be fused.

Incisors: The tips of the incisor tusks are worn and/or broken in FCM 3693. The more complete one has a remaining crown height

Figure 5. *Metaxytherium arctodites*, n. sp., holotype mandible, FCM 3693, from La Misión, Baja California; a, dorsal view; b, right lateral view.

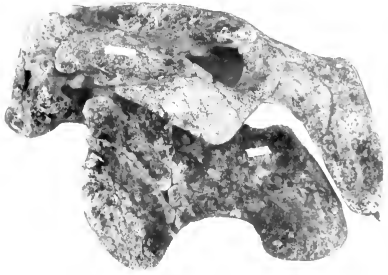

Figure 6. *Metaxytherium arctodites*, n. sp., holotype cranium and mandible in articulation, FCM 3693, from La Misión, Baja California; right lateral view.

of 13.5 mm, crown diameters of 12.0 and 9.1 mm, and root diameters of 18 and 11 mm.

Upper cheek teeth: In FCM 3693, the heavily worn DP^4's are still in place; no alveoli for DP^3 are present in front of them, having presumably been obliterated by the forward progression of DP^4. This three-rooted, submolariform tooth retains a slightly worn anterior cingulum connected lingually to the protoloph and surrounding a small basin open labially. DP^5 and M^1 are also heavily worn, M^2 only slightly so. The transverse valley of the latter tooth is blocked lingually by a posterior spur of the protocone; the metaconule lies anterolingual to the metacone; the posterolabial spur of the hypocone is steep and smooth. M^3 is like M^2 but with a thicker anterior cingulum connected labially as well as lingually and a distinct although low posterior cingular cuspule on the left side.

In LACM 127720, M^2 shows only slight wear on the anterior cingulum, which has slight swellings or cuspules anteriorly and anterolingually (Fig. 7). The anterior valley is open labially; no accessory cuspule blocks it. The protoloph is straight, and the transverse valley is constricted only slightly by the metaconule, which lies anterolingual to the metacone and completely anterior (and slightly labial) to the hypocone. The steep, smooth posterolabial spur of the latter nearly encloses the posterior basin; there are no posterior cingular cusps.

In FCM 3100, M^3 on both sides has a large, central anterior cingular cusp that protrudes posterolabiad into the anterior basin and contacts the paracone (Figs. 8, 9). A large posterolingual spur of the protocone (larger and more distinct from the protocone on the left side) blocks the transverse valley lingually. The right M^3 also has a tiny cuspule in the labial part of the valley. The metaconule lies about level with the metacone and anterolabial to the hypocone. The posterior cingulum bears two large cuspules, separated on the left side by a smaller one; on the right side, the basin they enclose contains a central cuspule.

Lower cheek teeth: In FCM 3693, M_2 does not exhibit the Y-shaped hypoconulid usual for *Metaxytherium* but only two posterior cingular cuspules and a small central spur from the hypolophid. On M_3, the summit of the protolophid is compressed mediolaterally, and the "G" pattern is not well developed. The "Y" pattern of the hypoconulid is again lacking, although the hypoconulid itself is large and prominent and bears two cingular cuspules, the labial larger.

COMPARISONS AND DISCUSSION

All previous identifications of *Metaxytherium* from the North Pacific are no longer accurate or valid. The new specimens that we report here are the only published correct identifications of *Metaxytherium* in the North Pacific and confirm the presence of the genus in middle Miocene time in Baja California and southern California. "*Metaxytherium*" *allisoni*, known from early to middle Miocene rocks of southern California and Baja California, was reassigned to the genus *Dioplotherium* by Domning (1978). Specimens from the early Miocene of Brazil have also been tentatively referred to this species (Toledo and Domning 1991). In the North Pacific, *D. allisoni* was contemporaneous with both *Metaxytherium arctodites* and *Dusisiren reinharti* Domning, 1978, also described from middle Miocene rocks of Baja California. "*Metaxytherium*" *jordani* is now referred to the genus *Dusisiren* and is the type species of that genus.

Dusisiren appears to have evolved in the eastern North Pacific from *Metaxytherium*. All species of *Dusisiren* (including the earliest but incompletely known species, *D. reinharti*) are distinguished from *Metaxytherium* (including *M. arctodites*) by the following derived characters: greater body size, lack of functional tusks, lesser rostral deflection, and a more slender horizontal mandibular ramus with a more moderately concave ventral border.

The second evolutionary stage of the *Dusisiren* lineage [termed *Dusisiren* Species B by Domning (1978) and known from an adult specimen of probable late Barstovian age] shows still more differences from species of *Metaxytherium* other than *M. arctodites*. The differences include the palatines not extending as far forward as the zygomatic–orbital bridge of the maxilla, a dorsolateral flange present on the exoccipital, the jugal contacting the premaxilla, the lacrimal beginning to be reduced, and the processus retroversus of the squamosal not inflected. A premaxilla–jugal contact and incipient lacrimal reduction are, however, observed in *M. arctodites* and suggest that this species is the sister taxon of the more derived genus *Dusisiren*; these states may also have been present in *D. reinharti*. An additional difference of possible taxonomic value is that the processus retroversus in *Dusisiren* never has two distinct terminations, as it does in *M. arctodites* and many, though not all, other specimens of *Metaxytherium*.

Because the specimens of *M. arctodites* described here are similar in age to the species of *Metaxytherium* from the Montera Formation in Peru (the latter unit is ca. 14–17 Ma in age; Dunbar et al. 1990), it may be asked whether the latter are also referable to our new species. Although this possibility cannot be absolutely excluded, neither can it be positively affirmed, and we prefer to retain the Peruvian specimens provisionally in *M. crataegense* until such time as the diagnostic (i.e., hydrodamaline-like) features of *M. arctodites* are observed in Peruvian specimens. The critical characters in this issue are contact of the premaxilla with the jugal and reduction of the lacrimal. In these characters *M. arctodites* differs from all other specimens of *Metaxytherium*.

Muizon and Domning (1985:193) stated that "the portion of the nasal process [of the premaxilla] in contact with the jugal, lacrimal, and frontal extends slightly more than half the length of the mesorostral fossa." This was an overstatement in that it was meant to describe the extent of the contact of the premaxilla with the collective group of bones lying lateral to it; it should not be read as an affirmation that the premaxilla and jugal are in direct contact. In fact, owing to damage to this region of the skull in the Peruvian *Metaxytherium* specimens, the full extent and contacts of the jugal cannot be clearly determined, and the lacrimal is not preserved at all.

Although our specimens clearly represent *Metaxytherium*, their phyletic position within the complex of New World *Metaxytherium* is problematical. These latter comprise *M. crataegense* and *M.*

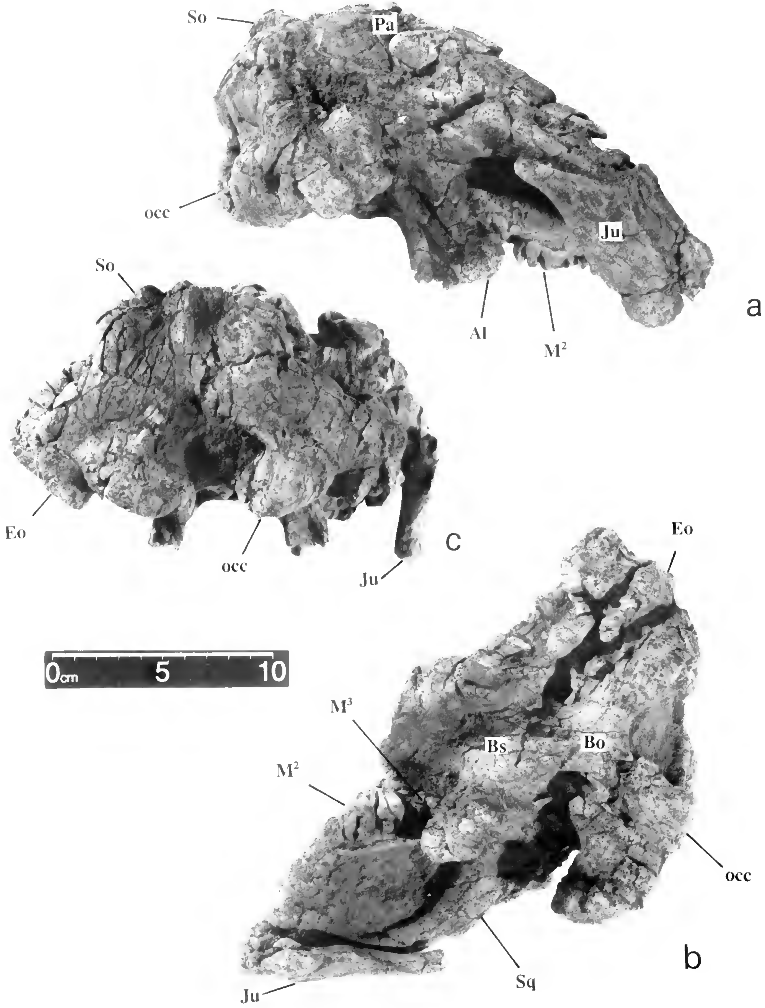

Figure 7. *Metaxytherium arctodites*, n. sp., referred cranium, LACM 127720, from LACM locality 5511, Oso Creek area, Orange County, California; a, right lateral view; b, ventral view; c, posterior view.

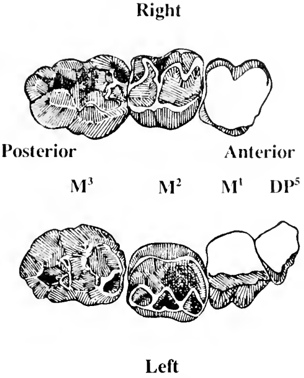

Figure 8. *Metaxytherium arctodites*, n. sp., dentition (DP^5 and M^{1-3}) of referred cranium, FCM 3100, from La Misión, Baja California; posterior end to left.

floridanum, together with *M. riveroi* Varona, 1972 (likely to be a synonym of *M. crataegense*). There also exist unpublished specimens that may be distinct from *M. crataegense*. All these named species are early to middle Miocene in age (*M. floridanum* survived into the late Miocene) and known only from the West Atlantic and Caribbean, except for *M. crataegense* which has also been identified in Peru (as "*M. calvertense*"; Muizon and Domning 1985). ("*M.*" *ortegense* Kellogg, 1966, from Colombia is now considered a synonym of the trichechid *Potamosiren magdalenensis* Reinhart, 1951; Domning in press).

These New World species of *Metaxytherium* differ among themselves only in body size and subtly in rostral deflection, mandibular proportions, and other cranial details, and it remains to be demonstrated which, if any, of these differences are worthy of taxonomic recognition. These forms are likewise almost indistinguishable from their European contemporaries, *M. krahuletzi* (early Miocene) and *M. medium* (middle Miocene). Furthermore, the late Oligocene European taxon *Halitherium christolii* Fitzinger, 1842, which has been proposed as the direct ancestor of *Metaxytherium* (see Domning and Thomas 1987), also seems to be represented in eastern North America during the late Oligocene, together with a smaller halitheriine that could represent the earliest known *Metaxytherium* (Domning, unpublished data).

Within this complex of fossils it is not yet possible to discern distinct evolutionary lineages, if indeed more than one New World lineage coexisted, or even to find much morphological evidence that the New and Old World forms were genetically isolated during the early and/or middle Miocene. The available data appear, however, to fit the following pattern: whereas the European halitheriines maintained approximately the same, relatively large body size throughout the late Oligocene and Miocene, and this size was shared by the North American form that resembled *H. christolii*, in the New World *Metaxytherium* started out smaller and attained the size of its European contemporaries only in the middle Miocene with the appearance of *M. crataegense* and *M. floridanum*. Concomitant with this increase in body size, there may have been a deepening of the horizontal mandibular ramus consequent upon an increase in rostral deflection, but the evidence for these latter changes is equivocal and their magnitude was slight in any case. Finally, although these comments imply that *M. floridanum* was a direct descendant of the earlier New World forms, even this is not certain and we cannot exclude the possibility that it was a direct immigrant from Europe (Domning 1988).

It is against this confused taxonomic background that we must attempt to place our new specimens. As stated above, these are Barstovian in age and coeval with or slightly younger than the late Hemingfordian or early Barstovian type material of *M. crataegense* from eastern North America (see Bryant 1991), as well as coeval with early *Dusisiren* on the Pacific coast.

Size.—The three individuals reported here are similar enough in size (Tables 1 and 2) to represent a single species, but they do show evidence of individual as well as ontogenetic size variation. Judged from dental eruption and wear, LACM 127720 is ontogenetically the youngest, followed by FCM 3693 and then FCM 3100, which is fully adult. However, the latter is smaller than FCM 3693 in most cranial dimensions and is even smaller than LACM 127720 in many. The dental dimensions of all three (Table 3) fall within the range of variation of the sample of *M. floridanum* from the Bone Valley Formation of Florida. The cranial dimensions of FCM 3693 are close to the Bone Valley mean and in many cases are above it.

The holotype of *M. calvertense* (USNM 16757), which is dentally immature, is similar to or smaller than our specimens in both cranial and dental dimensions. In comparison with the "*M. calvertense*" specimens (herein reidentified as *M. crataegense*) from Peru (Muizon and Domning 1985), which are also dentally immature, LACM 127720 is slightly smaller in cranial dimensions and FCM 3693 is somewhat larger; the teeth of all are similar in size.

North American *Metaxytherium* specimens of late Oligocene early Miocene age are slightly smaller than those discussed above. We conclude that our new species was similar in body size to *M. floridanum* and similar to or slightly larger than *M. crataegense*.

Rostral deflection and mandibular depth.—The rostral and mandibular deflections (Figs. 4b, 6) can be measured only in FCM 3693 (71° and 76°, respectively). These are within the range of variation of Bone Valley *M. floridanum* (sample sizes of five and eight for these two measurements, respectively). The rostral and mandibular deflections of both North American and Peruvian *M. crataegense* are $\leq 60°$ ($N = 2$), less than those observed in any *M. floridanum*; this apparent difference, however, may be attributable to immaturity of the *M. crataegense* specimens and/or sampling error. Minimum depth of the horizontal mandibular ramus (dimension "MO," character 128 of Domning 1994, this volume) in dugongids tends to vary directly with rostral and mandibular deflection. In FCM 3693 it is 81 mm, again within the range of Bone Valley *M. floridanum*, and evidently greater than in *M. crataegense* (67 mm in the Maryland specimen USNM 16757, 65 mm or more in a Peruvian specimen). However, neither of the latter mandibles is well preserved, and both fall within the range of immature *M. floridanum* in this dimension and in overall proportions. We conclude that our new specimens are indistinguishable from *M. floridanum*, and probably from *M. crataegense*, in regard to these characters.

Other cranial characters.—With regard to the other cranial characters considered taxonomically and phylogenetically informative by Domning (1994, this volume), our new specimens differ from *M. floridanum* and/or *M. crataegense* only in the following. (Character numbers are those from Domning 1994, this volume.)

Character 14 (zygomatic–orbital bridge of maxilla shortened anteroposteriorly): The zygomatic–orbital bridge retains its primitive proportions in FCM 3693 as in most *Metaxytherium*, but it is anteroposteriorly shortened in *M. floridanum*. Although this dimension can be measured precisely in only two specimens of the latter,

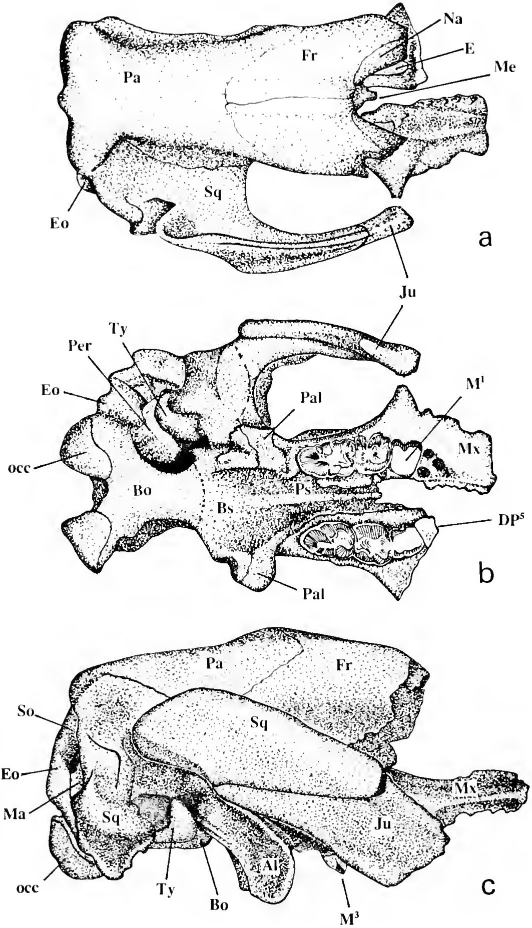

Figure 9. *Metaxytherium arctodites*, n. sp., referred partial cranium, FCM 3100, from La Misión, Baja California; a, dorsal view; b, ventral view; c, right lateral view.

TABLE 1. Measurements (in mm) of crania of *Metaxytherium arctodites*, n. sp.

	LACM 127720	FCM 3693	FCM 3100
Condylobasal length (AB)[a]	—	415	—
Height of jugal below orbit (ab)	—	58	47e[b]
Length of premaxillary symphysis (AH)	—	180	—
Rear of occipital condyles to anterior end of interfrontal suture (BI)	—	233+[c]	—
Zygomatic breadth (CC')	—	247	217
Breadth across exoccipitals (cc')	152	168	144
Top of supraoccipital to ventral sides of occipital condyles (de)	104	143	123
Length of frontals, level of tips of supraorbital processes to frontoparietal suture (F)	—	146e	—
Breadth across supraorbital processes (FF')	—	156	—
Breadth across occipital condyles (ff')	111	119	98
Breadth of cranium at frontoparietal suture (GG')	—	79	79
Width of foramen magnum (gg')	50e	52	45
Length of mesorostral fossa (HI)	—	175e	—
Height of foramen magnum (hi)	45e	60	42
Width of mesorostral fossa (JJ')	—	65	—
Maximum height of rostrum (KL)	—	87	—
Posterior breadth of rostral masticating surface (MM')	—	73	—
Anteroposterior length of zygomatic–orbital bridge of maxilla (no)	—	51	—
Length of zygomatic process of squamosal (OP)	118e	146e	128
Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen (OT)	—	177e	160
Length of parietals, frontoparietal suture to rear of external occipital protuberance (P)	—	102e	89
Length of row of tooth alveoli (pq)	—	99	89
Anteroposterior length of root of zygomatic process of squamosal (QR)	—	63	47
Maximum width between labial edges of left and right alveoli (rr')	—	83	73
Length of cranial portion of squamosal (ST)	—	109	98
Breadth across sigmoid ridges of squamosals (ss')	182	211	181
Dorsoventral thickness of zygomatic–orbital bridge (T')	—	14	7
Anterior breadth of rostral masticating surface (tt')	—	54	—
Height of posterior part of cranial portion of squamosal (UV)	108	127	111
Dorsoventral breadth of zygomatic process (WX)	40e	58	48
Maximum width between pterygoid processes (yy')	47e	52	41
Length of jugal (YZ)	—	181	—
Length of interfrontal suture	—	60+	82
Height of supraoccipital	51	64	68
Width of supraoccipital	88	90	93

[a] Letters in parentheses denote measurements used by Domning (1978: table 2).
[b] e, estimated.
[c] +, broken.

TABLE 2. Measurements (in mm) of holotype mandible of *Metaxytherium arctodites*, n. sp. (FCM 3693).

Total length (AB)[a]	303
Anterior tip to front of ascending ramus (AG)	233
Anterior tip to rear of mental foramen (AP)	117
Anterior tip to front of mandibular foramen (AQ)	176
Length of symphysis (AS)	107
Posterior extremity to front of ascending ramus (BG)	95
Posterior extremity to front of mandibular foramen (BQ)	137
Height at coronoid process (CD)	206
Distance between anterior and posterior ventral extremities (DF)	171
Height at mandibular notch (DK)	176
Height at condyle (DL)	193
Height at deflection point of horizontal ramus (EF)	144
Deflection point to rear of alveolar row (EU)	51e[b]
Minimum anteroposterior breadth of ascending ramus (GH)	79
Front of ascending ramus to rear of mental foramen (GP)	114
Maximum anteroposterior breadth of dorsal part of ascending ramus (IJ)	101
Top of ventral curvature of horizontal ramus to line connecting ventral extremities (MN)	50
Minimum dorsoventral breadth of horizontal ramus (MO)	81
Maximum breadth of masticating surface (RR')	69
Rear of symphysis to front of mandibular foramen (SQ)	72
Length of alveolar row (TU)	93e
Maximum width between labial edges of left and right alveoli (VV')	91
Minimum width between angles (WW')	72
Minimum width between condyles (XX')	158

[a] Letters in parentheses denote measurements used by Domning (1978: table 7).
[b] e, estimated.

shortening of the bridge is unusual in sirenians and appears to be a real though inconstant autapomorphy of *M. floridanum*. Its absence here is consistent with our specimens' representing an earlier stage of evolution than the Bone Valley sample.

Character 37 (nasal incisure extended or enlarged): The median incisure in the frontals extends abaft the supraorbital processes in FCM 3693 and probably in FCM 3100. This is a derived condition contrasting with other *Metaxytherium* except, possibly, for some *M. floridanum*. This needs to be verified for the latter species by means of more specimens in which the delicate frontal margin is preserved.

Character 87 (preorbital process of jugal contacts premaxilla): The jugal contacts the premaxilla in FCM 3693. This derived feature is otherwise unknown in halitheriines but is constant in hydrodamalines.

Character 91 (lacrimal reduced or absent): Although still relatively large, the lacrimal in FCM 3693 is more reduced than in *M. crataegense* or *M. floridanum*. This could also be seen as a tendency in the direction of hydrodamalines, and is probably linked with character 87.

Character 97 (incisure in posterior border of palatine extended): The palatal incisure is deeper in FCM 3693 than in other *Metaxytherium*, reaching as far forward as the front of M^1 and almost to the posterior edge of the zygomatic–orbital bridge. This is a derived state not seen in other halitheriines or hydrodamalines (except *Dusisiren jordani*, in which its anatomical basis is different), although *M. floridanum* approaches this condition. However, the cheek teeth of FCM 3693 were still undergoing mesial drift, and it is likely that at maturity this individual would not have merited a derived score for this character. Therefore it seems best to regard *M. arctodites* as not differing from other *Metaxytherium* in this character.

An additional character possibly suggestive of relationship with *Dusisiren* is the dorsoventral thinness of the zygomatic–orbital bridge of the maxilla observed in FCM 3100 (although not in FCM 3693). A general thinning of the bridge is seen in *Dusisiren jordani* and *D. dewana*, but in those species the posterior edge of the bridge

TABLE 3. Measurements (in mm) of teeth of *Metaxytherium arctodites*, n. sp.

		LACM 127720	FCM 3693		FCM 3100	
Tooth[a]		Right	Left	Right	Left	Right
DP^4	L	—	—	17.4w[b]	—	—
	AW	—	12.9	13.7	—	—
	PW	—	14.3e[c]	15.0	—	—
DP^5	L	—	—	19.3	—	—
	AW	—	—	18.8e	—	—
	PW	—	—	18.8w	—	—
M^1	L	—	21.3	21.1	17.8w	19.1w
	AW	—	21.3	21.6	—	20.7
	PW	—	19.8	21.3	—	18.8
M^2	L	27.1	26.3	25.7	21.9w	21.0w
	AW	25.5	23.8	23.3	21.7	22.1
	PW	22.6	20.9	20.4	20.3	20.3
M^3	L	—	26.8	27.1e	28.7	28.9
	AW	—	21.6e	21.5	22.6	22.6
	PW	—	18.6e	19.7e	19.5	19.3
DP_5	L	—	16.5w	17.6w	—	—
	AW	—	13.2w	12.9w	—	—
	PW	—	13.5w	13.3w	—	—
M_1	L	—	22.7	22.9	—	—
	AW	—	16.0	16.0	—	—
	PW	—	17.9	17.2	—	—
M_2	L	—	25.9	25.8	—	—
	AW	—	19.5	20.1	—	—
	PW	—	19.6	19.2	—	—
M_3	L	—	27.9e	27.8	—	—
	AW	—	20.7	21.0	—	—
	PW	—	19.8	18.7	—	—

[a] L, crown length; AW, anterior width; PW posterior width.
[b] w, dimension reduced by wear.
[c] e, estimated.

is thin and sharp like the anterior edge, rather than thick and rounded as in all species of *Metaxytherium* and in most other sirenians. However, the posterior edge is also thick in *Dusisiren reinharti* and *Dusisiren* Species B. Therefore, the most that can be said is that probably the bridge thinned in some individuals of populations ancestral to *D. jordani* but the thinning of its posterior edge developed or became common only in *D. jordani* itself.

Dentition.—The lack of a Y-shaped hypoconulid on the lower molars in FCM 3693 is not without precedent in, for example, *M. floridanum*, but is also in agreement with the general reduction of the hypoconulid in *Dusisiren*. In other respects, however, the teeth of our specimens differ in no significant way from those of other species of *Metaxytherium*, showing neither the subtle rearrangements of the molar cusps seen in some *D. jordani* nor any reduction of the tusks.

In summary, our new specimens possibly contrast with *M. crataegense* and resemble *M. floridanum* in characters 37 and, to a certain extent, 97, but are more primitive than *M. floridanum* in character 14. On this basis they seem to be intermediate between these two species in stage of evolution. However, they resemble hydrodamalines in characters 87 and 91 (which probably form a single character complex) and possibly in a tendency to thinning of the zygomatic–orbital bridge. They consequently do not seem to be on a line of descent from *M. crataegense* to *M. floridanum*. Therefore, we place them in a new species, *Metaxytherium arctodites*.

These data present a generally congruent, although in some ways unexpected, phylogenetic pattern. The character complex of lacrimal reduction and premaxilla–jugal contact unites these specimens with *Dusisiren* (at least with *Dusisiren* Species B and later species; the states of these characters are unknown for *D. reinharti*). Setting aside the apparently incongruent and possibly autapomorphic character 37, there is, in fact, no good reason to exclude the present specimens from the structural ancestry of hydrodamalines. This is surprising in view of the previous suggestion (Domning 1978) that hydrodamalines were derived from a species of *Metaxytherium* with relatively slender mandibles. However, Domning's (1978) impression that *M. krahuletzi* (early Miocene, Europe; oldest and most primitive of the named species of *Metaxytherium*) and "*M. calvertense*" had mandibles more slender than those of other *Metaxytherium* was probably an illusion based on inadequate sample size and the representation of these species by only immature specimens, which may differ in this regard from adults. *Dusisiren* diverged from the *Metaxytherium* morphotype by reverting to lesser rostral deflection and mandibular depth (Muizon and Domning 1985), but there now seems to be no reason to believe that the starting point of this divergence was other than a *Metaxytherium* of normal, deep-jawed proportions, such as we now have before us in *M. arctodites*.

Domning (1978) sought to explain hydrodamaline origins in zoogeographic terms by postulating a "Mexican barrier" of habitat unsuitable for sirenians, located along the Pacific coast south of Baja California. Caribbean–East Pacific halitheriines dispersing northward across this barrier by the early or middle Miocene supposedly gave rise to *Dusisiren* in the relative isolation of California and Baja California. We now know that *M. crataegense* from the Caribbean reached the eastern Pacific by the early or middle Miocene (Muizon and Domning 1985), and it is plausible that some of these dispersed north of the barrier as hypothesized and there began to evolve hydrodamaline traits. Our new specimens could well represent such a population ancestral to *Dusisiren*, except for their Barstovian age, which postdates the earliest record of hydrodamalines (viz., *D. reinharti* from supposedly Hemingfordian-correlative deposits in Baja California; Domning 1978). Unless the latter occurrence is dated too early (and its date is uncertain), *Metaxytherium* appears to have coexisted with *Dusisiren* north of the barrier for some time. This would be most simply explained by a cladogenetic event (of unknown cause) occurring among the animals north of the barrier subsequent to their acquisition of the hydrodamaline traits of the lacrimal and jugal that we see here. Our specimens would then represent an almost unmodified survival of this intermediate evolutionary stage, living alongside the early hydrodamalines. Deeper nasal and palatal incisures might have evolved autapomorphically in this surviving population.

Metaxytherium arctodites may therefore be viewed as the sister taxon of *Dusisiren* and other hydrodamalines, since, in contrast to all other species of *Metaxytherium*, it shares with hydrodamalines at least two derived characters. Cladistically, it could be argued that for this reason *M. arctodites* should be placed in *Dusisiren*, or at least in the Hydrodamalinae, rather than in *Metaxytherium*. As currently understood, however, the latter genus would remain paraphyletic in any event, so the generic placement of our new species is really arbitrary. We prefer to emphasize its phenetic similarity to other *Metaxytherium* (especially in regard to obviously adaptive traits such as body size, rostral deflection, and tusk morphology) by placing it in this genus.

The discovery of *Metaxytherium arctodites* brings the total number of sirenian taxa coexisting in Baja California and California in the middle Miocene to three. This was also the case in other parts of the world during the Oligocene and Miocene, although sirenian diversity later declined. One possible explanation for this is that food resources in these areas in middle Miocene time were more diverse, capable of supporting a greater diversity of sirenians.

The three taxa undoubtedly had different feeding behaviors. For example, the middle Miocene *Dioplotherium allisoni* has a strongly deflected rostrum and a large pair of upper tusks with bladelike posterior margins. This suggests that the animal was a bottom-feeder, probably specializing on rhizomes of robust seagrasses as well as eating the leaves of seagrasses in general (Domning 1989b). *Metaxytherium arctodites*, with its deflected snout but very small tusks, was probably a more generalized bottom-feeder, consuming rhizomes of smaller seagrasses but depending primarily on the leaves of diverse species (Domning 1989a). *Dusisiren* spp. have less downturned snouts and lack functional tusks altogether. This suggests that they fed on plants such as kelps that grew higher in the water column in addition to benthic seagrasses, and this was probably the beginning of the hydrodamalines' characteristic adaptation for feeding on kelps (Domning 1978).

The North Pacific specimens of *Metaxytherium*, although associated with certain near-shore animals, were all found in true marine deposits with predominantly open-ocean faunas. At La Misión, *Metaxytherium arctodites* is associated with large mysticete whales, small odontocete whales, seabirds, marine turtles, bony fishes, and large pelagic sharks of the genera *Isurus*, *Hemipristis*, *Galeocerdo*, and *Carcharocles* (Aranda-Manteca 1987; Deméré et al. 1984; Gonzalez-Barba 1990). The La Misión fossil marine vertebrate assemblage is a mix of subtropical and warm-temperate taxa.

The sirenians in the Rosarito Beach Formation at La Misión are not especially rare. They constitute an unusually high percentage of the marine mammal skeletal associations that we have located. In addition to the two partial skeletons with crania, we have also located parts of three other individuals, for a total of five. Among the other marine mammals at the site, we have found one pinniped, one desmostylian, and approximately seven cetaceans. Although many of these field data are preliminary, it appears that sirenians are unusually abundant in the Rosarito Beach Formation.

ACKNOWLEDGMENTS

We thank Carmen Aranda, Susan E. Barnes, Jorge Bustamante, Robert L. Clark, Denny V. Diveley, Gustavo Gascon-Romero, Gerardo González-Barba, R. Ewan Fordyce, Miguel Hernandez, Erika Castañon, Rolando Petterson, Albert E. Sanders, Hector Barradas, Hector Trinidad, Alejandro H. Rosado, and all Aranda-Manteca's paleontology students for help in the field, collecting the skeletons of *Metaxytherium* at La Misión. We also thank the UABC and the LACM and its Foundation (partly through the Fossil Marine Mammal Research Fund) for providing support for our field work at La Misión. The Baja California specimens were prepared and photographed by Aranda-Manteca with the support of UABC and the Secretaria de Educación Publica (SEP).

We thank Raymond L. Price for collecting and making available the cranium of *Metaxytherium* from Orange County. This specimen was prepared by Rodney E. Raschke, and his work was supported by NSF grant BSR 82-18194 to the LACM Foundation for curatorial support of vertebrate paleontological collections and preparation of fossil marine vertebrates. The specimen was photographed by John De Leon, former LACM staff photographer, and the prints were made by Donald Meyer, former LACM staff photographer.

Domning's work on the taxa discussed above has been supported by NSF grants DEB 80-20265, BSR 84-16540, and BSR 86-03258. The manuscript was reviewed and improved by Annalisa Berta, James M. Clark, Thomas A. Deméré, John M. Harris, and Gary S. Morgan. We also thank Joaquín Arroyo-Cabrales and Samuel A. McLeod for assistance in revising the manuscript.

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A New Specimen of *Behemotops proteus* (Order Desmostylia) from the Marine Oligocene of Washington

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ABSTRACT.—A new specimen of the most primitive known desmostylian, *Behemotops proteus*, from marine middle or upper Oligocene rocks of Washington State, USA, increases our knowledge of the species' dentition and confirms the close similarity of *Behemotops* to the Eocene anthracobunid tethytheres of Asia. This material and new specimens from Japan indicate that *B. emlongi* is a synonym of *B. proteus* and enable reinterpretation of the anterior dentition of the immature type specimen of *B. proteus*: we now view P_1 of our former interpretation as the true canine. M_2 and M_3 of *B. proteus* are closely similar in pattern to M_2 and M_3 of *Anthracobune pinfoldi*, although the enamel is thicker and the main cusps are more conical and more apically worn in *Behemotops*. Despite suggestions that anthracobunids may be desmostylians, we continue to regard *Anthracobune* as either a proboscidean or a primitive tethytherian more closely related to the Proboscidea than to the Desmostylia.

INTRODUCTION

Domning et al. (1986) described the new desmostylian genus *Behemotops*, which included two new species: *B. proteus*, from the marine middle or (more likely) upper Oligocene Pysht Formation of Clallam County, Washington State, USA, and *B. emlongi*, from the uppermost Oligocene Yaquina Formation of Lincoln County, Oregon. These were interpreted to be the most primitive known desmostylians, with significant resemblances to primitive Paleogene proboscideans and tethytheres from Africa and Asia.

Since the completion of that paper, an additional specimen from near the type locality of *B. proteus* has been obtained and prepared. It adds significantly to our knowledge of the morphology of the species, particularly of the anterior lower premolars and upper dentition (Domning et al. 1991). It was collected by William R. Buchanan on 2 February 1985 and generously donated by him to the Natural History Museum of Los Angeles County, California, where it now bears the catalog number 124106. Its preparation was completed in May 1986 just as our original paper was published.

In addition, *Behemotops* has been reported and partly described from Japan (Inuzuka 1984, 1987, 1989), and an undescribed maxillary fragment bearing molars, referable to *Minchenella*, is now available but remains undescribed. Also, various authors have written much about relationships of and within the Tethytheria (McKenna 1987, 1992; Novacek 1992: fig. 1). Moreover, a new Asian "moerithere" (anthracobunid?) specimen includes undescribed cranial material (Bajpai et al. 1989). Meanwhile, however, the new American specimen of *Behemotops* enables us to add to knowledge of the genus and to discuss its broader implications.

The teeth illustrated in Figures 2–11 were whitened for photography. Where matrix or adjacent teeth obscured given views, casts were substituted for the actual teeth, as indicated.

Abbreviations.—The following abbreviations are used to identify the institutions listed: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York; H-GSP: Howard University–Geological Survey of Pakistan Project, Washington, D.C.; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; USGS, United States Geological Survey; USNM, formerly United States National Museum, now National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Superscripts on I, C, P, M denote upper incisors, canines, premolars, and molars, respectively; subscripts denote lower counterparts.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Mirorder[1] Tethytheria McKenna, 1975

Order Desmostylia Reinhart, 1953

Family Uncertain

Behemotops Domning, Ray, and McKenna, 1986

Behemotops proteus Domning, Ray, and McKenna, 1986

Figures 1–13

Type species.—*Behemotops proteus* Domning, Ray, and McKenna, 1986:6.

Synonym.—*Behemotops emlongi* Domning, Ray, and McKenna, 1986:23 (new synonymy).

Holotype.—USNM 244035, immature right mandibular ramus with DP_4, canine tip (reidentification), P_3–M_3, and apparently associated skeletal fragments.

Type locality.—Present-day intertidal zone 34 km (21 miles) west of Port Angeles and 3.6 km (2.2 miles) east of mouth of East Twin River, north shore of Olympic Peninsula, Clallam County, Washington, USA.

Previously described, newly referred specimens.—USNM 244033, adult, left mandibular ramus with M_3 (holotype of *B. emlongi*); USNM 186889, adult, anterior end of right mandibular ramus with canine tusk (formerly referred to *B. emlongi*), both from the Yaquina Formation, latest Oligocene, Lincoln County, Oregon.

New specimen.—LACM 124106 (J. L. Goedert, field no. JLG 76), associated teeth of young adult, including left and right P^4 (possibly one or both of these teeth could be P^3, although we doubt this); right M^{2-3}; fragment of left M^3; left P_{1-4} and M_{2-3}; right P_2, M_2, and M_3; and a possible tusk fragment.

New locality.—LACM locality 5123, Disque Quadrangle, Washington, 7.5-minute series, USGS. Collected as float in inter-

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[1] Wiley (1979:335), Tassy (1981) and Tassy and Shoshani (1988) advocated the ranking of the Tethytheria as a superorder. McKenna used the superordinal category at a still higher taxonomic rank. In contrast, Prothero and Schoch (1989:530) reduced the Tethytheria to an order, thereby implicitly reducing also the rank of orders Sirenia, Proboscidea, and Desmostylia.

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tidal zone, approximately 2.3 km (1.5 miles) east of the type locality of *B. proteus*.

Horizon.—Lower part of the type section of the Pysht Formation, of late (?) Oligocene age. We discussed the complex geology and difficult correlation of the deposits in this area previously (Domning et al. 1986:6–12, figs. 1, 3). The Pysht Formation was regarded as upper Zemorrian, late Oligocene, by Feldmann et al. (1991) and thought to represent a deep marine sequence that shoals upward into the overlying shallow-water Clallam Formation. We are aware of no new information to add to those discussions. Unfortunately, efforts by David Bukry and John Barron, USGS, Menlo Park, California, to determine a biostratigraphic age based on nannofossils or diatoms from matrix associated with the new specimen and the holotype failed to produce diagnostic specimens (J. Barron, pers. comm. to C. E. Ray, 12 September 1989).

Revised diagnosis (modified from Domning et al. 1986:6).—Desmostylian more primitive than other members of the order in having seven lower postcanine cheek teeth, without marked diastemata; P_1 still present (in contrast to *Paleoparadoxia* and the other known desmostylians), small, single-rooted, with a high protoconid to which a smaller paraconid is appressed, and with a tiny heel cusp; P_2 large, with a high protoconid to which are appressed a columnar, recurved paraconid and a smaller recurved heel cusp. Lower molars brachydont and bunodont, with four principal cusps neither cylindrical nor appressed, and forming a square followed by a broad posterior cingulum; metaconids of lower molars not twinned. All permanent teeth in use together at maturity. Lingual surface of mandible lacks swelling at rear of tooth row. *Behemotops proteus* also exhibits the following independently derived characteristics: canine of adults enlarged, procumbent, and mediolaterally compressed; heel cusp pair of P_4 small; body size increased. In contrast to *Anthracobune pinfoldi*, ?P^4 with paracone and protocone converted to columnar cusps, joined by one or two columnar conules; M^2 and M^3 similar to those of *A. pinfoldi* but cusps more columnar and metaconules almost or completely incorporated in anterolabial crest from hypocone.

Description.—The new specimen was collected as a boulder that had been broken into several pieces, in part along weathered joints, exposing several teeth and bone fragments. The best of the latter, a fragment of the right mandibular ramus, is shown in Figure 1, prior to reassembly of the split blocks. Unfortunately, preparation failed to reveal a skull or jaws, only a number of upper and lower cheek teeth, with scraps of poorly preserved associated bone. Several of the teeth (the right M^{2-3} and P_2 and M_{2-3}) were still in or near their original relative positions, indicating that at the time of burial enough bone remained to keep them joined together. In some way not clear to us, most of the bone appears to have been subsequently destroyed, without, however, damaging the crowns of the teeth. All other teeth were randomly distributed in the matrix. The roots of the teeth also are absent or poorly preserved and only indistinctly separable from the matrix, except where they were exposed in the split block (Fig. 1).

Preserved bone.—As revealed in Figure 1, and reflected in the association of parts of the upper and lower dentition in or near natural position, considerable remnants of the bone of the skull and jaws survived until burial. No well-preserved natural bone surface was found in the specimen, however, and even internal structure was not preserved well. Apparently, burial occurred after the bone was much weathered but before the enamel-covered parts of the teeth were damaged. Enough of the bone of the right lower jaw remains to suggest, but only suggest, a very large alveolus for an enlarged, protruding lower canine tusk similar to that of "*B. emlongi*." We make this suggestion with trepidation, pending recovery of better material, while calling attention to the enlarged tusk of the Japanese *Behemotops* (Inuzuka 1989: fig. 2–45).

Teeth.—The fine wrinkling of the enamel surface seen on most of the teeth of USNM 244035 has been mostly worn away in LACM 124106 but is detectable in all teeth wherever the enamel has been protected from wear polishing. The teeth are similar to their counterparts in the holotypes of *B. proteus* and *B. emlongi* except as noted in the following descriptions.

Fourth (?) upper premolar: Preserved from both left and right sides (Fig. 2). (Judging from demonstrable differences in P_3 and P_4 of *Behemotops* and by analogy with P^3 and P^4 of *Paleoparadoxia tabatai*, we believe that both of these teeth represent P^4 and that it is less likely that either one or both could be P^3.) The right P^4 crown is dominated by a cluster of two pairs of principal cusps, all robust, steeply conical, circular in worn cross section, and closely appressed. The linguolabial pair (protocone and paracone) are the larger, approximately twice the diameter of the anteroposterior pair. These cusps are bordered basally by a strongly developed cuspulate cingulum, in part obliterated anteriorly and posteriorly by interdental wear. The anterior cusp (paraconule?) of the left P^4 is much less developed than its counterpart in the right P^4, being little more than an accentuation of the precingulum. It does not form a cone and is not breached apically by a circular wear surface. We believe these differences to be within the limit of bilateral variation.

First upper molar: Not preserved.

Second upper molar: Preserved from right side only (Fig. 3). Two distinct labial roots are present; the lingual root is indented just below the crown and may be longitudinally grooved or even divided but is mostly concealed by matrix. As on the lower teeth, the cusps are massive, blunt cones, appressed at their bases but otherwise distinct. Because of its confluence with the paraconule, the protocone appears much larger than the paracone. Both protoloph and hypoloph are aligned obliquely (anterolabially) to the long axis of the crown. The transverse valley is similarly oblique and also sinuous, and is constricted lingually by the proximity of the protocone to the hypocone and hypoloph. The cingulum bears a more or less distinct cuspule at each end of the transverse valley. The hypocone is larger than the metacone; at the foot of the valley between them, a confluent pair of cingular cuspules forms the posterolabial margin of the tooth.

The crown is moderately worn, especially lingually; all four cusps have been breached by wear. A complete basal cingulum encircles the tooth and bears well-developed interdental wear facets anteriorly and posteriorly. The paracone has an oblique facet on its anterolingual wall, bordered basally by a less highly oblique, anteriorly sloping precingular facet. The posteromedial slope of the paracone has a broad, oblique facet, weakly subdivided into three subequal confluent facets. The protocone and paraconule are too deeply and roundly worn to show most of the original facets, although the protocone displays a flattened, transversely concave surface obviously continuous functionally with an anterolingual oblique facet on the hypocone. Labial to that facet, on the anterolabial surface of the hypocone at the site of a formerly more prominent metaconule, is a more transversely oriented facet, divided weakly into anterior and posterior subfacets, which are in turn confluent with a slightly oblique facet on the anterolingual slope of the metacone. The metacone also has a large, highly oblique facet on its anterior wall. The hypocone has a small sharply defined facet on its posterolingual surface, and a larger facet on its posterolabial surface, continuous functionally with wear on the two elevated cingular cuspules at the posterolabial margin of the tooth.

Third upper molar: Completely preserved from the right side (Fig. 4), but only the anterolabial portion of the left tooth is present. The roots are as on M^2. M^3 is nearly identical to M^2 but displays much more clearly the paraconule, which even when unworn is only partly distinct from the protocone. No metaconule is present. The crown is slightly worn; the enamel is completely penetrated only on

Figure 1. *Behemotops proteus*, LACM 124106, split block showing remnants of right lower postcanine dentition, prior to reassembly and preparation. A, medial block in labial aspect. B, lateral block in lingual aspect. The crowns of P_3-M_1 have been lost to weathering, as have much of their roots. Only the tip of the anterior root of M_1 remained.

the right protocone and left paraconule, though almost so on the paracones. Wear facets can be discerned on the anterior surfaces of the former two cusps, as well as on the posterior surfaces of all the cusps. An anterior interdental wear facet is also present. The paracone has only one distinctive wear facet, occupying its posterolingual slope. The paraconule has three distinct facets, one on its posterior slope, the other two on its anterior and anterolingual slopes. The latter is confluent with the anterolingual facet of the protocone. The protocone also has a small facet on its labial slope and a much larger one on its posterior slope, opposite a still larger, similar one on the anterior slope of the hypocone. The hypocone has a small labial facet near its apex. The little-worn metacone has one, still smaller, facet on the posterior slope of its apex.

Lower canine: A small fragment of what appears to be the dentinal proximal tip of an enlarged canine was found isolated in the matrix. The dentinal wall is some 2.5 mm thick, and represents less than half of the circumference of the tooth. It resembles closely in cross-sectional shape the basal end of the broken mandibular tusk of the Japanese *Behemotops* (Inuzuka 1989: fig. 2–45) and lends some credence to our speculation (above) that we see an alveolus for a massive tusk of "*B. emlongi*" magnitude in the rotten, macerated remnants of bone preserved in LACM 124106. The caniniform tooth that we regarded as P_1 in the holotype of *B. proteus* we now think probably represents an incompletely formed canine (as suggested to us by Earl Manning).

First lower premolar: What appears to be the single-rooted left P_1 (Figs. 5, 12) is moderately worn, with both principal cusps breached and truncated by wear. The central cusp (protoconid) is a high, thick cone bowed somewhat toward the lingual side. Closely appressed to it anteriorly and almost fused with it is a smaller cusp (paraconid). A vertical crest descends the posterior side of the protoconid to the summit of a tiny basal cuspule. This crest, together with the anteroposterior alignment of all three cusps, lends a somewhat bladelike aspect to the crown as a whole.

Second lower premolar: The specimen includes the complete crown of the right P_2, with slightly damaged posterolingual base, and the anterior two-thirds of the left P_2 (Figs. 1, 6, 12). Both are slightly worn apically, with a dentinal lake in the center of the

Figure 2. *Behemotops proteus*, LACM 124106, stereophotographs of left (A–E) and right (F–J) P^4, in occlusal (A, F), anterior (B, G), lingual (C, H), posterior (D, I), and labial (E, J) aspects.

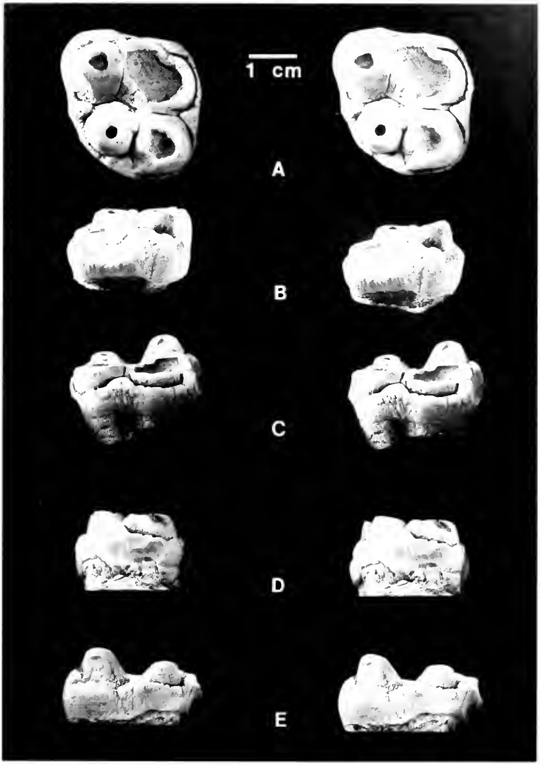

Figure 3. *Behemotops proteus*, LACM 124106, stereophotographs of right M^2 in occlusal (A), anterior (B), lingual (C), posterior (D, cast), and labial (E) aspects.

protoconid, and with the surface of wear inclined somewhat posteriorly, especially in the right P_2; the enamel of the subsidiary cusps has not been breached by wear. On the posterior side of the protoconid near the apex of each tooth is a steeply inclined flat wear facet. The right paraconid shows no evidence of wear. In the left P_2 there is a common rounded wear surface developed anterolabially on the paraconid and protoconid. The protoconid is a high, columnar cusp, slightly compressed laterally to produce the suggestion of anterior and posterior crests; from apex to root, it is somewhat concave lingually and straight labially. The paraconid is also high and columnar, tightly appressed to the anterior (slightly medial) wall of the protoconid, and recurved posteriorly so that its apex immediately adjoins the protoconid. The posterior or heel cusp is much smaller, but also columnar and similarly bent toward and against the protoconid. These three cusps together give the tooth a bladelike appearance. There is a faint swelling on the lingual surface of the base of the protoconid which probably represents the metaconid. A basal cingulid encircles the tooth completely except on the anterolingual side of the protoconid, where it is faint (left) or absent (right). The damaged area at the posterolingual base shows a broadened area that is either a heel cusp or part of the basal cingulid. The two large roots of P_2 are subequal in size and splayed (Figs. 1, 12), not appressed as suggested in our earlier paper (Domning et al. 1986:7, figs. 4, 15). However, near the level where the tooth emerges from the jaw the roots are fused.

Third lower premolar: Only the left P_3 is preserved (Figs. 1, 7, 12). It is moderately worn, all three principal cusps having been breached by wear. Wear is also visible on the heel cuspules at the

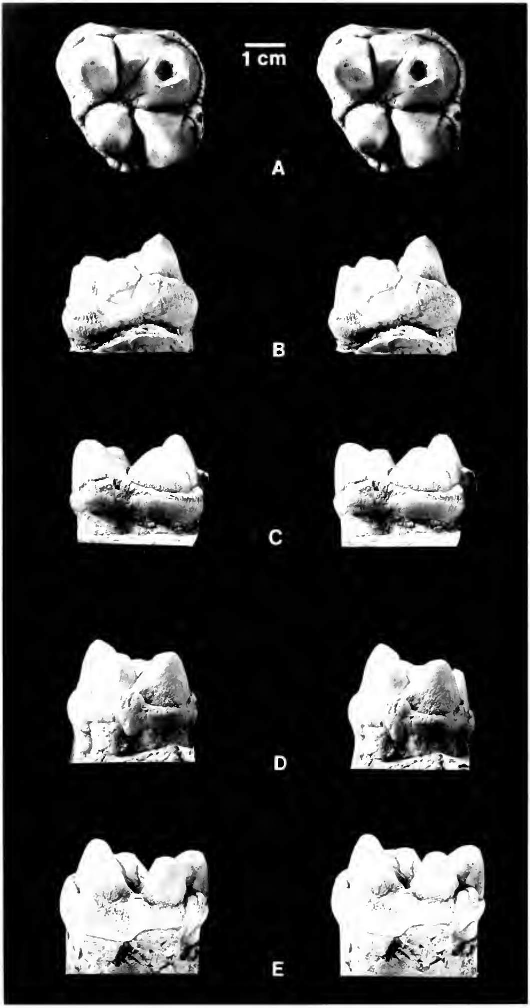

Figure 4 *Behemotops proteus*, LACM 124106, stereophotographs of right M^3 in occlusal (A), anterior (B, cast), lingual (C), posterior (D), and labial (E) aspects.

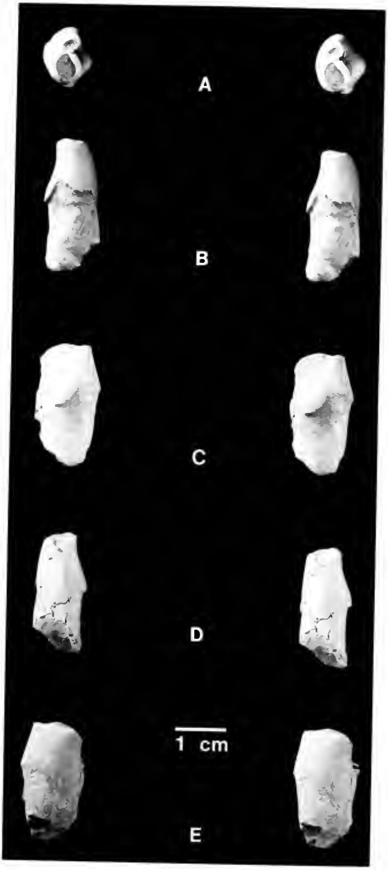

Figure 5. *Behemotops proteus*, LACM 124106, stereophotographs of left P$_1$ in occlusal (A), anterior (B), lingual (C), posterior (D), and labial (E) aspects.

posterior end of the base of the crown. The protoconid is a high, massive, conical cusp. Its truncated and worn tip slopes posteriorly, and the posterolingual side of the truncated surface bears an even more steeply inclined, almost flat surface, divided into two distinct wear facets by a faint line that descends posterolabially. The smaller paraconid is closely appressed to its anterior side, and is the highest part of the tooth in its worn state. The paraconid is very similar to that of P$_2$; its anterior edge bulges forward and is labiolingually compressed, accentuating the bladelike character of the tooth. It is a much taller, more robust, more bladelike cusp than its counterpart in the holotype of *B. proteus*. A small metaconid forms a slight spur on the lingual side of the protoconid. Its steeply, lingually inclined, rounded wear surface is continuous with that on the posterolingual wall of the protoconid and with the polished lingual wall of the crown, all of which combine to deemphasize the metaconid. Prior to this wear, it may have differed little from P$_3$ of the holotype. A well-developed cingulid encircles the base of the tooth except on part of its lingual side, where it may have been obliterated by polishing. Posteriorly, this cingulid forms a heel bearing a cluster of six cuspules, the largest of which occupies the posterolabial corner of the tooth. There is no cuspule in this position in the holotype of *B. proteus*. The largest cuspule bears a steeply inclined posterolabial wear surface. It apparently was appressed lingually to three smaller, lightly worn cuspules, aligned fore and aft along the posteriorly descending slope of the protoconid and contributing to the bladelike aspect of the tooth, as in the holotype of *B. proteus*. The posterolingual corner of the heel bears an independent robust cuspule, almost as large as the posterolabial one, and much less worn, as reflected by a transverse apical facet. It is bordered labially by a much smaller cuspule. Two cuspules of subequal size occupy this area in the holotype of *B. proteus*. The two large, subequal roots of LACM 124106 (Figs. 1, 12) are widely splayed deep in the jaw but fuse well below the top of the alveolus.

Fourth lower premolar: We tentatively identify as the left P$_4$ crown (Fig. 8) a deeply and apparently anomalously worn tooth crown found in the matrix. This identification is based in part on similarity in size and plan to P$_4$ in the holotype of *B. proteus*. The major cusps have been reduced to a single confluent lake of dentine, obtusely pointed in outline anteriorly and constricted both labially and lingually about two-thirds of its length from the front. Small basal pre- and postcingulids are present; the postcingulid broadens to form a slight shelf labially. It must be emphasized that our identification of this tooth remains very uncertain. There are ill-defined surfaces of interdental wear anteriorly and posteriorly. Neither can be fit to the P$_3$, nor to any other preserved tooth. The roots of P$_4$ (Figs. 1, 12) are large, long, and subequal, but do not splay widely deep in the jaw. Presumably they fused near the top of the alveolus.

First lower molar: Not preserved.

Second lower molar: Preserved from both left and right sides (Fig. 9); a robust, rectangular bunodont tooth with four massive cusps and two roots. This tooth does not differ significantly from M$_2$ in the holotype of *B. proteus* except in ways attributable to deeper wear. It is moderately worn, more so on the labial side, and the enamel is breached on all four cusps, most deeply on the hypoconid. There is a simple, straight precingulid. The protoconid and metaconid are low subconical cusps lying side by side with their bases closely appressed. The transverse valley is blocked by a low cristid obliqua connecting the metaconid and hypoconid, and a single low cuspule lies at the valley's labial outlet. The hypoconid and entoconid resemble each other and the anterior cusps in size and shape, and their bases are likewise closely appressed. The hypoconid gives the impression of larger size owing to its deeper wear. The postcingulid is straight and worn flat on top but is wider and more prominent than the precingulid.

Third lower molar: Also preserved from both left and right sides (Figs. 10 and 11). It is slightly worn, especially labially, and the enamel is breached on the protoconid, metaconid, and hypoconid. Distinct wear facets are present on the anterolabial slopes of the metaconid, hypoconid, and entoconid, on the cristid obliqua, and on both anterolabial and anterolingual surfaces of the hypoconulid. Aside from the rounded apical wear on the protoconid, the tooth also

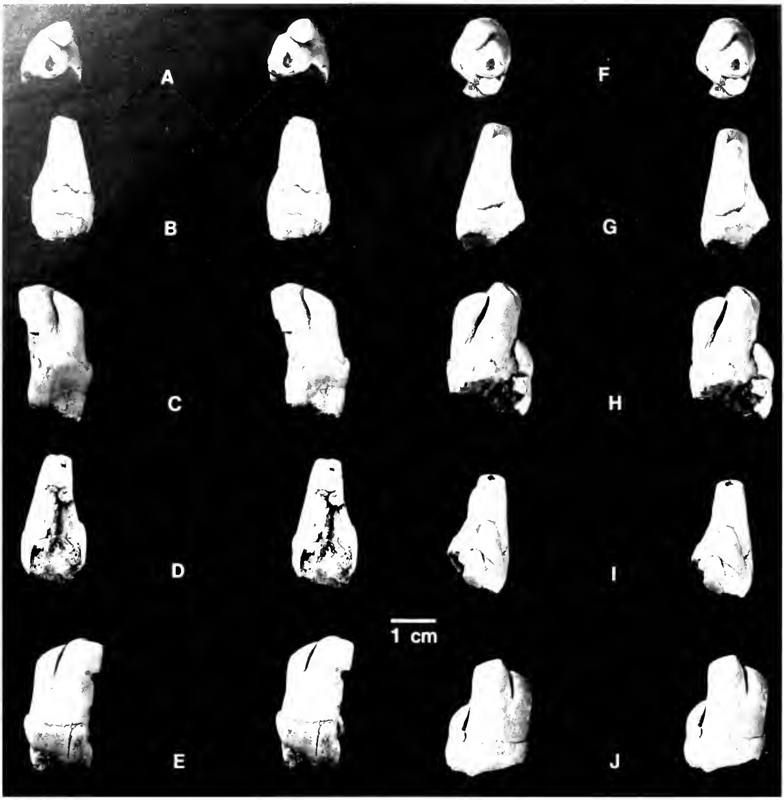

Figure 6. *Behemotops proteus*, LACM 124106, stereophotographs of left (A–E) and right (F–J) P_3, in occlusal (A, F), anterior (B, G), lingual (C, H), posterior (D, I), and labial (E, J) aspects.

has two distinct but conjoined wear facets anterolingually and one posterolingually. The metaconid has a strongly developed large concave facet on its posterolabial wall, complementing that on the anterolabial wall of the entoconid. The cristid obliqua has a posterolingual facet essentially opposite its anterolabial facet. There is a straight, minutely crenulated precingulid. The four major cusps and cristid obliqua differ in no way from those on M_2, but the cuspule at the labial end of the transverse valley is much less distinct. There is also more of a suggestion of basal cingulids on the sides of the crown, especially labially. The chief distinguishing feature of the M_3 is its posterior prolongation by an enormous hypoconulid, which almost attains the bulk of the other cusps but is lower. Its anterior surface bears two low, irregular longitudinal ridges, one median and the other more labial, which contact a spur of the hypoconid. An irregular cuspule on either side forms a cingulid linking the hypoconulid basally to both the hypoconid and entoconid.

This specimen confirms our earlier conclusion (Domning et al. 1986) that the unerupted M_3 of the holotype did not reflect the adult form of the tooth. Also, it demonstrates that the adult's hypoconulid is much larger than would be suspected from that immature and

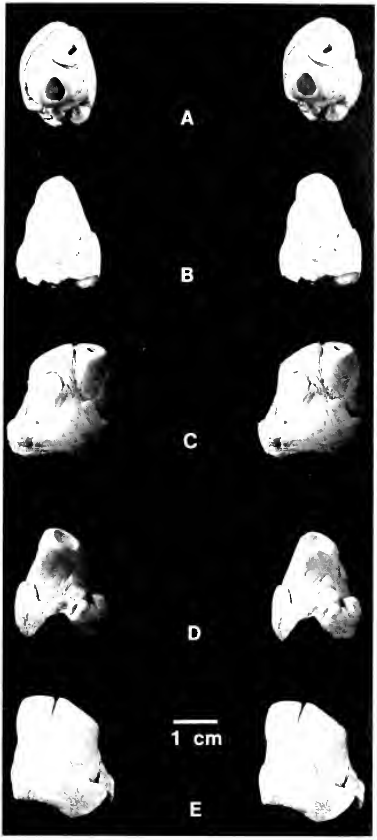

Figure 7 *Behemotops proteus*, LACM 124106, stereophotographs of left P_3 in occlusal (A), anterior (B), lingual (C), posterior (D), and labial (E) aspects

Figure 8 *Behemotops proteus*, LACM 124106, stereophotographs of left P_4? in occlusal (A), anterior (B), lingual (C), posterior (D), and labial (E) aspects

incompletely formed specimen, even larger, indeed, than in the otherwise similar mature referred M_3 of USNM 244033.

Our concept of the lower dentition of *Behemotops proteus*, based mainly on the new specimen, is represented in Figures 12 and 13. Unfortunately, the upper dentition is not sufficiently known to support a similar representation.

DISCUSSION

The overall similarity in size and character of postcanine teeth in LACM 124106 and USNM 244035 (holotype of *B. proteus*), detailed similarity between P_3 and M_2 in each, and topotypic occurrence lead us to assign the new specimen to *B. proteus*.

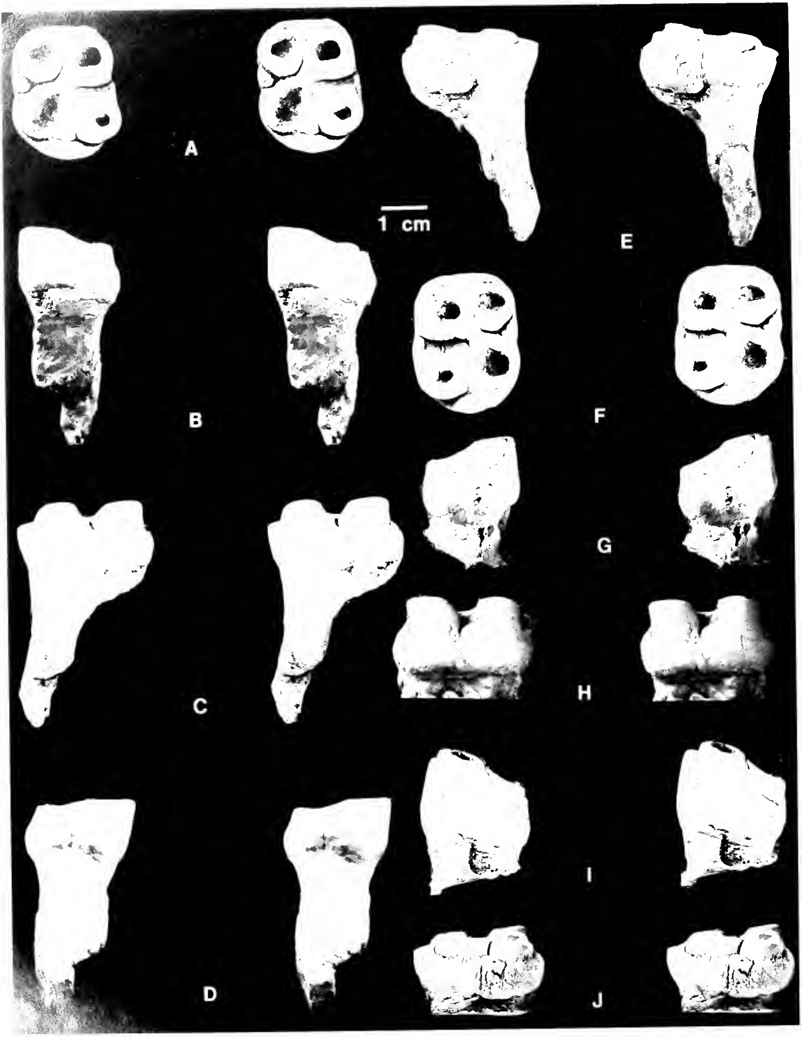

Figure 9 *Behemotops proteus*, LACM 124106, stereophotographs of left (A–E) and right (F–J) M_2, in occlusal (A, F), anterior (B, G, cast), lingual (C, H, cast), posterior (D, I, cast), and labial (E, J, cast) aspects

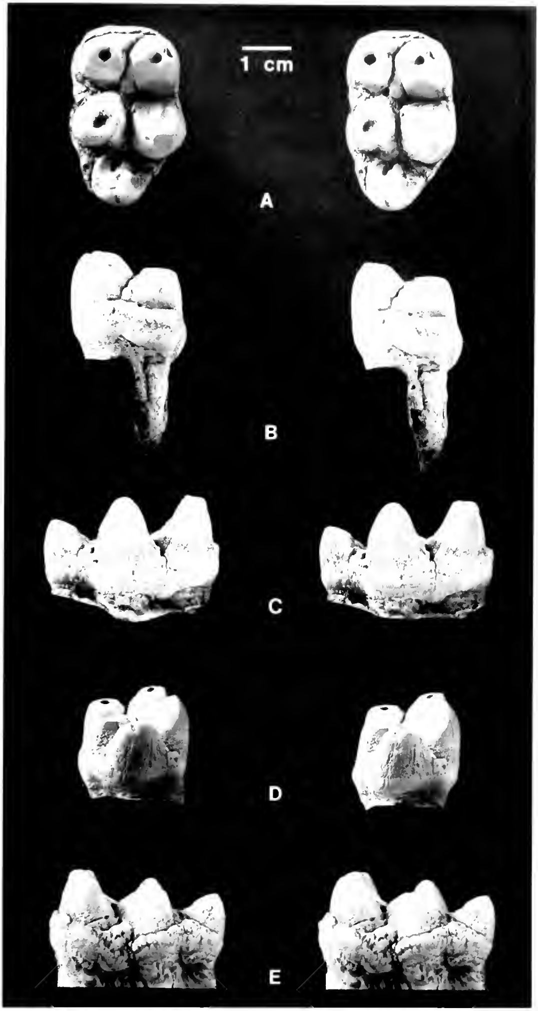

Figure 10. *Behemotops proteus*, LACM 124106, stereophotographs of left M_3 in occlusal (A), anterior (B), lingual (C), posterior (D), and labial (E) aspects.

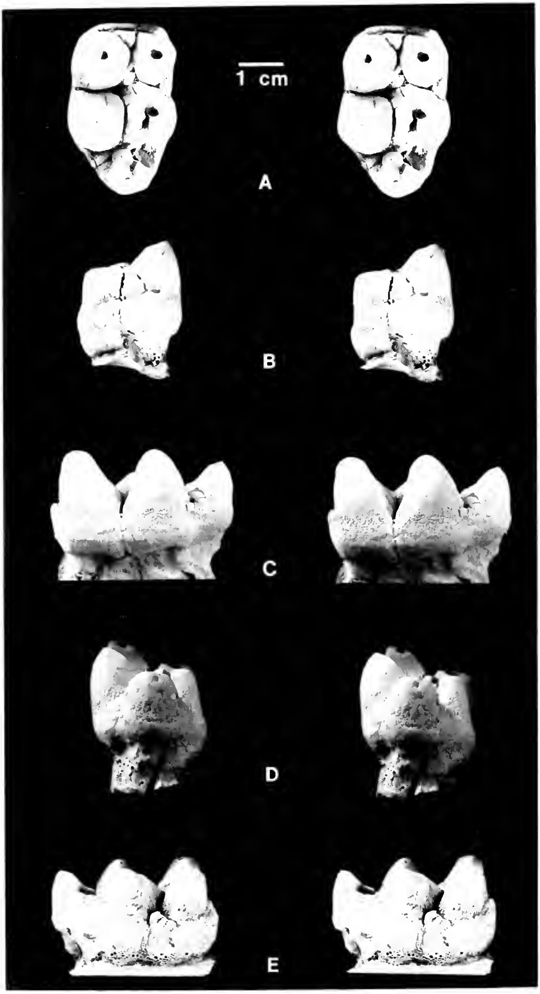

Figure 11. *Behemotops proteus*, LACM 124106, stereophotographs of right M_3 in occlusal (A), anterior (B, cast), lingual (C), posterior (D, cast), and labial (E, cast) aspects.

The dissimilarity of M_3 in the two specimens, and their similarity in the new specimen and in the holotype of *B. emlongi*, USNM 244033, confirm our earlier opinion that the peculiarities of M_3 in the holotype of *B. proteus* are attributable to its incomplete development in the juvenile animal.

Moreover, the suggestion, however equivocal, of a greatly enlarged canine in the mandible of the new specimen further tends to draw the two nominal species together. Recent observations on the genus *Desmostylus* by Domning indicate that large lower tusks may be absent in young individuals but develop and extend posteriorly in older animals.

We now believe that the specific separation of the Oregon animal as *B. emlongi*, always questionable in our minds, can no longer be supported on morphological grounds; accordingly we here relegate *B. emlongi* to the junior synonymy of *B. proteus*.

Japanese *Behemotops*

Although the first specimen of *Behemotops*, USNM 186889, a massive tusk in a mandibular remnant, was found in Oregon in 1969, nothing definitive could be done with it until more informative material was found. This occurred in 1977 when Douglas Emlong discovered at the same locality a half mandible overlapping sufficiently with the first specimen to leave no doubt that they represented a single species. This latter specimen, USNM 244033, became the holotype of *B. emlongi* in 1986. On 11 March 1976, Emlong found the juvenile's mandible, USNM 244035, in Washington State. This became the holotype of *B. proteus* in 1986. The specimen forming the primary basis for this paper, LACM 124106, was collected in 1985 from the same rock unit on Washington's Olympic Peninsula.

Meanwhile, in Japan, beginning in the fall of 1976, parts of more than one individual of a primitive desmostylian were discovered in the Morawan Formation along the Morawan River in eastern Hokkaido (Saito et al. 1988:269). Although these were first mentioned in print as early as 1984 (Inuzuka 1984) and, according to Saito et al. (1988:269), regarded as a new genus ancestral to all other desmostylians, we were unfortunately not aware of the existence of the material until after publication of our original paper in 1986. The material has now been in part described (in Japanese) and illustrated by Inuzuka (1987, 1989).

Dr. Inuzuka, during a research visit to the USNM in April and May 1990, generously made information about the Japanese specimens available to us and provided excellent casts of the dentition and two mandibular fragments. Extensive skeletal materials and a cranium exist as well (Inuzuka 1989: figs. 2–20, and others). When these materials have been fully described, they will unquestionably add greatly to understanding of the Desmostylia, but in the meantime published information, along with the casts provided by Dr. Inuzuka, has aided significantly in developing our own evolving concept of these fascinating animals, particularly as regards number of taxa and ontogeny.

It is beyond our scope here to specify the infrageneric relationship between the North American and Japanese *Behemotops*. We note only that a case could be made for specific separation of the

Figure 12. *Behemotops proteus*, composite right lower postcanine dentition in occlusal aspect. Based primarily on the right P_2, M_2, and M_3, and left (reversed) P_1 and P_3 of LACM 124106. The P_4 and M_1 are based on the holotype, USNM 244035, with hypothetical, deeper wear. No doubt m1 at least would have been worn even more deeply than shown. However, no objective basis is available to show the details of such wear. For clarity, P_4–M_3 are shown separated by slight spaces, but in life they would have been tightly appressed, as demonstrated by interdental wear facets.

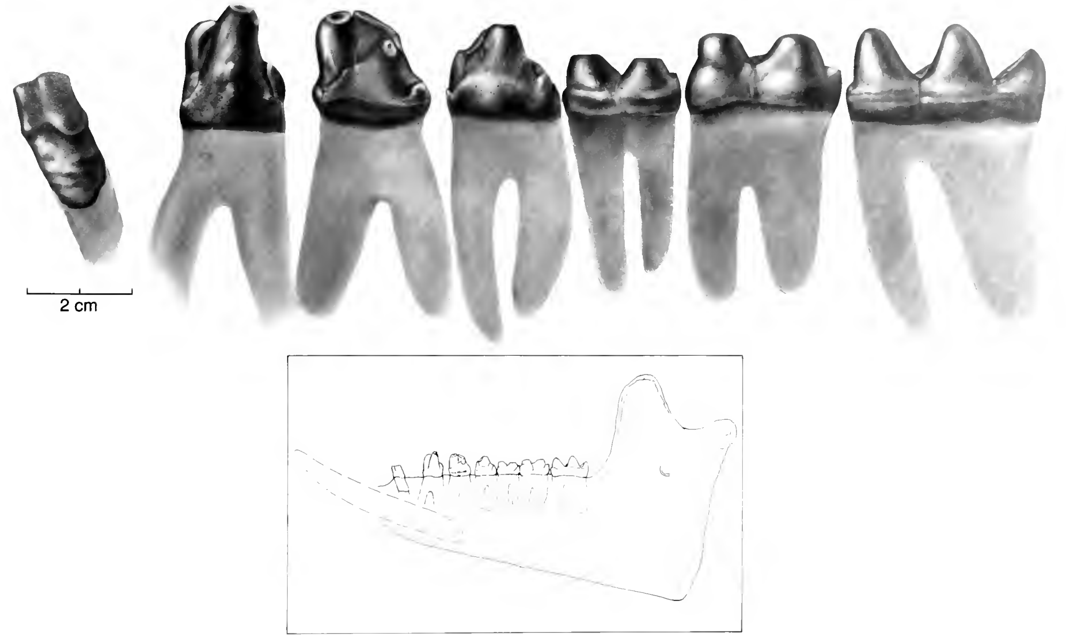

Figure 13. *Behemotops proteus*, composite right lower postcanine dentition in lingual aspect. The roots are based primarily on the split block as shown in Fig. 1. The crowns are based primarily on the right P_2, M_2, and M_3 and left (reversed) P_1 and P_3 of LACM 124106. The crowns of P_4 and M_1 are based on the unworn holotype, USNM 244035, with hypothetical, deeper wear, instead of on the excessively worn LACM specimen. The inset drawing, also in lingual aspect, is intended to suggest our concept of a complete right mandibular ramus, with the probable canine but without incisors, based on all available mandibular material of *Behemotops*.

Figure 14. *Anthracobune pinfoldi*, H-GSP 82-31P, stereophotographs (reversed) of left maxilla with P^3–M^3 in occlusal aspect. See West (1983) for discussion.

Japanese material on the basis of its smaller size, stronger cingula [in this and other dental details perhaps even more like *Anthracobune* (Fig. 14) and *Moeritherium* than is the North American *Behemotops*], smaller tusk than in USNM 186889 (holotype of *B. emlongi*), lacking the resulting massive lateral bulging at the front of the jaw (possibly sexually dimorphic?), and detailed dental differences, especially salient in the premolars.

Much more important to present purposes is our belief that all known specimens of *Behemotops*, even if not conspecific, at least constitute a tightly clustered group for purposes of developmental and biogeographical interpretations.

Ontogeny

From these observations, we now believe that *Behemotops* underwent a striking degree of ontogenetic change, possibly exacerbated by sexual dimorphism. This may have been driven largely by the late development of its enormous mandibular canine tusk and facilitated by the capacity, particularly in the premolars, to continue long past maturity to enlarge already large roots out of all proportion to the size of crowns, mainly by persistent heavy deposition of cementum. We were formerly unable to accept such marked alterations as being intraspecific (Domning et al. 1986:31–33), but the addition of LACM 124106 and the Japanese specimens, although still not completely satisfying, does in our opinion substantiate the ontogenetic leap from the juvenile holotype of *B. proteus* to the old adult holotype of *B. emlongi*.

We argued in 1986 (p. 33) as follows: "there does not appear to have been space in the mandible below P_1 (or DP_1) for an enlarged canine tusk like that of *B. emlongi*. Rather, any canine or incisor tusks that were present must have been medial to P_1 (or DP_1). It seems highly unlikely that enough tusk growth or mandibular remodeling could have taken place in the time remaining until eruption of M_3 for *B. proteus* to take on the form of *B. emlongi*.

Principally for the latter reason, we prefer to regard the Washington and Oregon animals as representing separate species of a single genus, pending additional knowledge of their anatomy and ontogeny."

We now regard the caniniform tooth developing deep within the mandible of the holotype of *B. proteus* as the true canine. Its further development and enlargement at the growing tip must have been retarded, pending eruption of P_{1-4} and M_3. All postcanine teeth were erupted, worn, and with long roots in LACM 124106, a fully adult but not old individual. We believe that a very large canine tusk was also present in this specimen, as in the holotype and referred specimen of *B. emlongi*. The two latter specimens, however, represent ontogenetically older individuals, on the basis of greater wear of M_3 and on the changes in alveoli and roots of the postcanine teeth. The roots, separate and discrete in LACM 124106 and USNM 244035, evidently were drawn together and were more or less coalesced through deposition of cementum in USNM 244033 and 186889, judged from the alveoli of these latter specimens. The premolars have inclined progressively forward as the tusk came to dominate the anterior part of the jaw so that they lie highly oblique to the original occlusal plane and occupy the shallow space left to them atop the massive tusk. These relationships are illustrated in Figure 13.

The Japanese material strongly corroborates this interpretation. The tusk is smaller so that the premolars have not been laid so nearly horizontal, but the roots of P_{1-3} preserved in an anterior mandibular fragment are enormously enlarged (Inuzuka 1989: figs. 2–45), as are some other preserved roots. On the other hand, the preserved crowns of P_3 and P_4 are normally behemotopsian in size and configuration.

Phylogeny

Figure 15 presents our current notion of the cladistic relationships of *Behemotops* to other desmostylians and to certain other tethytheres. This cladogram was constructed by hand, hence tree statistics for this or alternative arrangements are not available. As discussed in our earlier paper (Domning et al. 1986), the Sirenia are an outgroup to both the Proboscidea and Desmostylia. On the basis of its lower dentition, *Minchenella* is possibly ancestral to both the Proboscidea and the Desmostylia. *Anthracobune* (and other anthracobunids) are excluded from the Desmostylia. They are possibly to be excluded from the Proboscidea as well (see Tassy 1988); however, we still place them in that order, in agreement with Shoshani et al. (1989) and Gingerich et al. (1990). The Desmostylia and Proboscidea are sister groups, in contrast to the views expressed by Tassy (1981: fig. 12).

Behemotops proteus (now including *B. emlongi*) no longer appears to have only characters plesiomorphic to, and therefore possibly be ancestral to, all other desmostylians. The mediolateral compression of its lower canine tusk and the reduction of the posterior cusps of its P_4, as well as its large body size (not included in the cladistic analysis), appear to be autapomorphies that set it apart as an early collateral branch of the order (although *Behemotops* is still, on the whole, the most primitive desmostylian known). This conclusion is in accord with its stratigraphic position, because *Behemotops* and *Cornwallius* were contemporaries or near-contemporaries in the late Oligocene. We predict from this cladogram that early representatives of *Paleoparadoxia* will also turn up eventually in upper Oligocene marine rocks.

Other known desmostylians are separated from *Behemotops* by five or more unequivocal character transformations and clearly form a monophyletic group. However, it is not yet apparent whether this group would be most usefully ranked as a family or whether it should be subdivided into families. Pending resolution of the specific status and cladistic position of the Japanese *Behemotops*, it is likewise unclear whether a separate family based on this genus (Behemotopsidae Inuzuka, 1987:16) would or would not be paraphyletic. Therefore we continue to defer to a later date a formal proposal for the familial classification of the Desmostylia.

ACKNOWLEDGMENTS

As ever, the *sine qua non* for progress in vertebrate paleontology is finding good fossils. William R. Buchanan discovered the specimen that forms the primary basis for the present paper, and generously donated it to the LACM, where it was immediately catalogued and sent on to us by Dr. Lawrence G. Barnes for preparation and study. James L. and Gail H. Goedert assisted with field data and shipping. The difficult preparation of the split blocks was carried out expertly by Gladwyn B. Sullivan, USNM. The photographs for Figures 1–11 and 14 were made by Victor E. Krantz; the figures were prepared by Mary Parrish with the assistance of David J. Bohaska, USNM. The drawings for Figures 12 and 13 were made by Mary Parrish. Figure 15 was drafted by Lorraine Meeker, AMNH. Yoko Zoll of the Smithsonian Behind-the-Scenes Volunteer Program provided expert translation of Japanese into English.

Norihisa Inuzuka very generously made available to us casts of the dentition of the Japanese *Behemotops*, as yet incompletely described. Robert M. West loaned the maxilla of *Anthracobune pinfoldi*. John A. Barron and David Bukry attempted to recover diatoms and nannofossils from matrix associated with the holotype and the new specimen of *Behemotops proteus*.

We thank Earl Manning, Storrs Olson, and Adele Panofsky for pointing out errors in our original paper, and Earl Manning in particular for a detailed and helpful critique of it. James M. Clark kept us abreast of his research on *Paleoparadoxia* and provided advance information now published (Clark 1991) on a new species of that genus. Both Manning and Clark helped to persuade us that *Behemotops proteus* and *B. emlongi* are conspecific. Philip D. Gingerich, J. G. M. Thewissen, and J. Shoshani also aided us in several ways.

ERRATA AND CORRIGENDA

In our former paper characters 49–51 were inadvertently omitted from the cladogram (Domning et al. 1986: 37, fig. 22) because a label became detached from the drawing prior to printing. As can be deduced from the distribution of other numbered characters, these three characters apply to the same node as characters 33 (parallelism), 47, and ?48. This node unites *Prodeinotherium*, *Deinotherium*, *Palaeomastodon*, and other Proboscidea.

The "Brezina animal" (Domning et al. 1986: figs. 22, 23) has now been named *Numidotherium koholense* (Mahboubi et al. 1986).

The reference to page 000 (Domning et al. 1986: 46, line 32) refers to p. 15.

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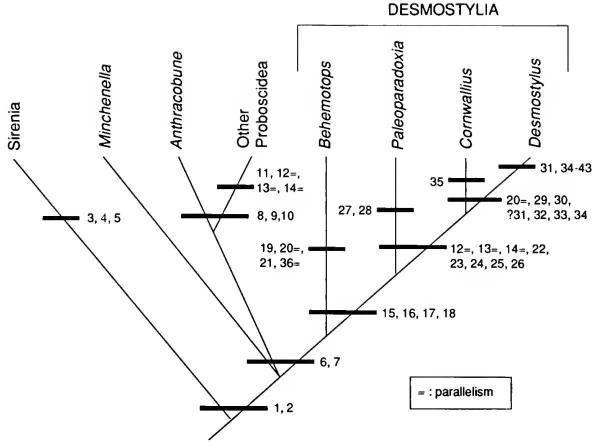

Figure 15. Cladogram of desmostylians (*Behemotops*, *Paleoparadoxia*, *Cornwallius*, and *Desmostylus*) and some closely related tethytherian outgroups. 1, Anterior border of orbit lies over or forward of M^1. 2, Zygomatic process of squamosal bone expanded far laterally. 3, Pachyostosis and osteosclerosis. 4, Incipient bilophodonty. 5, Number of premolar loci increases to five (here we treat possession of five premolar loci as a synapomorphy of the Sirenia or character reversal rather than as a retention by Eocene sirenians of the plesiomorphic condition exhibited by various Mesozoic mammals). 6, Last lower molar with hypoconulid shelf transversely broad, but the hypoconulid still central. A small entoconid II (postentoconulid, a new entoconid situated behind the true entoconid) can be present adjacent to it lingually (*Minchenella*) and tiny cuspules can be present labially. 7, External auditory meatus high, nearly enclosed ventrally by mutual contact of squamosal post-tympanic and postglenoid processes. The status of this character is unknown in *Minchenella* and *Anthracobune*. 8, Last lower molar with two definite cuspids at rear: a labially displaced hypoconulid and a large entoconid II (postentoconulid). 9, Astragalus with strongly projecting tuberculum mediale (Gingerich et al. 1990:76). 10, Scapula with large downcurved coracoid process (Shoshani et al. 1989). 11, Tusk formed from incisor. 12, Astragalar foramen lost. 13, Crista capitalis of astragalar head lost (Gingerich et al. 1990:76). 14, First premolar lost. Diastema separates incisors and canines from remaining premolars. 15, Lower incisors transversely aligned. 16, Enlarged passage (postzygomatic foramen of VanderHoof 1937:178, figs. 9, 11) present through squamosal from external auditory meatus to roof of skull. This character unites at least *Paleoparadoxia*, *Cornwallius*, and *Desmostylus*, but apparently applies as well to *Behemotops* (see Inuzuka 1989:56, fig. III-2-21). This passage may well be the same as the canalis temporalis seen in *Moeritherium* (Tassy 1981:109–110) but not in advanced Proboscidea. In that case this character would join characters 7 and 8 at a more inclusive node. 17, Roots of P_1 fuse. This assumes the double-rooted condition to be plesiomorphic, an inversion of the polarity of character 19 of our previous cladogram (Domning et al. 1986:36, fig. 22). 18, Paroccipital process elongated. The status of this character is not yet reported in *Behemotops* but is possibly determinable in the Japanese specimen (Inuzuka 1989). 19, Reduction of heel cusp pair of P_4. 20, Lower canine becomes an enlarged procumbent tusk. 21, Tusk mediolaterally compressed. 22, Roots of P_2 fuse; crown reduced. 23, Roots of P_3 fuse; paraconid lost. 24, Roots of P_4 fuse. 25, All cusps on posterior cheekteeth become desmostylodont (swollen, columnar, and appressed). 26, On P_4 through M_3, hypoconulid and (especially) entoconid II (postentoconulid) enlarge. 27, On M_2, well-developed extra cuspid present between and labial to protoconid and hypoconid. 28, Mandibular symphysis horizontally oriented and faces ventrally (character 29 of Clark 1991). 29, Premolars at 2nd, 3rd, and 4th loci lost in adults (but in young individuals three upper loci and at least one lower locus are occupied by deciduous or permanent premolars). 30, Molar cingula reduced (see character 39 for further development). 31, Mandibular symphysis becomes elongate. Status not yet reported in *Cornwallius*. 32, Sagittal crest reduced (see character 43 for further development). 33, Additional anterolingual and anterolabial cusps on upper molars. 34, Reduction of lower incisors to one pair. 35, Loss of lower incisors. 36, Body size increased. 37, Medially positioned bony swelling occurs at the rear of the tooth row. 38, Cusp height increases. 39, Molar cingula lost (see character 30). 40, Suprasymphysial depression reduced. 41, Rear molars very high-crowned, with enamel extending below gum line and into alveolus. 42, Zygomatic process further broadened. 43, Sagittal crest lost (see character 32).

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TABLE 1. Measurements of *Behemotops* teeth (mm).

	LACM 124106		USNM 244035[a]	USNM 244033[a]	Japanese specimen[b]	
	left	right	left	right	left	right
P^4, A–P[c] diameter, crown	20.0	20.0				
P^4, Transverse diameter, crown	21.2	21.7				
M^2, Length, crown		31.3				25.6
M^2, Maximum anterior width, crown		30.2				24.5
M^3, Length, crown		31.8			(25.4)[a]	[d]26.3
M^3, Maximum anterior width, crown		32.4			24.6	25.0
P_1, A–P diameter, crown	14.8					
P_1, Transverse diameter, crown	11.4					
P_2, A–P diameter, crown		19.5				
P_2, Transverse diameter, crown	14.8	(14.9)				
P_3, A–P diameter, crown	22.9		20.8			
P_3, Transverse diameter, crown	17.0		14.4			
P_4, A–P diameter, crown	23.9		23.1			
P_4, Transverse diameter, crown	16.3		15.8			
M_2, Length, crown	31.3	31.0	31.7			
M_2, Anterior width, crown	22.6	23.2	23.7			
M_2, Posterior width, crown	24.0	24.4	23.6		18.6	
M_3, Length, crown	41.0	40.0	(31.7)	37.6	(31.8–)	
M_3, Anterior width, crown	25.5	24.4	(19.0)	24.2	(20.0+)	
M_3, Posterior width, crown	25.6	25.9	(21.0)	28.6	21.3	

[a] From Domning et al. (1986).

[b] From Inuzuka (1987:16).

[c] A–P, anteroposterior.

[d] Measurements in parentheses are approximate, based on incomplete, worn, damaged, or incompletely accessible parts.

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Neogene Climatic Change and the Emergence of the Modern Whale Fauna of the North Atlantic Ocean

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ABSTRACT.—Fossil Cetacea of Neogene age are present on the east coast of the United States in strata ranging in age from ca. 17 to 4.5 Ma. At the beginning of this period the cetacean fauna was almost entirely assignable to families now extinct. By its end, represented by the assemblage of the Yorktown Formation, the vast majority of taxa belonged to families and genera extant today. The Yorktown assemblage is dominated by large baleen whales of modern aspect, and by a diversity of Delphinidae, the latter unknown in pre-Yorktown strata on the east coast. These faunal changes can be correlated with physical events in the North Atlantic Ocean. Establishment of the West Antarctic ice sheet (between 8 and 5 Ma) and closure of the western portal of the Mediterranean (6.4 to ca. 5.3 Ma) contributed to cooling, steeper temperature gradients, and probably more complex current patterns. The resulting variety of pelagic habitats may have facilitated adaptive radiation of both baleen and toothed whales, with increasing partitioning of food resources. The appearance of the modern cetacean fauna in the North Atlantic was essentially contemporaneous with that in the Southern Hemisphere, and reflects worldwide change in environmental conditions.

INTRODUCTION

The modern cetacean fauna is typified by large baleen whales of the families Balaenopteridae (rorquals and humpbacks) and Balaenidae (right whales) and by toothed whales of the family Delphinidae, a family of great diversity, ranging in size up to that of the killer whale, *Orcinus orca*. Fordyce (1989) pointed out that marine-mammal faunas of high latitudes in the Southern Hemisphere were ecologically and/or taxonomically similar to extant faunas by the late Miocene to Pliocene. This was also true in the eastern North Pacific Ocean (Barnes 1976) and in the North Atlantic Ocean, as will be pointed out below.

Fordyce (1989) described the physical changes in the Southern Ocean that accompanied the evolution of the austral marine-mammal fauna. In the late Neogene especially, progressive cooling resulted in new water-mass patterns and increased thermal gradients. Similar phenomena accompanied faunal development in the North Atlantic, and it is the purpose of this article to consider the results of recent paleoceanographic research and their possible correlation with the evolution of the cetacean fauna.

In our present state of knowledge the modernization of the cetacean fauna appears to have been roughly contemporaneous throughout the world. It may be, however, that refined stratigraphic correlation and increased knowledge of paleoceanography will allow reconstruction of the temporal and geographical patterns of adaptive radiation of Cetacea that took place over the world during the late Neogene.

MIDDLE AND LATE MIOCENE FAUNAS

The middle Miocene (ca. 16.5–10.5 Ma) cetacean fauna of the North Atlantic Ocean, represented by assemblages in the Calvert, Choptank, and St. Mary's formations of Maryland and adjacent areas (Fig. 1), was archaic in contrast to today's fauna, being dominated by genera now extinct. Most of the baleen whales of the time can be assigned to the extinct family Cetotheriidae, a paraphyletic grouping of small mysticetes. The Delphinidae, now the dominant odontocetes, are not known in Calvert, Choptank, or St. Mary's time (see Barnes et al. 1985: 21; Gottfried et al. 1994, this volume).

In the Eastover Formation of late Miocene age, which unconformably overlies the St. Mary's Formation from southern Maryland to North Carolina, there is fossil evidence of large mysticetes assignable to the Balaenopteridae (rorquals and humpbacks). The age of the base of the Eastover Formation is not well constrained, as no radiometric dates have been obtained for that part of the formation (the Claremont Manor Member). Blackwelder (1981:96) reported a K/Ar date, based on glauconite, of 8.9 ± 0.4 Ma for the base of the upper part of the Eastover (the Cobham Bay Member) and a date of 6.6 ± 0.05 Ma for the top of the Eastover (Fig. 1). Other authors (Ward and Blackwelder 1980; Andrews 1986) placed the base of the Eastover Formation at 11 Ma. Balaenopterid bones are found near the base of the Eastover Formation; thus it is apparent that large mysticetes of modern aspect appeared in the North Atlantic Ocean perhaps as early as 11 Ma. The modern aspect of the Eastover assemblage is paralleled by essentially contemporaneous faunas in the Southern Hemisphere (Fordyce 1989).

Unfortunately, outcrops of the Eastover Formation are not as extensive as those of the underlying middle Miocene formations, and many of the fossil bones found in the Eastover are disarticulated, presenting difficulties in identification. Further collecting and study will contribute to knowledge of this critical time in whale evolution.

PLIOCENE FAUNA—YORKTOWN FORMATION

Our first good view of the emerging modern whale fauna of the North Atlantic is in the Yorktown Formation of early Pliocene age (Table 1, Fig. 1). In Virginia the Yorktown unconformably overlies the Eastover Formation. In North Carolina, where it unconformably overlies the middle Miocene Pungo River Formation (14.5–13.5 Ma, correlative with the Calvert Formation), the Yorktown is exposed in the pits of the Lee Creek phosphate mine (Fig. 2). Here it has yielded hundreds of fossil whale bones, the study of which is the principal basis of this paper. The deposition of the Yorktown Formation lasted from about 4.8 Ma to about 3.0 Ma (Snyder et al. 1983; Dowsett and Wiggs 1992).

Another valuable source of information about the early Pliocene whales of the North Atlantic is the huge collection at the Institut Royal d'Histoire Naturelle in Brussels, Belgium, consisting of whale bones of Scaldisian age, correlative with the Yorktown Formation (Ray 1976:392). The bulk of the Belgian material was excavated in the 1860's during the construction of a ring of forts around Antwerp and since then during excavation of additional basins for the harbor of Antwerp (van Beneden 1882; de Meuter and Laga 1976).

The availability of extensive collections of fossil bones from the Lee Creek mine and from Antwerp is the result of large-scale excavations. At Antwerp, Belgian army engineers carted bone by the wagonload to the Musée Royal (now the Institut Royal). At Lee Creek, paleontologists collected specimens from the spoil piles on which they had been dumped by draglines (McLellan 1983; Whitmore and Kaltenbach, unpublished). In both instances, associated bones of an individual were rarely collected; hence emphasis is

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
Proc. San Diego Soc. Nat. Hist. 29:223–227, 1994

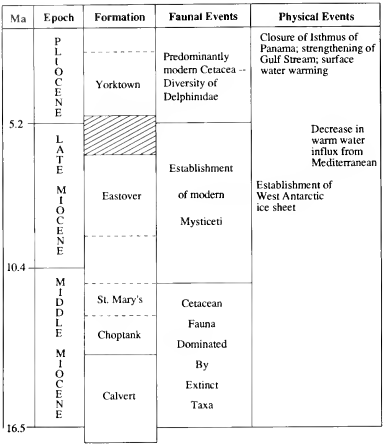

Figure 1. Late Neogene physical and faunal events in the North Atlantic Ocean.

Table 1. Cetacean assemblage of the Yorktown Formation.

- Odontoceti
  - Ziphiidae
    - *Mesoplodon longirostris* (Cuvier)
    - *Ziphius*, cf. *Z. cavirostris* Cuvier
    - Ziphiidae *incertae sedis*
  - Pontoporiidae
    - cf. *Pontoporia*
  - Delphinidae
    - cf. *Delphinus*
    - aff. *Lagenorhynchus*
    - *Stenella* n. sp.
    - *Tursiops* sp.
    - *Globicephala* sp.
    - *Pseudorca* sp.
  - Monodontidae
    - *Delphinapterus* sp.
  - Physeteridae
    - Kogiinae n. gen. & sp.
    - Physeterinae *incertae sedis*
- Mysticeti
  - Cetotheriidae
    - *Herpetocetus* n. sp.
  - Balaenopteridae
    - *Balaenoptera acutorostrata* Lacépède
    - *B. borealina* Van Beneden
    - *Megaptera* sp.
  - ?Eschrichtiidae
    - new gen. & sp.
  - Balaenidae
    - *Balaenula* sp.
    - *Balaena* n. sp.

placed on the study of skulls and of individual bones such as the periotic and tympanic, which in the Cetacea are diagnostic to genus and sometimes to species.

The Pliocene whale bones at the Lee Creek mine are concentrated in the lower part of the Yorktown Formation (ca. 4.5 Ma; Gibson 1983:75). Whale material has also been found elsewhere in the lower Yorktown Formation: a nearly complete skeleton of *Balaena*, very close to *B. mysticetus* [U.S. National Museum of Natural History (USNM) 22553], was collected at Hampton, Virginia, and partial skeletons of both *Balaena* and *Balaenoptera* have been collected at Williamsburg, Virginia. Remains of these taxa, and of the humpback whale *Megaptera*, have been found at Lee Creek.

There is therefore a modern aspect to the mysticete fauna of the Yorktown Formation. Some specimens, however, cannot readily be assigned to living taxa. For example, a large skull I am now studying shows some characters of the Eschrichtiidae, others of the Balaenopteridae. As in the Eastover Formation, the Pliocene assemblage contains Mysticeti whose differences from living taxa are subtle and complex.

Another member of the North Atlantic Pliocene assemblage is the cetotheriid *Herpetocetus*. This small whale (skull length ca. 1 m) is distinguished by a mandibular articulation unlike that of any other mysticete. The articulation of the mandible with the postglenoid process is on the dorsal side of the mandible rather than at its proximal end. Thus it appears that the mouth of *Herpetocetus* could not achieve as wide a gape as can species of *Balaenoptera* or, probably, other cetotheriids. *Herpetocetus* is biostratigraphically significant: with a relatively short stratigraphic range (upper Miocene to upper Pliocene) it has wide geographic distribution. It is known from the Pliocene of Belgium (van Beneden 1872; Whitmore and Barnes, unpublished), the early Pliocene of North Carolina, the late Miocene to late Pliocene of California (Barnes 1976), and the early Pliocene of Japan (Hatai et al. 1963; Hasegawa et al. 1985; Oishi 1987). Its dispersal into the Pacific must have taken place during this period, when the Middle American Seaway between the Atlantic and Pacific oceans was open (Whitmore and Stewart 1965).

Among the Odontoceti the Physeteridae (sperm whales) and the Ziphiidae (beaked whales) were early residents of the North Atlantic Ocean. As shown by collections from both sides of the ocean both families were well represented by middle Miocene time and probably earlier (Gottfried et al. 1994, this volume; van Beneden and Gervais 1868–1879). It may be that the Paleogene North Atlantic was a fruitful feeding ground for these mesopelagic and deep-water feeders but that its relatively warm surface waters did not offer a rich supply of food to pelagic mysticetes and delphinids, which feed near the surface.

In addition to the large baleen whales, a striking characteristic of the early Pliocene North Atlantic cetacean fauna was the presence, already in considerable diversity, of the family Delphinidae. Three delphinid genera have been identified from Lee Creek on the basis of skulls: *Stenella* n. sp., aff. *Lagenorhynchus*, and *Pseudorca* sp. Three other genera have been identified from ear bones, sometimes accompanied by fragments of skull or mandible, and very occasionally associated postcranial elements: *Tursiops* sp., *Globicephala* sp., and cf. *Delphinus*. *Delphinus* is very difficult to distinguish from *Stenella* on the basis of ear bones alone.

Even when a reasonably complete fossil skull is available, taxonomic assignment is difficult because one skull may combine characteristics of several living taxa. Caution in establishing new taxa of Pliocene odontocetes is encouraged by our knowledge of intraspecific variation and interspecific hybridization in living Delphinidae. A wise conservative approach to some Pliocene

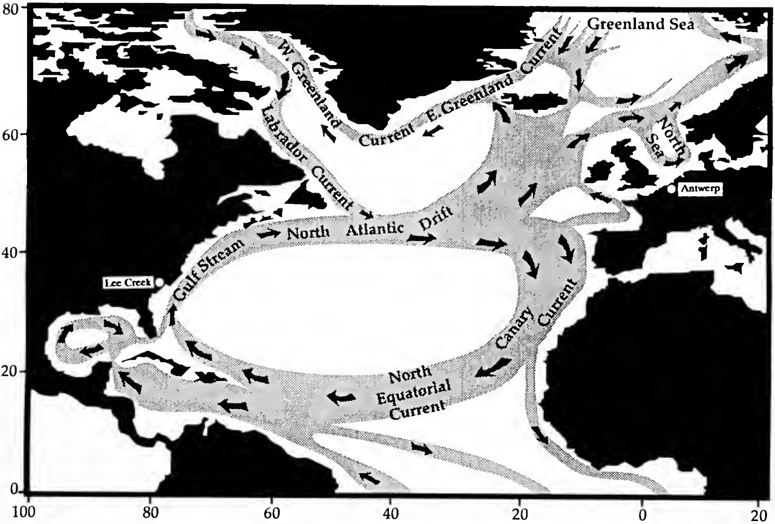

Figure 2. General circulation of the modern North Atlantic Ocean. Modified from Dowsett (1990).

Delphinidae might be to refer them to the "*Lagenorhynchus–Stenella–Delphinus* complex." But regardless of the degree of differentiation of these and other delphinid genera in Yorktown time, it is apparent that such differentiation was well under way.

Also present in the Yorktown Formation at Lee Creek are ear bones of a pontoporiid odontocete related to the La Plata dolphin, *Pontoporia blainvillei*, of South America. Its presence in northern waters in early Pliocene time fits Gaskin's (1976) concept of the "Atlantic Tethyan fringe," extending approximately from southern Brazil to North Carolina, the southern part of which was colonized by *Inia* and *Pontoporia* (Gaskin 1976, fig. 4). The Pontoporiidae extended into the Northern Hemisphere also in California between 9 and 3 Ma (Barnes 1985).

A prominent member of the Yorktown assemblage is the beluga, *Delphinapterus*, represented by a skull from Hampton, Virginia (USNM 25819), and by many ear bones from Lee Creek, far south of the genus' current arctic–subarctic range. On the west coast of North America, fossil belugas belonging to other genera have also been found well south of the present range of *Delphinapterus* (Barnes 1984).

As determined by numbers of ear bones collected at Lee Creek, three odontocete taxa predominate: cf. *Delphinus*, *Delphinapterus*, and a new genus and species of pygmy sperm whale (Kogiinae). The last, also represented by a skull (USNM 187015), is remarkable in that, unlike living species of *Kogia*, it has a set of robust and deeply rooted upper teeth.

In summary, the Yorktown cetacean assemblage includes at least 18 genera, of which 12 are living today (Table 1).

THE NORTH ATLANTIC OCEAN IN NEOGENE TIME

With two notable exceptions, discussed below, the physical borders of the North Atlantic Ocean were little different in the Neogene than they are today. The many marine transgressions and regressions had a profound effect on coastal and estuarine life but affected an area minuscule compared to the expanse of the open ocean. Changes in oceanic temperature and current patterns have accompanied the evolution of the cetacean fauna (Gaskin 1976; Fordyce 1989). They influenced the pattern and distribution of the pelagic food chain, and this in turn led to adaptive radiations among the Cetacea.

The establishment of the West Antarctic ice sheet between about 8.0 and 5.0 Ma renewed global cooling, caused in part by a north-flowing cold bottom current whose effects eventually reached the North Atlantic (Ciesielski et al. 1982; Kennett and von der Borch 1985; Benson et al. 1991). This cold bottom current first reached the north during Eastover time, which also marked the beginning of the dominance of large modern mysticetes in the North Atlantic (Fig. 1).

The cooling effect of the West Antarctic ice sheet was intensified in the North Atlantic between 6.4 and about 5.3 Ma, when tectonic events closed the western portal of the Mediterranean, shutting off what had been a flow of warm water into the North Atlantic. The thermal gradient in the upper part of the water column was steepened, increasing the speed of the gyre (Benson et al. 1991; Fig. 2). The resulting current and temperature patterns were probably more complex than before. Their appearance approximately coincided with, or perhaps shortly preceded, the first known adaptive radiation of the Delphinidae in the North Atlantic and the establishment there of modern baleen whales (Fig. 1).

Steep temperature gradients, both horizontal and vertical, support concentrations of prey species that attract Cetacea (Gaskin 1976: 311–315). Such gradients, occurring in zones of upwelling on continental margins, are exemplified today by upwelling off the Peruvian coast. Similar upwelling has been postulated on the basis of phosphate deposits of Miocene and Pliocene age in Florida, of probable Oligocene age in South Carolina, and of middle Miocene age in North Carolina (Pungo River Formation: Gibson 1983). Such upwelling must have had a marked effect on the productivity of coastal waters; in addition, although not so visible in the geologic record, temperature gradients farther out at sea were probably intensified because of current convergence and oceanic eddies resulting from the increasing strength of the North Atlantic Gyre coupled with a greater supply of cold bottom water. Such eddies would have supported high plankton productivity and in turn would have attracted not only baleen and sperm whales but also Delphinidae, many species of which are notably opportunistic feeders.

The other major physical event affecting the North Atlantic in Neogene time was the closure of the Middle American Seaway or Balboa Portal between 3.2 and 2.5 Ma (Lundelius 1987; Marshall 1988). By the time that the North Atlantic Gyre was well developed, water flow through the seaway between the equatorial Atlantic and Pacific had become a "mere leak" (Benson et al. 1991:176). As a result of this closure the Gulf Stream was strengthened. It may also have migrated northward (Dowsett and Wiggs 1992). The resulting increased northward flow of warm water was accompanied by warming of surface water in the North Atlantic. Between 3.15 and 2.85 Ma, surface seawater temperatures in coastal waters of Virginia were 2° to 6° C higher than today (Dowsett and Poore 1991). Similar warm temperatures extended as far north as Massachusetts (Cronin 1991).

This warm interval does not appear to have harmed the newly established modern cetacean fauna of the North Atlantic, although it undoubtedly affected their migration and feeding patterns. One aspect of this warm period, which probably began after the earliest Yorktown deposition (Fig. 1; see also Dowsett and Wiggs 1992), may bear upon the question of the presence of belugas in early Pliocene time along the mid-Atlantic coast of North America. Belugas now commonly range as far south as the Bay of Fundy, although stragglers have been seen as far south as New Jersey (Reeves and Katona 1980). They breed at a temperature of 15° C (Paul F. Brodie, pers. comm., 11 November 1975). Cronin (1991) estimated that winter temperatures during deposition of the Yorktown Formation at Lee Creek (ca. 4.5 Ma) were between 12.9° and 14°C, a range tolerated by the beluga. The summer water temperatures at Lee Creek, however, as estimated by Cronin (1991), between 22.2° and 23.7° C, were warmer than would be tolerated by the present-day beluga. Reeves and Katona (1980) pointed out that belugas undertake seasonal migrations of as much as 2000 km. It is therefore possible that, in early Yorktown time, the beluga frequented coastal waters of what is now North Carolina in winter months, moving northward during the summer. With the onset of warming between 3.15 and 2.8 Ma, winter temperaturers were too warm and the beluga could have abandoned middle latitudes.

Reeves and Katona (1980) suggested that, in addition to water temperature, competition for food may be a factor limiting the beluga to boreal waters. They pointed out that, along the North Atlantic continental shelf and in adjacent deeper waters, the beluga must compete for food with dolphins, pilot whales, and seals. They speculated that such competition may have helped drive the beluga to a more northerly range. This hypothesis is not borne out by the Lee Creek fossil assemblage, in which belugas are numerous and apparently contemporary with the postulated competing species.

PLEISTOCENE CETACEA OF THE NORTH ATLANTIC

The fossil record of Pleistocene Cetacea in eastern North America is poor. The only extensive record is for the very late Pleistocene of the Champlain Sea, the precursor of the St. Lawrence River and Lake Champlain (Harington 1988). Belugas are very common in this assemblage. Also present are finback (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), and bowhead (*Balaena mysticetus*) whales, but belugas were relative latecomers. The Mysticeti have been dated at ca. 11.5 Ka; the beluga at ca. 10.5 Ka (Harington 1988).

The record of Pleistocene Cetacea in the eastern North Atlantic is also sparse. Isolated ear bones of balaenopterids and balaenids have been reported from the Red Crag of England and its equivalents in Belgium (Owen 1846: 543; Lydekker 1915). Although the Red Crag is regarded as early Pleistocene (Mitchell et al. 1973), it also contains reworked fossils as old as Eocene.

A strange omission in the fossil record is the almost complete absence of precursors of the living gray whale, *Eschrichtius robustus*. As mentioned above, an undescribed skull from the Yorktown Formation of North Carolina shows some features characteristic of the Eschrichtiidae. This specimen cannot, however, be assigned to the genus *Eschrichtius*. The only well-established fossil record of *Eschrichtius* is from the late Pleistocene of California (Barnes and McLeod 1984). Mead and Mitchell (1984) recorded subfossil gray whales from North Atlantic shores (see also van Deinse and Junge 1937) and reported C^{14} age determinations on subfossil specimens ranging from 10,140 ± 125 to 320 years B.P. Apparently, despite the lack of Pleistocene evidence, gray whales were established in the North Atlantic in Holocene time.

CONCLUSIONS

Cooling, steepened temperature gradients, and altered circulation patterns in the North Atlantic Ocean coincided, between about 11 and 4 Ma, with the establishment there of the modern whale fauna. The pioneer members of the fauna, present before the beginning of the late Miocene–Pliocene cooling trend, were the Physeteridae and Ziphiidae (sperm and beaked whales). The establishment of a current and temperature regime dominated by cold water, increasing the availability of plankton, opened the way for large baleen whales, especially balaenopterids (rorquals and humpbacks), including *Balaenoptera*, the only living mysticete genus to have undergone adaptive radiation. Later, as more prey opportunities arose, the Delphinidae began their own adaptive radiation, which may still be going on. These stages represent a continuing process of partitioning the pelagic resource base.

ACKNOWLEDGMENTS

I particularly thank Richard H. Benson for discussions that helped establish the theme of this paper. Lucy E. Edwards helped bring me up to date on North Atlantic paleooceanography, and she and Thomas M. Cronin gave helpful reviews of the manuscript. I thank Mark Holmes and Michael Gottfried for help in preparing Fig. 1, and Harry J. Dowsett for permission to use Fig. 2.

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Miocene Cetaceans of the Chesapeake Group

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ABSTRACT.—The Chesapeake Group of the mid-Atlantic coastal plain of North America consists of nearshore marine sediments that range in age from late Oligocene to Pliocene. The lower to upper Miocene portion of the Chesapeake Group is divided into four formations—in ascending order, the Calvert, Choptank, St. Mary's, and Eastover—which contain a rich and diverse cetacean fauna. General trends within the fauna of these four Miocene formations include the absence of cetotheriid-grade mysticetes in the lower Calvert, absence of squalodontid odontocetes above the Calvert, and an overall reduction in cetacean diversity and total numbers in the post-Calvert formations (possibly associated with environmental changes). Peak diversity and total numbers occur in the upper third of the Calvert, where the dominant forms are long-snouted rhabdosteid odontocetes and cetotheriid-grade mysticetes. Major differences between the cetaceans of the Miocene portion of the Chesapeake Group and the Recent northwestern Atlantic Ocean include the absence of delphinids and large mysticetes and the presence of long-snouted dolphins in the Miocene. Bones of relatively young cetaceans are common in the Miocene Chesapeake Group deposits, probably reflecting the expected high mortality of young individuals, rather than suggesting that the Chesapeake region was a cetacean breeding/calving ground during the Miocene.

INTRODUCTION

The Chesapeake Group deposits of the mid-Atlantic coastal plain of North America have long been known as one of the world's richest accumulations of late Tertiary marine fossils. Originally called the "Chesapeake Formation" (Darton 1891), the Chesapeake Group (terminology first adopted by Dall and Harris 1892) encompasses upper Oligocene through Pliocene marine claystones, mudstones, siltstones, and sandstones from the Atlantic coastal plain of Delaware, Maryland, Virginia, and North Carolina. According to Ward (1985), the Chesapeake Group consists of the following seven formations (see Fig. 1):

Chowan River Formation	upper Pliocene
Yorktown Formation	upper to lower Pliocene
Eastover Formation	upper Miocene
St. Mary's Formation	upper to upper middle Miocene
Choptank Formation	middle Miocene
Calvert Formation	lower middle to lower Miocene
Old Church Formation	lower Miocene to upper Oligocene

Extensive exposures in the Chesapeake Bay region of the Calvert, Choptank, St. Mary's, and Eastover formations, and the abundance of fossil remains, combine to make this part of the Chesapeake Group sequence the best record of Miocene marine life available from eastern North America. Both marine and (less frequently) terrestrial fossils are found, allowing for extraregional correlations with terrestrial and marine sequences from other localities (e.g., Wright and Eshelman 1987). The biota includes palynomorphs, diatoms, terrestrial plants, foraminifers, sponges, annelid worms, corals, abundant and diverse bivalves and gastropods, scaphopods, and a nautiloid, decapod crustaceans, barnacles, an inarticulate brachiopod, echinoderms, abundant sharks and rays, bony fishes, sea turtles and rarer terrestrial turtles, crocodiles, seabirds, occasional land mammals, sirenians, seals, and, rather commonly, cetaceans. General summaries of the geology and paleontology of the Miocene portion of the Chesapeake Group were provided by Clark et al. (1904), Vogt and Eshelman (1987), Ward and Powars (1989), and Ward (1992).

Fossil cetaceans from the Chesapeake Group deposits have been of special interest since the pioneering days of North American paleontology. Explorers and naturalists noted cetacean remains in the Chesapeake region as early as the 17th century (Simpson 1942, Ray 1983). The first formal scientific name assigned to a Chesapeake Group cetacean was *Delphinus calvertensis* Harlan, 1842, among the earliest vertebrate fossils from North America to be formally described (Simpson 1942). Harlan described a specimen (Fig. 2) from the well-known Calvert Cliffs section along the western shore of Chesapeake Bay in southern Maryland. This taxon was later removed from *Delphinus* and placed into *Pontoporia* (Cope 1866) and then *Lophocetus* (Cope 1868c), and was eventually redescribed by Eastman (1907), a history that appropriately symbolizes the taxonomic complications arising from much of the earlier research on Chesapeake Group cetaceans.

Since Harlan's 1842 publication, many prominent paleontologists, including Leidy, Cope, Gill, Eastman, True, Abel, Hay, Case, and most notably Kellogg, have studied Miocene cetaceans from the Chesapeake Group. The bulk of this research has focused on describing new taxa, with comparatively little in the way of more general comparisons and syntheses [see Case in Clark et al. (1904), Kellogg and Whitmore (1957), Kellogg (1957, 1966, 1968), and Whitmore (1971) for earlier general discussions].

This paper enlarges on previous studies of one of the world's richest deposits of fossil cetaceans by providing an overview of Miocene Chesapeake Group cetaceans, including the geologic and paleoenvironmental setting, overall taxonomic diversity, major faunal trends, comparison with modern cetacean assemblages, and aspects of Miocene cetacean paleobiology. We focus on the four formations (see above) that constitute the Miocene portion of the Chesapeake Group; the upper Oligocene to lower Miocene Old Church Formation (named by Ward 1985) is not included because it has not been extensively investigated and to date has not produced significant vertebrate remains. The cetacean fauna of the Pliocene Yorktown Formation is discussed separately (Whitmore 1994, this volume).

GEOLOGICAL AND PALEOENVIRONMENTAL SETTING

Geology of the Miocene Chesapeake Group formations.—The most extensive exposures of the Miocene formations within the Chesapeake Group are found in the Calvert Cliffs (Fig. 3), which extend for approximately 50 km along the western shore of Chesapeake Bay in Calvert and southernmost Anne Arundel counties, southern Maryland; other important localities are found along the

In A. Berta and T. A. Deméré (eds.)
Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.
Proc. San Diego Soc. Nat. Hist. 29:229–238, 1994

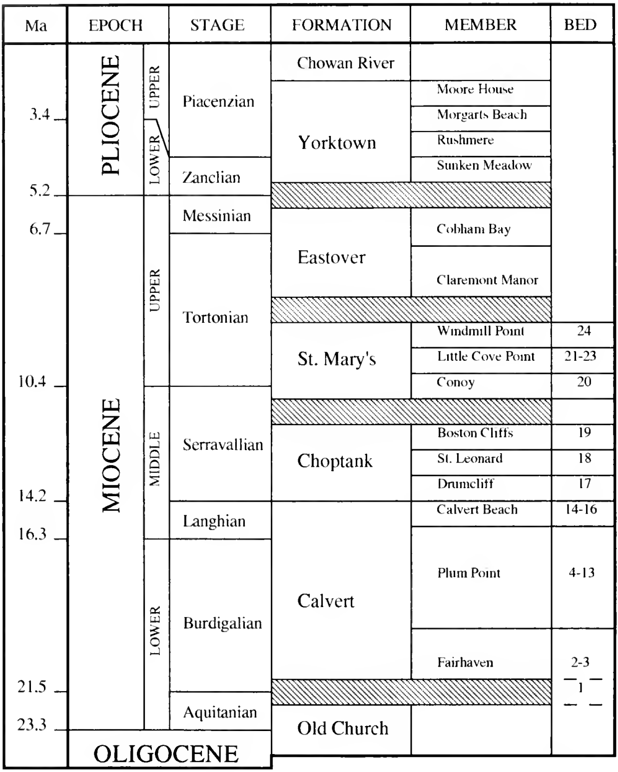

Figure 1. Composite stratigraphy of formations constituting the Chesapeake Group, modified after Wright and Eshelman (1987) and Ward (1992). Dates in million years ago (Ma) in left-hand column are at stage boundaries, from Harland et al. (1990). Position of stage boundaries relative to Chesapeake Group formations is approximate; note also that the Eastover Formation extends as far down as 11 Ma according to Ward and Blackwelder (1980) and Andrews (1986).

Maryland and Virginia sides of the Potomac River and in tidewater Virginia (Fig. 4). A newly discovered lower Calvert Formation site in Delaware has produced a more terrestrially influenced fauna than is typical for the Calvert Formation (Ramsey et al. 1992).

Shattuck (1902) subdivided the Chesapeake Group in Maryland into the Calvert, Choptank, and St. Mary's formations; he later (in Clark et al. 1904) divided the three formations into 24 "zones," with "zone" 1 at the base of the Calvert (which lies unconformably above the Eocene Nanjemoy Formation in much of the region) and "zone" 24 at the top of the St. Mary's. Ward (1985) placed Shattuck's "zone" 1 in the Old Church Formation, but later (Ward 1992) maintained that it was a "distinct unit, younger than the Old Church" (p. 5). In the most recent treatment of these formations the Calvert Formation extends up through "zone" 16, the Choptank includes "zones" 17–19, and the St. Mary's includes "zones" 20–24 (Ward 1992). Shattuck's "zones" are based on changes in lithology, as well as relative abundances—but not unique assemblages—of mollusks; because they are not biostratigraphic zones in the strict sense, we refer to Shattuck's 24 divisions as beds, following Gernant et al. (1971), Wright and Eshelman (1987), and Ward

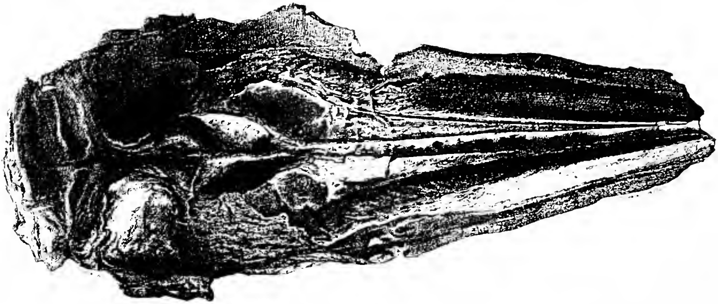

Figure 2. *Lophocetus calvertensis* holotype skull (USNM 16314), in dorsal view. Reproduction of the figure in Harlan's (1842) original description of this specimen as *Delphinus calvertensis*.

(1992). The 24 divisions, however they are referred to, remain useful because they have become the traditional means of indicating relative stratigraphic position within most of the Miocene portion of the Chesapeake Group (Fig. 1). Some of the beds or "zones" have been combined and renamed as members (Fig. 1), as summarized by Ward and Powars (1989) and Ward (1992). Ward (1992) also divided the entire Chesapeake Group into 19 depositional events, with each depositional event representing a unique transgressive depositional episode, and named eight molluscan zones within the Miocene portion of the Chesapeake Group.

The Eastover Formation, the youngest Miocene formation within the Chesapeake Group, was not recognized at the time of Shattuck's 1904 study, and it has not been incorporated into the framework of the 24 divisions first laid out by Shattuck. The Eastover Formation was named by Ward and Blackwelder (1980) and includes beds referred to as the "Virginia St. Mary's" in earlier literature of this century. The formation lies stratigraphically above the St. Mary's and below the Pliocene Yorktown Formation (Fig. 1).

According to Vogt and Eshelman (1987), the Miocene sediments of the Chesapeake Group were deposited as part of a complex package representing a first-order transgressive/regressive cycle with numerous superimposed smaller-scale perturbations of sea level. The deposits formed in inner shelf to marginal marine conditions associated with the Salisbury Embayment, a Miocene depocenter that was one of a series of embayments along the mid-Atlantic coast of North America during this time (see Ward and Powars 1989). Maximum transgression of the Salisbury Embayment occurred during Calvert time, with the extent of the embayment becoming reduced during deposition of the sediments that constitute the Choptank and St. Mary's formations (Ward and Powars 1989).

Fine sandstones, siltstones, mudstones, claystones, and occasional diatomite beds are represented in the Miocene Chesapeake Group. The thickness and lithic and biotic composition of the beds vary considerably. The reasons for this variation may include a trend toward shoaling and climatic cooling, concurrent uplift of the Atlantic Coastal Plain, uneven subsidence of the Atlantic Coastal Plain, and eustatic changes in sea level (Vogt and Eshelman 1987, and references therein). The highly fossiliferous shell beds have been interpreted variously as being formed by single brief episodes of rapid accumulation, high natural population levels, or relatively slow sedimentation rates (Kidwell 1982a,b; Kidwell and Jablonski 1983; Vogt and Eshelman 1987).

Age of the deposits.—The Miocene age of the portion of the Chesapeake Group we address is well established and has been recognized since the early researches of Rogers (1836) and Lyell (1845). Correlation of the local deposits with other marine sequences is difficult because the Chesapeake Group sediments were deposited in relatively shallow water, so the planktonic foraminifera that are the primary basis for the global marine microfossil zonations are often lacking. Microfossil studies, based on foraminifera and diatoms (summarized by Vogt and Eshelman 1987), corroborate the Miocene age of the formations being considered here. This is further supported by the land mammal fauna, which Wood et al. (1941), Gazin and Collins (1950), Tedford and Hunter (1984), and Wright and Eshelman (1987) all regarded as indicating a Hemingfordian to Barstovian age for the Calvert and Choptank formations. The only three radiometric dates (based on glauconite) obtained for the Miocene of this region (Blackwelder and Ward 1976) suggest late middle and late Miocene ages for the St. Mary's and Eastover formations, respectively. While additional radiometric, microfossil, and land mammal data could prove helpful in refining the formations' ages, enough information is available to bracket the absolute age of the Eastover through Calvert formations as ranging from ca. 6.5 to ca. 20 Ma (see Fig. 1). The duration of possible missing intervals (due to erosion or nondeposition) has not been accurately estimated; according to Vogt and Eshelman (1987) the long-term accumulation rate for the Chesapeake Group in Maryland averages 15 m/Ma.

Paleoclimate.—There is general consensus that the Chesapeake Bay region was somewhat warmer during Calvert time than it is presently, and gradually cooled during deposition of the younger Miocene formations. Leopold (1970), as discussed by Whitmore (1971), pointed out that the palynological record of the Chesapeake Group during Calvert time suggests a warm-temperate terrestrial flora with some subtropical elements, similar to the coastal environment of the Carolinas today, succeeded during Choptank time by a slightly cooler warm-temperate climate and a still cooler but temperate regime, similar to the current climate of this region, during deposition of the St. Mary's Formation. A more recent palynologi-

Figure 3. View north along typical Calvert Cliffs exposures through the the Miocene portion of the Chesapeake Group, western shore of Chesapeake Bay, Calvert County, Maryland (locality 1, Fig. 4). Arrows indicate boundary between Choptank (below) and St. Mary's formations.

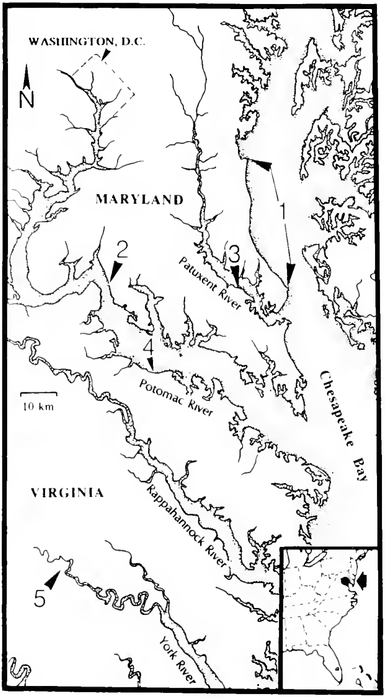

Figure 4. Mid-Chesapeake Bay region of Maryland and Virginia, showing major collecting sites for Miocene Chesapeake Group cetaceans. 1, Calvert Cliffs, Calvert and Anne Arundel counties, Maryland (the cliffs extend between the arrows for ca. 50 km); 2, Popes Creek, Charles County, Maryland; 3, Drum Cliff (and other nearby localities) along the Patuxent River, St. Mary's, Calvert, and Charles counties, Maryland; 4, Stratford and Horsehead cliffs, Westmoreland County, Virginia; 5, Exposures along the upper reaches of the Pamunkey River, Hanover, Caroline, and King William counties, Virginia.

cal study (de Verteuil 1986) generally agrees with this scenario and found that dinocyst assemblages in the Calvert and Choptank formations were dominated by estuarine and estuarine–neritic taxa indicating a subtropical to warm temperate climate. De Verteuil (1986) also inferred cooling during the late Miocene from the increasing proportion of *Pinus*. The vertebrate fauna is consistent with this interpretation in that indicators of a warm climate—sirenians and a gopher turtle—are found in the Calvert Formation (Whitmore 1971). Müller (1992) postulated a relatively sharp temperature decrease in the late middle Miocene on the basis of a shift to a cooler-water fish fauna during St. Mary's time.

DIVERSITY OF CHESAPEAKE GROUP CETACEANS

Overview.—The Chesapeake Group deposits contain one of the world's richest and most diverse assemblages of fossil cetaceans. This summary of the Miocene part of that record is based on the extensive holdings of fossil cetaceans at the National Museum of Natural History (USNM) and specimens from the Calvert Marine Museum (CMM) collection. The long history of research on Chesapeake Group cetaceans carries with it a tradition of confusing nomenclatural problems, suspect and erroneous taxonomic assignments, and new taxa erected on the basis of nondiagnostic incomplete specimens. These practices were prevalent during but not exclusive to the time of Leidy, Cope, and their contemporaries and immediate successors. A significant portion of this taxonomic disarray was addressed by Kellogg in a series of papers between 1923 and 1969; however, many problems still remain. It is not the intent of this paper to undertake a systematic revision of Miocene Chesapeake Group cetaceans—in this review we have focused only on those forms whose taxonomic validity we consider well-established.

To date, some 45 generic names have been applied to Miocene cetaceans from the Chesapeake Group. We provisionally consider 25 of these to be well-substantiated (Table 1); material that is yet assigned only to the families Ziphiidae and Balaenopteridae suggests at least two other genera. These Miocene genera include 16 or 17 odontocetes (about two-thirds of the total) and 9 or 10 mysticetes. The odontocete

Table 1. Miocene Cetaceans from the Chesapeake Group.

Taxon	Occurrence[a]
Order Odontoceti	
Family Squalodontidae	
Squalodon calvertensis	Cal
Squalodon cf. *S. tiedemani*	Cal
Family Platanistidae	
Zarhachis flagellator	Cal
Zarhachis sp. or *Pomatodelphis inaequalis*	Cal, Ch
Zarhachis sp.	StM
Family Rhabdosteidae	
Eurhinodelphis bossi	Cal
Rhabdosteus latiradix	Cal
Family Squalodelphidae	
Phocageneus venustus	Cal
Notocetus sp.	Cal
Family Kentriodontidae	
Kentriodon pernix	Cal
"Delphinodon" dividum	Cal
Liolithax pappus	Cal
Hadrodelphis calvertense	Cal, Ch?
Lophocetus calvertensis	StM
Kentriodontid indet.	Ch, StM, Ea
Family Physeteridae	
Orycterocetus crocodilinus	Cal, Ch
Orycterocetus mediatlanticus	StM
Physeterid indet.	StM
Family Ziphiidae	
Ziphiid indet.	Ch?
Odontoceti incertae sedis	
Tretosphys gabbi	Cal
Araeodelphis natator	Cal
Pelodelphis gracilis	Cal
Order Mysticeti	
Family "Cetotheriidae"	
Parietobalaena palmeri	Cal
Mesocetus siphunculus	Cal
Diorocetus hiatus	Cal, Ch
Aglaocetus patulus	Cal, Ch
Pelocetus calvertensis	Cal, Ch
Thinocetus arthritus	Ch
Halicetus ignotus	Ch
Cetotherium sp.	StM
Cephalotropis coronatus	StM
Family Balaenopteridae	
Balaeonopterid? indet.	Ea

[a] Cal, Calvert Formation; Ch, Choptank Formation; StM, St. Mary's Formation; Ea, Eastover Formation.

outnumbering the mysticete genera is in keeping with, but not quite as pronounced as, the overall pattern seen in the fossil record and among Recent cetaceans. Worldwide, 76% of all fossil cetacean genera are odontocetes (128 odontocetes vs. 41 mysticetes; Carroll 1988), whereas 84% (32 odontocetes vs. 6 mysticetes) of all living genera are odontocetes (Leatherwood et al. 1983).

The relatively high proportion of mysticete genera in the Chesapeake Group Miocene, as compared to the overall pattern among all fossil cetaceans and Recent forms, has several potential explanations. These include possible collecting bias, environmental bias resulting from ancient habitats that favored mysticetes, or artificially high diversity resulting from taxonomic oversplitting. Another possible factor is the high post-Miocene diversity of odontocetes (at least 10 odontocete genera first appear after the Miocene), whereas Miocene mysticetes were relatively diverse, owing to the early "cetothere" radiation.

The Miocene Chesapeake Group mysticetes that have been described in the literature have typically been assigned to the "Cetotheriidae," a catch-all category into which the majority of primitive and relatively small Tertiary mysticetes have been placed. The forms traditionally classified as "cetotheres" are in serious need of detailed taxonomic revision, and monophyly of the family has yet to be corroborated by shared derived features. The lack of a rigorous phylogenetic analysis that includes cetotheriid-grade mysticetes undermines efforts to study the early evolutionary history of the baleen whales.

The following section summarizes the cetacean fauna known to date from each of the four Miocene formations of the Chesapeake Group. References are given for the original description and subsequent important papers dealing with the named species; catalog numbers from the Calvert Marine Museum and National Museum of Natural History collections are provided for pertinent specimens that have not been published.

Calvert Formation cetaceans.—The Calvert Formation has the highest vertebrate diversity as well as the greatest thickness and extent of the formations within the Miocene portion of the Chesapeake Group. The most phylogenetically primitive of the Calvert odontocetes is the squalodontid *Squalodon calvertensis* Kellogg, 1923 (Fig. 5A). An additional larger species referred to *S. tiedemani* Allen, 1887, is also present (A. Dooley, pers. comm.).

The dominant odontocetes in terms of number of specimens are the long-snouted rhabdosteid dolphins *Eurhinodelphis* and *Rhabdosteus*. Kellogg (1955) held that *Rhabdosteus latiradix* Cope, 1868a (also see Cope 1868b; True 1908b), is the most common odontocete in the Calvert; however, computerized records of the USNM collection suggest that *Eurhinodelphis* may be more common, while Myrick (1979) maintained that the two genera are roughly equal in numbers of specimens. *Eurhinodelphis bossi* Kellogg, 1925b, is the only formally described species within the genus from the Calvert; Kellogg originally (1924c) implied the presence of additional taxa, but not in subsequent papers. Myrick (1979) distinguished 10 or 11 rhabdosteid species from the Calvert Formation; however, descriptions of these have not been published.

Muizon (1988) considered *Rhabdosteus* a *nomen dubium* and instead referred specimens from the Maryland Miocene that had been assigned to that genus to the European form *Schizodelphis*, a conclusion he reached after studying the type material of *Schizodelphis*. *Schizodelphis* had been previously reported from the Calvert fauna by True (1908a), who referred *Priscodelphinus crassangulum* Case, 1904, to *Schizodelphis*. Bohaska is currently reinvestigating the issue of whether or not *Schizodelphis* occurs in the Maryland Miocene (and in Florida); until that study is completed we consider North American records of *Schizodelphis* questionable and therefore have not included it on our list of Calvert Formation genera.

In addition to the rhabdosteids, the long-snouted possible platanistoid *Zarhachis* is also present in the Calvert. Kellogg (1924a, 1926) referred specimens from the lower Calvert to *Z. flagellator* Cope, 1868c. A possible second species of this genus, or perhaps the related form *Pomatodelphis inaequalis* Allen, 1921 (see Kellogg 1959), also occurs in the upper Calvert (USNM 11343, 24868, 25168, 205302).

A relatively diverse assemblage of shorter-beaked kentriodontid odontocetes has been reported from the Calvert Formation. The largest of these is *Hadrodelphis calvertense* Kellogg, 1966, originally described on the basis of a single pair of associated partial dentaries and now known from a complete skull, lower jaws, and associated skeleton (CMM-V-11). This large odontocete likely reached a length of over 4 m. Dawson (1992) has been studying the associated CMM material and is preparing a revision of the genus. The rarity of *Hadrodelphis* in the Chesapeake Group may relate to its being a pelagic taxon and therefore not as common in the coastal Salisbury Embayment environments as the more nearshore-adapted long-snouted forms.

Figure 5. A, Squalodontid odontocete *Squalodon calvertensis*, cast of skull of USNM 206288, ×0.20. (B) Cetotheriid-grade mysticete *Parietobalaena palmeri*, USNM 24883, skull and lower jaws, ×0.15. Both specimens on exhibit at the Calvert Marine Museum.

Smaller kentriodontids in the Calvert include *Delphinodon dividum* True, 1912, and *Kentriodon pernix* Kellogg, 1927, each well-represented by fairly complete specimens; Kellogg (1957) questioned whether "*D.*" *dividum* was properly assigned to that genus. Somewhat rarer than these is a medium-sized form originally named *Lophocetus pappus* Kellogg, 1955, which was revised and placed into the genus *Liolithax* by Barnes (1978).

The largest odontocete, and the largest cetacean recorded from the Calvert Formation, is the physeterid *Orycterocetus crocodilinus* Cope, 1868b (discussed in some detail by Kellogg, 1965). Unlike Recent sperm whales, this Miocene form retained functional teeth in its upper jaws.

Other, relatively poorly known Calvert Formation odontocetes have been assigned to the Squalodelphidae, including *Phocageneus venustus* Leidy, 1869 (more complete material of this taxon was discussed by Kellogg in 1957), and *Notocetus* sp. (Muizon 1987). Three additional forms have to date been placed only as Odontoceti incertae sedis: *Tretosphys gabbi* Cope, 1868c (restudied from additional remains by Kellogg, 1955), *Pelodelphis gracilis* Kellogg, 1955; and *Araeodelphis natator* Kellogg, 1957. These species are all represented by relatively limited material with no well-preserved skulls known.

Nominal mysticetes from the Calvert Formation have almost all been placed in the "Cetotheriidae," which as previously discussed is a problematic grade-level assemblage. The most common Calvert mysticete is *Parietobalaena palmeri* Kellogg, 1924b (see Fig. 5B and Kellogg 1968), which is the smallest of the Maryland Miocene baleen whales (adult length approximately 4 to 5 m). Other "cetotheres" from the Calvert include *Diorocetus hiatus* Kellogg, 1968, *Aglaocetus patulus* Kellogg, 1968, *Mesocetus siphunculus* Cope, 1895 (redescribed by Kellogg 1968), and *Pelocetus calvertensis* Kellogg, 1965 (the largest form, length 7–8 m).

Although no non-cetotheriid-grade mysticetes have been definitively reported from the Calvert Formation, *Eschrichtius cephalum* Cope, 1868a (which is not a gray whale, despite Cope's assigning it to what is now considered the proper genus for gray whales; see Barnes and MacLeod 1984) is a large, possibly balaenopterid mysticete represented by a single partial skeleton (Kellogg 1968) that has been considered Miocene in age. However, the stratigraphic position of this material is unclear, and Cope's precise locality is uncertain. It is possible that the specimen was collected from a Pliocene deposit, which would be more consistent with the relative abundance of balaenopterids in the Pliocene Yorktown Formation exposures of Virginia and North Carolina. In addition, a typically Pliocene mustelid was apparently collected at the same site (Ray et al. 1981). For these reasons we continue to regard the occurrence of balaenopterid mysticetes in the Calvert Formation as unsubstantiated.

Choptank Formation cetaceans.—The Choptank Formation is not as thick or extensive as the Calvert and cetacean (and other vertebrate) specimens are markedly fewer and less diverse than in the Calvert Formation. In Shattuck's original division (in Clark et al. 1904), the Choptank included beds (or "zones") 15 through 20, but more recently beds 15 and 16 have been placed in the Calvert Formation, and bed 20 has been transferred to the St. Mary's (Ward and Strickland 1985; Ward 1992). Beds 17, 18, and 19, currently considered to constitute the Choptank Formation, are sandier than the underlying Calvert Formation and may represent a shallow-shelf open-marine setting rather than the nearshore depositional setting proposed for the Calvert (Ward and Powars 1989). This environmental shift may be at least partially responsible for the decrease in number and diversity of cetacean specimens in the Choptank.

Choptank odontocetes include a long-snouted taxon (or taxa) identifiable as either *Zarhachis* sp. or *Pomatodelphis inaequalis*.

This long-snouted material has been recovered from bed 17 of the Choptank (USNM 13768, 187414, 206000), and the same form may also occur in beds 10 and 12 of the Calvert Formation. The two most conspicuous long-snouted genera in the Calvert Formation, *Eurhinodelphis* and *Rhabdosteus*, have not been recovered from the Choptank.

A large kentriodontid is known from one skull (CMM-V-15) found in bed 17 of the Choptank. A small as yet undescribed kentriodontid, probably *Kentriodon pernix*, is also present in bed 17, on the basis of a periotic (CMM-V-239). A section of a large physeterid mandible has also been collected from the Choptank (USNM 16552).

The only ziphiids known from the Chesapeake Group are three partial rostra (USNM 412120, 412124, 425487), presumably all from the Choptank Formation. None of these ziphiid specimens were found *in situ*, but all were collected along the southern (geologically younger) end of Calvert Cliffs in Calvert County, Maryland, several kilometers from any Calvert Formation outcrops, and vertebrates are quite rare in the overlying St. Mary's Formation in this area. It is likely therefore that the ziphiid specimens are out of the Choptank Formation. Whitmore et al. (1986) discussed the association of ziphiids with offshore upwelling zones, phosphorites, and large squid populations (a primary food source for extant ziphiids). The absence of ziphiids in the Calvert and their scarcity in the Choptank may be an environmental artifact in that the Salisbury Embayment was not an environment pelagic enough to support a substantial ziphiid population.

The mysticete record of the Choptank Formation includes two forms not known from the Calvert, *Thinocetus arthritus* Kellogg, 1969, and *Halicetus ignotus* Kellogg, 1969. Other cetotheres from the Choptank include the genera *Pelocetus*, *Diorocetus*, and *Aglaocetus* (all also known from the Calvert). Although the number of specimens is smaller, the diversity of mysticetes in the Choptank Formation is about the same as in the Calvert (see Table 1).

St. Mary's Formation cetaceans.—The St. Mary's Formation is now considered to include beds 20 through 24 from Shattuck's original division of the Chesapeake Group (Ward 1992). Outcrops referred to in the older literature as the "Virginia St. Mary's" pertain mainly to the Eastover Formation (Blackwelder and Ward 1976, and below), although there are St. Mary's sites along the rivers of the coastal plain of Virginia. Exposures of the St. Mary's are not as extensive as those of either the Calvert or Choptank and are poorer in vertebrate remains.

St. Mary's Formation cetaceans are relatively scarce and not as diverse as those from the Calvert or the Choptank. Long-snouted dolphins are represented by a possible third Chesapeake Group Miocene species of *Zarhachis* or a related form, based on four specimens (USNM 22500, 214759, 447490, 464067). The only kentriodontid described from the St. Mary's is the historically important *Lophocetus calvertensis* (Harlan, 1842) (Fig. 2), still known only from the holotype specimen. Much of the material of the relatively small odontocetes from the St. Mary's Formation is incomplete and relatively undiagnostic, and probably includes specimens of kentriodontid and/or delphinoid affinities.

Physeterids from the St. Mary's include a skull of *Orycterocetus mediatlanticus* Cope, 1895, restudied by Kellogg (1925a). Isolated sperm whale teeth include a specimen (USNM 464139) with an enamel crown similar to that seen on the European and Australian genus *Scaldicetus*. One additional very large tooth (USNM 167608) is comparable in size but not in morphology to teeth of the extant sperm whale, *Physeter catodon*. Clearly, significantly more attention needs to be paid to fossil physeterids from the Miocene Chesapeake Group.

"Cetotheres" have also been recovered from the St. Mary's Formation. A number of undescribed skulls have been collected by watermen dredging for oysters in Chesapeake Bay—such specimens often include enough adhering matrix to reveal their geologic context. Baum and Wheeler (1977) assigned vertebrae and a mandible from the St. Mary's in Virginia to Cope's (1895) "cetothere" genus *Siphonocetus*; Kellogg (1968) implied that material assigned to this genus actually pertains to *Cetotherium*. An additional "cetothere," *Cephalotropis coronatus* Cope, 1896, is known from a skull out of the St. Mary's Formation.

Eastover Formation cetaceans.—The Eastover Formation was named by Ward and Blackwelder (1980) and includes upper Miocene beds overlying the St. Mary's and underlying the Pliocene Yorktown Formation. The molluscan fauna of the Eastover indicates a temperate climate cooler than the warm-temperate conditions that predominated lower in the Chesapeake Group section.

The Eastover Formation is not as well exposed as the formations lower in the section. In addition, relatively little attention has been paid to this formation, with the result that our knowledge of the Eastover fauna is still inadequate. Whitmore (1984) noted a large kentriodontid, which he considered close to *Kentriodon*, from an Eastover exposure near the Pamunkey River in Caroline County, Virginia. Whitmore also mentioned that bones of a "large mysticete" had been collected out of the Eastover along the Pamunkey River in New Kent County, Virginia. It has yet to be determined if these latter remains are from a large "cetothere" or if they represent a relatively early record of a balaenopterid mysticete.

DISCUSSION

Major temporal trends.—Several trends in the pattern of cetacean diversity and distribution through the Miocene portion of the Chesapeake Group are apparent. First, squalodontid odontocetes (represented by *Squalodon calvertensis* and *S.* cf. *S. tiedemani*), the most phylogenetically primitive odontocetes in the Chesapeake Group, persist only through the upper part of the lower-to-middle Miocene Calvert Formation. This is in keeping with the worldwide pattern of squalodontids becoming extinct partway through the Miocene as more derived odontocetes appear (Barnes et al. 1985).

A somewhat unexpected situation exists with regard to the first appearance of "cetotheres" in the Calvert Formation. The oldest known "cetotheres" from the Calvert were collected from bed 8; no specimens are known from the lower part (beds 1–7) of the Calvert, which is late early to early middle Miocene and contains several species of odontocetes. "Cetotheres" are known from lower Miocene and Oligocene deposits in Europe, New Zealand, and South America (Barnes et al. 1985), so their absence from a richly fossiliferous lower-to-middle Miocene marine deposit is somewhat surprising. It is not possible to determine whether this reflects collecting bias, environmental bias, or an actual pattern of Miocene mysticete distribution, but it would not be surprising if "cetothere" remains were eventually found in the lower beds of the Calvert Formation.

Perhaps the most striking pattern observed is the decline in diversity (see Table 1) and number of specimens above the Calvert Formation. Maximum diversity is reached in the upper part of the Calvert Formation, centered around beds 12 to 14, which together contain 17 genera. In comparison, the most diverse post-Calvert assemblage is bed 17 of the Choptank Formation, which has produced about seven genera to date. This decline in diversity may be connected to cooling and general climatic deterioration, or it may be an artifact of facies changes, the post-Calvert sediments apparently being deposited in somewhat more open marine settings, with a less diverse cetacean fauna, than those of the Calvert Formation. It may also reflect a real change in the diversity of cetaceans along the mid-Atlantic coast of North America during the latter half of the Miocene.

Comparison with Recent cetacean assemblages.—Chesapeake Group cetaceans reach their highest diversity in the upper Calvert Formation, where they are comparable to modern cetaceans in total diversity and in the variety of forms represented. The upper Calvert includes at least 5 mysticete and 12 odontocete genera; in comparison, the Recent cetacean assemblage in the northwest Atlantic Ocean consists of 4 mysticete and 20 odontocete genera (Leatherwood et al. 1976). The total number of genera (17 in the upper Calvert versus 24 Recent) suggests that the cetacean record from this interval of the Chesapeake Group provides a reasonable approximation of cetacean diversity in the northwestern Atlantic Ocean during the middle Miocene.

Among the major size classes of cetaceans, only large mysticetes of modern aspect are missing from the Miocene portion of the Chesapeake Group. It is possible that balaenopterids first appeared in the region near the end of the Miocene, as suggested by the Eastover Formation material discussed by Whitmore (1984), but they have yet to be identified definitively, and it is clear that relatively small and primitive cetotheriid-grade mysticetes were the dominant baleen whales in the Chesapeake region during the Miocene. Balaenopterids did not become well-established in the northwest Atlantic until the Pliocene (see Whitmore 1994, this volume). Also missing from the Miocene Chesapeake Group deposits are delphinids, the open-ocean dolphins that today constitute the most diverse and abundant group of odontocetes, and phocoenids, the porpoises.

Paleobiological considerations.—Past authors, including Kellogg (1966, 1968), Whitmore (1971), and Vogt and Eshelman (1987), have speculated that the relative abundance in the Chesapeake Group of cetacean bones with unfused epiphyses and of skulls with incompletely closed sutures indicates that the Salisbury Embayment was the site of a breeding and/or calving ground for Miocene cetaceans. Kellogg (1966:67) summarized this view as follows: "The presence of such a preponderance of immature or young marine mammals suggests that this region was the calving ground for the mysticetes, the sperm whales and probably some of the smaller odontocetes." This idea has become firmly entrenched in the popular literature and among fossil collectors active in the Chesapeake Group.

We find several problems with this scenario. First, skeletal fusion of the cetaceans studied to date is not completed until after sexual maturity. Mead and Potter (1990) provided evidence that bottlenose dolphins become reproductively active at six to eight years of age, whereas the epiphyses in their forelimb bones do not completely fuse until several years later. This suggests that lack of skeletal fusion is not a reliable indicator of a specimen's being a neonate or even a juvenile. Incompletely fused skeletons might well represent cetaceans that had reached sexual but not complete physical maturity.

Furthermore, thousands of stranding records compiled over many years show that the majority of stranded cetaceans are relatively young animals (up to two years old, J. G. Mead, pers. comm.) whose skeletons are not completely fused. Thus the apparent demographic skew of Chesapeake Group cetaceans may in fact reflect the normal mammalian pattern of high mortality rates in the younger age classes (as expected in a random sample) and is not an unusual or unexpected phenomenon requiring a special explanation.

Finally, there are no modern instances of several cetacean species breeding or calving in the same nearshore habitat. The only comparable modern example is the gray whale *Eschrichtius robustus*, which breeds in protected lagoons along the Pacific coast of Baja California, Mexico. However, this apparently specialized behavior is unique to gray whales among Recent cetaceans. It may be that the breeding/calving scenario concerning the Miocene Chesapeake Group cetaceans arose at least in part out of the earlier idea that "cetotheres" are ancestral to gray whales (as implied by Kellogg 1928) and therefore similar in certain habits. Barnes and MacLeod (1984) argued against a close gray whale–"cetothere" relationship and maintained that the evolutionary history of gray whales can be traced back only as far as the Pleistocene.

One well-substantiated aspect of Chesapeake Group cetacean paleobiology is that both mysticetes and odontocetes were preyed upon and/or scavenged by sharks. Cetacean bones regularly show linear grooves and gouges caused by shark bites during attacks and/or scavenging on carcasses. Deméré and Cerutti (1982) demonstrated that similar grooves on the mandible of a late Pliocene "cetothere" from San Diego, California, resulted from a shark attack or scavenging, probably by the Pliocene great white shark *Carcharodon sulcidens* Agassiz, 1843. More recently, Cigala-Fulgosi (1990) described and figured bite marks of a great white shark on the skeleton of a Pliocene dolphin from Italy. Similar grooves and gouges seen on Miocene cetacean bones from the Chesapeake Group can also be ascribed to sharks, whose teeth are common fossils in the region and which include the giant megatooth shark *Carcharodon* [= *Carcharocles* of some authors] *megalodon* (Charlesworth, 1837). *Carcharodon carcharias* (Linnaeus, 1758), the Recent species of great white shark, and other large sharks are also known to prey on marine mammals (Ames and Morejohn 1980; Leatherwood et al. 1983; Corkeron et al. 1987; Cigala-Fulgosi 1990).

FUTURE RESEARCH

This overview of Miocene Chesapeake Group cetaceans leads to some suggestions on where future research efforts might be concentrated to address problems that have not been resolved.

(1) More effort should go into elucidating phylogenetic interrelationships and classification of the mysticetes. The lack of any testable phylogenetic hypothesis of mysticete interrelationships that includes fossil taxa makes it difficult to discuss baleen whale evolution meaningfully and leaves unresolved the question of what, if anything, is a "cetothere."

(2) More collecting and research attention should be paid to cetaceans from the upper Miocene St. Mary's and Eastover formations to yield a better understanding of the transition from the mid-Miocene cetacean faunas, which include relatively primitive forms, to the Pliocene assemblages (discussed by Whitmore 1994, this volume), in which the modern families of cetaceans begin to dominate.

(3) The interrelationships of fossil and living long-snouted dolphins remain unclear despite a recent increase in attention (Muizon 1990, 1991; Messenger 1991). A better understanding of the phylogeny of these taxa is necessary for the relationship between living and fossil long-snouted dolphins to be assessed and for the position within the Odontoceti of the Miocene long-snouted forms to be resolved.

(4) Alpha-level taxonomic problems remain to be addressed. These include questionable species named by Cope that are overdue for reexamination and complicated synonymies that require unraveling. A stable classification and more firmly established phylogenetic hypotheses will be possible when these problems are better resolved.

ACKNOWLEDGMENTS

We thank J. G. Mead for graciously sharing the cetacean stranding data he has accumulated and for discussions of cetacean biology. R. E. Eshelman contributed a number of insightful comments and criticisms on the manuscript. The paper was substantially improved by the review of C. Repenning. H. Fink provided helpful editorial comments. We are grateful to A. Berta and T. A. Deméré for inviting us to participate in the SVP Marine Mammal Symposium and this volume. W. Ashby helped tabulate and analyze computerized records of the fossil cetacean holdings at USNM that were provided by M. Brett-Surman. D. Weller assisted with preparation of the figures. A special thanks goes to the many amateur collectors, too many to name here, whose skill, dedication, and generosity over the years is responsible for much of what we know about the cetaceans of the Chesapeake Group.

Financial support to Gottfried was provided by the Calvert County Board of Commissioners and the CMM Lincoln Dryden Fund, and to Bohaska by the Remington and Marguerite Kellogg Fund of the National Museum of Natural History, Smithsonian Institution.

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Miocene and Pliocene Marine Mammal Faunas from the Bone Valley Formation of Central Florida

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ABSTRACT.—Three faunas recovered from the Bone Valley Formation of central Florida contain marine mammals: the middle Miocene (late Barstovian) Bradley Fauna, the late middle Miocene (early Clarendonian) Agricola Fauna, and the early Pliocene (late Hemphillian) Palmetto Fauna. The ages of the Bone Valley faunas are based on diagnostic land mammals that have been correlated with the North American Land Mammal biochronology. Only three species of marine mammals occur in the Bradley Fauna, the dugongid sirenian *Metaxytherium floridanum*, the long-beaked dolphin *Pomatodelphis inaequalis*, and a "cetotheriid" mysticete. The slightly younger Agricola Fauna has a more diverse fauna composed of 12 species of cetaceans and two sirenians. The most abundant taxa are *M. floridanum*, *P. inaequalis*, *P. bobengi* new combination, and two species of "cetotheres." Less common taxa from the Agricola Fauna include a ziphiid, the physeterid *Scaldicetus*, the odontocetes *Hadrodelphis*, *Delphinodon* cf. *D. mento*, and cf. *Lophocetus*, two additional "cetotheres," and the dugongid *Dioplotherium allisoni*. Pinnipeds are absent from both the Bradley and Agricola faunas. The sirenians and cetaceans from the Agricola Fauna occur in fine-grained sediments that frequently preserve complete skulls and articulated skeletons. Fossils of marine mammals are rarer and more fragmentary in the Palmetto Fauna than in the Agricola Fauna, although the late Hemphillian assemblage is more diverse, consisting of nine cetaceans, a sea otter, four pinnipeds, and one sirenian. The most common marine mammals in the Palmetto Fauna are the small balaenopterid *Balaenoptera floridana*, the iniid *Goniodelphis hudsoni*, the physeterid *Physeterula*, and the large phocid *Callophoca obscura*, whereas rarer species include an undescribed pontoporiid, an unidentified delphinid, the ziphiids *Mesoplodon* sp. and *Ninoziphius platyrostris*, the physeterid *Kogiopsis floridana*, the giant otter *Enhydritherium terraenovae*, the odobenid *Trichecodon huxleyi*, the phocid *Phocanella pumila*, and the dugongid *Corystosiren varguezi*. The record of the Desmostylia from the Bone Valley Formation is probably erroneous, as it was apparently based on tooth fragments of *Desmostylus* from California. Comparisons of mammalian faunas from the Bone Valley Formation and the Chesapeake Group of the Atlantic Coastal Plain suggest correlation of the Bradley Fauna with the Choptank Formation, the Agricola Fauna with the St. Mary's Formation, and the Palmetto Fauna with the lower Yorktown Formation.

The early Hemphillian (late Miocene) was a transitional period during which *Metaxytherium*, *Pomatodelphis*, "cetotheres," and many other contemporaneous taxa went extinct in Florida, while *Enhydritherium terraenovae* and two families of mysticetes, the Balaenidae and Balaenopteridae, first appeared. The late Hemphillian of Florida is characterized by a rarity of sirenians and the presence of small balaenopterids such as *Balaenoptera floridana*, the probable freshwater dolphin *Goniodelphis hudsoni*, and the pinnipeds *Callophoca obscura* and *Trichecodon huxleyi*. Most late Hemphillian marine mammals from the Bone Valley Formation are unknown from younger faunas, although *Balaenoptera floridana*, *Trichecodon huxleyi*, and *Callophoca obscura* survived until the late Blancan (late Pliocene). The humpback whale *Megaptera* and large species of *Balaenoptera* first appeared in Florida during the late Pliocene. The origins of the modern marine mammal fauna of Florida are poorly understood because deposits of Pleistocene age are depauperate in marine mammals. None of the 30 species of modern marine mammals recorded from Florida waters are definitely known prior to the Pleistocene. The manatee *Trichechus manatus*, West Indian monk seal *Monachus tropicalis*, and false killer whale *Pseudorca crassidens* are known from the early Pleistocene (Irvingtonian) of Florida, but other extant species are either restricted to the late Pleistocene or have no fossil record in the state.

INTRODUCTION

The Bone Valley region of central Florida became known for its rich fossil vertebrate faunas shortly after phosphate mining commenced early in this century (Sellards 1915, 1916; Allen 1921). Vertebrate fossils are often abundant in the extensive open-pit phosphate mines of the Bone Valley region, located principally in southwestern Polk County, but also in adjacent southeastern Hillsborough County and northwestern Hardee County (Fig. 1). Phosphatic sediments of the Bone Valley Formation exposed in these mines have produced a sequence of Neogene vertebrate faunas (Fig. 2) dating from the middle Miocene (about 15 Ma) through the early Pliocene (4.5 Ma).

Stratigraphically collected samples of fossil vertebrates from the Bone Valley Formation are uncommon because phosphate mining entails excavating huge volumes of sediment with draglines. Fossils are most often found as isolated specimens on spoil piles or in hydraulic wells, the latter being areas where the phosphatic matrix is turned into a slurry for processing by means of jets of water under high pressure. However, during the past 25 years, field parties from the Florida Museum of Natural History, mining geologists, and avocational paleontologists have collected numerous fossil vertebrates from the Bone Valley Formation *in situ*, including faunas of middle Miocene (late Barstovian), late middle Miocene (early Clarendonian), and early Pliocene (late Hemphillian) age. Several *in situ* faunas of early middle Miocene (early Barstovian) age are also known from the Bone Valley region, although they are derived from the older underlying Arcadia Formation. Some collections from spoil piles in a limited area produce a uniform fauna of similar age, presumably derived from a restricted stratigraphic interval.

The best known Bone Valley vertebrate faunas are early Pliocene and have been correlated with the late Hemphillian North American Land Mammal Age (MacFadden and Webb 1982; Berta and Morgan 1985; Webb and Hulbert 1986; Tedford et al. 1987). The composite late Hemphillian vertebrate assemblage from the upper portion of the Bone Valley Formation was designated the Palmetto Fauna by Webb and Hulbert (1986). The Palmetto Fauna, frequently called the Upper Bone Valley Fauna (e.g., Tedford et al. 1987), contains a diverse vertebrate assemblage of more than 150 species. The sediments containing the Palmetto Fauna appear to have accumulated in a variety of fluvial, deltaic, and nearshore marine depositional environments at a time when sea level was approximately 25–35 m higher than at present (Webb and Tessman 1968; MacFadden and Webb 1982). The marine and estuarine components of this fauna consist of sharks, rays, bony fish, sea turtles, pelagic birds, and at least 15 species of marine mammals, including a "sea" otter, four pinnipeds, one sirenian, and a minimum of nine cetaceans.

Prior to the 1970s, only marine mammal paleontologists recognized Miocene faunas in the Bone Valley Formation (Allen 1921; Kellogg 1924, 1944). The biochronologic age and stratigraphic position of the middle Miocene vertebrate faunas from the Bone Valley Formation have been established only recently (Webb and

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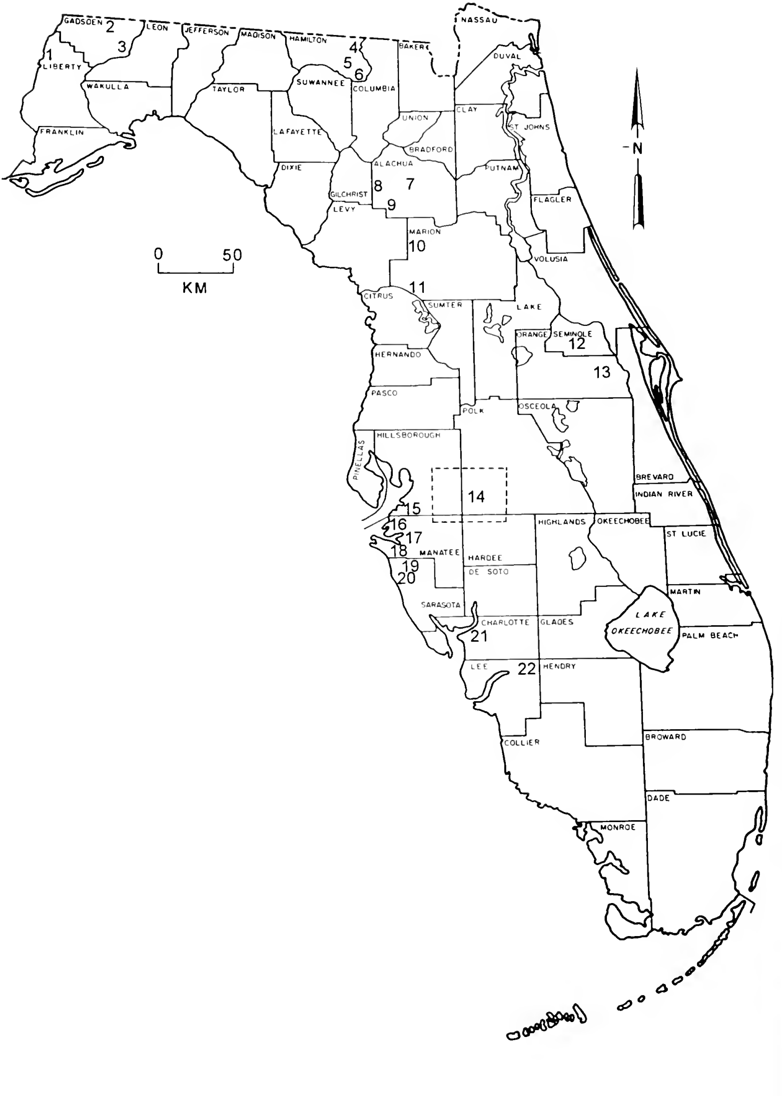
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Crissinger 1983; Webb and Hulbert 1986; Hulbert 1988a,b). Two composite middle Miocene vertebrate faunas from the Bone Valley Formation were named by Webb and Hulbert (1986) on the basis of land mammals, the late Barstovian Bradley Fauna and the early Clarendonian Agricola Fauna. The Bradley Fauna contains only three marine mammal species represented by mostly fragmentary material. At least 14 species of sirenians and cetaceans are known from the Agricola Fauna, including complete skulls and/or articulated skeletons of dugongids, long-beaked dolphins, and "cetotheriid" mysticetes.

A review of the cetaceans from the Bone Valley Formation (Allen 1921) can be taken as the beginning point for study of the Florida fossil marine mammal fauna, although Matson (1915) and Sellards (1915) had earlier mentioned the occurrence of marine mammals in this unit. Most of the earlier papers on the Bone Valley marine mammal fauna concentrated on descriptions of new taxa (e.g., Allen 1921, 1941; Kellogg 1929; 1944; Case 1934). However, several contributions, in particular Kellogg (1944), discussed the entire fauna and attempted to assign an age to this heterogeneous assemblage. The data accumulated over the past three decades now make it possible to place the marine mammal assemblages and associated land mammal fossils from the Bone Valley Formation in an accurate stratigraphic and chronologic context. This study summarizes the biochronology and systematics of the Bone Valley marine mammals and reviews briefly other Florida Neogene marine mammal faunas.

MATERIALS, METHODS, AND ABBREVIATIONS

The Cetacea from the Bone Valley Formation are the primary focus of this report. The Bone Valley sirenians were recently reviewed by Domning (1988, 1990), and C. E. Ray and I. Koretsky are currently studying the pinnipeds.

The cetacean fossil record in Florida is based primarily on fragmentary material, including partial skulls and mandibles, isolated teeth, periotics, and auditory bullae. The only geologic units in Florida that have produced complete cetacean skulls and skeletons are the lower Bone Valley Formation of middle Miocene age and the Tamiami Formation of Pliocene age.

Skulls and articulated skeletons of sirenians are considerably more common in Florida than are intact cetaceans. Besides the middle Miocene unit of the Bone Valley Formation, sirenian skeletons are known from the late Oligocene/early Miocene White Springs Local Fauna from the Parachucla Formation along the Suwannee River in Columbia and Hamilton counties (Domning 1989b; Morgan 1989), the late early Miocene Midway Fauna from Gadsden County in the Florida panhandle (Simpson 1932; Tedford and Hunter 1984), the middle Miocene Statenville Formation in the Occidental Mine and along the Suwannee River in Hamilton County (Domning 1989b; Morgan 1989), and the late Miocene Gainesville Creeks Fauna (new name) in Alachua County (Domning 1988).

Pinnipeds are the rarest fossil marine mammals in Florida. With the exception of a single phocid phalanx from the middle Miocene Occidental Fauna (Morgan 1989), all other Florida pinniped fossils are Pliocene and Pleistocene, including specimens from the Palmetto Fauna and Tamiami Formation. No articulated skeletons or skulls of pinnipeds are known from Florida. A few mandibles with teeth have been collected, but most pinniped fossils consist of isolated teeth and canine tusks, otic regions, and postcranial elements.

Use of the terms "local fauna" and "fauna" follows the definitions proposed by Woodburne (1987). A local fauna is a collection of vertebrate fossils from a restricted stratigraphic interval in one or a few sites in a limited geographic area, such as a phosphate mine (e.g., Fort Green Mine Local Fauna) or a specific site within a mine (e.g., Whidden Creek Local Fauna in the Gardinier Mine). A fauna is composed of a few to many local faunas of similar taxonomic composition and age from a relatively wide geographic area, such as the entire Bone Valley region (e.g., the Agricola Fauna includes all Bone Valley early Clarendonian local faunas).

Detailed locality and map data and field notes for the Bone Valley fossil sites discussed in the text are available in the vertebrate paleontology locality files of the Florida Museum of Natural History, University of Florida, and the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution.

The following abbreviations are used throughout the text: LF, local fauna; NALMA, North American land mammal age.

Fossil specimens of marine mammals from the Bone Valley Formation mentioned in this study are housed in the following museums: AMNH, American Museum of Natural History, New York, New York; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MOSI, Museum of Science and Industry, Tampa, Florida; UF, Florida Museum of Natural History (formerly the Florida State Museum), University of Florida, Gainesville, Florida; UF/FGS, Florida Geological Survey (formerly housed in Tallahassee and now merged with the UF collection in Gainesville); UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; USNM, U. S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

GEOLOGY AND AGE OF THE BONE VALLEY FORMATION

The lithostratigraphy of the various geologic units in the Bone Valley phosphate-mining district (Fig. 3) in central Florida was discussed by Scott and MacGill (1981) and Scott (1988). These two papers, as well as Domning (1988), should be consulted for a more detailed discussion of the geology of the Bone Valley Formation. Figure 4 summarizes the stratigraphy and chronology of the Bone Valley Formation, using the informal stratigraphic subdivisions

Figure 1. Locations of the Bone Valley region and other Neogene marine mammal localities discussed in the text. For each site, the name of the fauna, North American land mammal age (or epoch if land mammals are absent), and geologic unit (if known) are provided. 1, Alum Bluff, late Pliocene, Jackson Bluff Formation; 2, Willacoochee Creek, early Barstovian, Dogtown Member of Torreya Formation; 3, Midway, late Hemingfordian, Dogtown Member of Torreya Formation; 4, Upper Suwannee River, late Barstovian, Statenville Formation; 5, Occidental, early Clarendonian, Statenville Formation; 6, White Springs, early Arikareean, Parachucla Formation; 7, Gainesville Creeks, early Hemphillian, undifferentiated Hawthorn Group; 8, McGehee Farm, early Hemphillian, Alachua Formation; 9, Love Bone Bed, latest Clarendonian, Alachua Formation (sites 8 and 9 are combined into the Archer Fauna in Fig. 3); 10, Moss Acres Racetrack, late early Hemphillian; 11, Withlacoochee 4A, late early Hemphillian; 12, Meade Sand Pit, early Irvingtonian, Nashua Formation; 13, F & W Mine, early Irvingtonian, Nashua Formation; 14, Bone Valley region (sites range in age from early Barstovian to late Hemphillian and are derived from both the Arcadia Formation and Bone Valley Formation. See Figure 2 for an enlargement of the Bone Valley region showing the location of the various phosphate mines mentioned in the text); 15, Leisey 1C, late early Hemphillian, Bone Valley Formation (?); 16, Port Manatee, late early Hemphillian, Bone Valley Formation (?); 17, Manatee Dam, late early Hemphillian, Bone Valley Formation (?); 18, Braden River, late early Hemphillian, Bone Valley Formation (?); 19, Bee Ridge, late Pliocene, Tamiami Formation; 20, Lockwood Meadows, late early Hemphillian, Bone Valley Formation (?) (sites 15–18 and 20 are included in the Manatee Fauna in Fig. 3); 21, Forsberg Shell Pit, early Irvingtonian, Caloosahatchee Formation; 22, Hickey Creek, late Pliocene, Tamiami Formation.

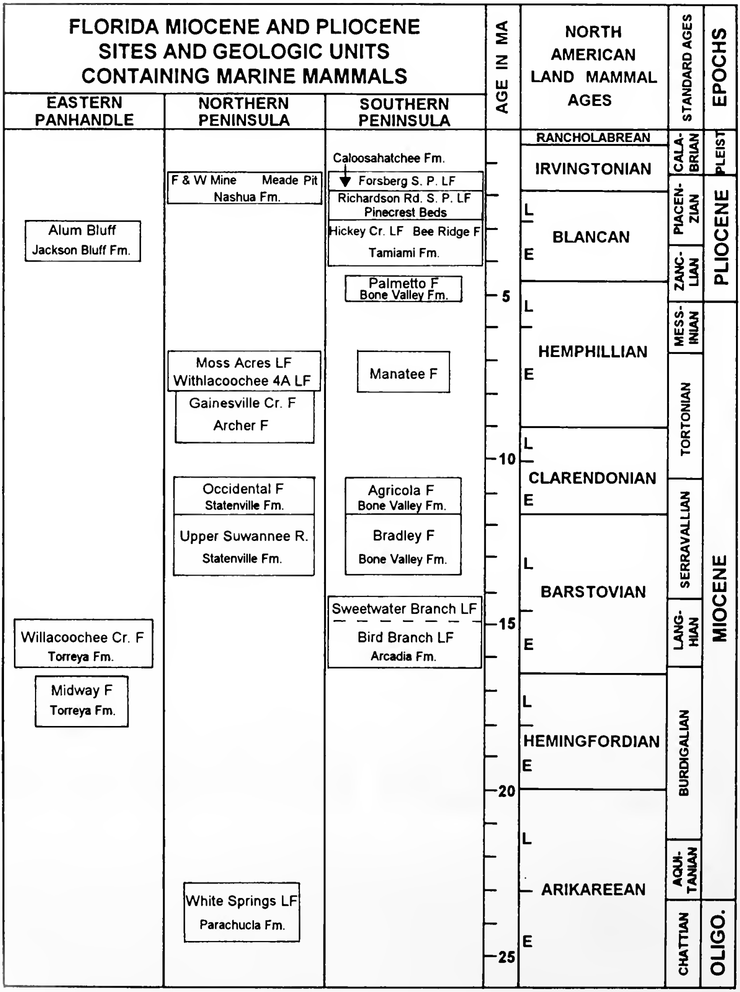

Figure 2. Stratigraphic correlation and chronology of Neogene faunas and sites in Florida that have produced fossils of marine mammals. The geographic location of each site is plotted in Fig. 1. The chronology and subdivisions of the North American Land Mammal Ages follow Tedford et al. (1987) for the Arikareean through the Hemphillian and Lundelius et al. (1987) for the Blancan and Irvingtonian. The chronology of the epochs and standard ages follows Berggren et al. (1985).

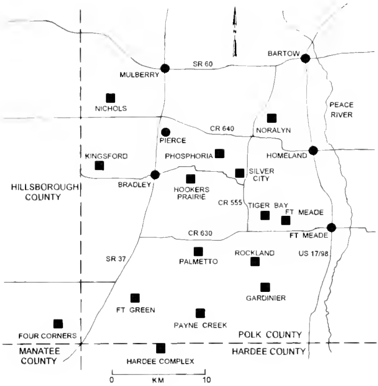

Figure 3. Detail of the Bone Valley region in central Florida (extent of geographic coverage is indicated by the box surrounding site 14 on Fig. 1), showing most of the phosphate mines, towns, and roads mentioned in the text. Squares, phosphate mines; cirles, towns. U.S. highways (US), state roads (SR), and county roads (CR) are indicated by solid lines, county boundaries by dashed lines.

(units 2–6) proposed by Crissinger (1977) and Webb and Crissinger (1983).

The Bone Valley Formation is a clastic rock unit consisting primarily of pebble- to sand-sized phosphate in a matrix of clay and quartz sand (Scott 1988). Coarse phosphatic gravels predominate in the upper portion of the formation, while fine-grained phosphatic sands are more abundant in the lower part of the unit, although phosphatic gravel beds are present in the lower Bone Valley Formation as well. The Bone Valley Formation extends over a wide area of central Florida (about 3500 km^2) and reaches a maximum thickness of 15 m in southwestern Polk County (Scott 1988). In much of its outcrop area the Bone Valley Formation unconformably overlies a light-colored phosphatic dolostone of the middle Miocene Arcadia Formation and is overlain by unnamed unconsolidated sands, mostly of Quaternary age.

The limited extent of the Bone Valley Formation, its gradational lateral and vertical boundaries, and its similarity in lithology to other units led Scott (1988) to reduce the Bone Valley Formation of earlier workers to a member of his newly proposed Peace River Formation. However, Scott (1988) also noted that the presence of phosphatic gravels in the Bone Valley Member is a diagnostic lithological character separating this unit from the remainder of the Peace River Formation. The Bone Valley Formation is a widespread, well-characterized geologic unit and its vertebrate faunas are internationally recognized (e.g., Savage and Russell 1983; Woodburne 1987). In the interest of maintaining consistency with the large body of published work on the vertebrate fauna of this important geologic unit, I continue to use the name Bone Valley Formation in its traditional sense and as an equivalent of the Bone Valley Member of the Peace River Formation of Scott (1988).

In his review of the Bone Valley cetacean fauna, Kellogg (1944) discussed specimens from both the pebble phosphate deposits that he referred to the Bone Valley Formation and the "laminated blue clays" immediately below the pebble phosphate that he tentatively referred to the Hawthorn Formation. Both of Kellogg's units are included in the Bone Valley Formation as recognized here. The "lower" Bone Valley Formation is composed primarily of fine-grained phosphatic sands and clayey sands, including Kellogg's "laminated blue clays" (Unit 4 of Webb and Crissinger 1983), but also incorporates several lower phosphatic gravel beds (units 3 and 5). The lower Bone Valley Formation contains vertebrate faunas of middle Miocene age (Barstovian and early Clarendonian). The upper pebble phosphates (Unit 6) are informally termed the "upper" Bone Valley Formation (Fig. 4) and contain faunas of early Pliocene age (late Hemphillian).

Chronology

Early collections from the Bone Valley Formation yielded conflicting evidence regarding the age of this unit, in large part because the majority of fossil vertebrates collected from the Bone Valley Formation prior to the late 1960s lacked precise stratigraphic data. The marine mammals were typical of Miocene faunas elsewhere (Allen 1921; Kellogg 1924, 1944). Indeed, the Bone Valley genera upon which Allen and Kellogg based their age assessment, the long-beaked dolphin *Pomatodelphis* and the sirenian *Metaxytherium*, among others, are now known to be restricted to Miocene faunas in Florida. However, when more taxa of marine mammals from the Bone Valley Formation became known, several cetaceans appeared characteristic of the Pliocene (Allen 1941; Kellogg 1944). The first paleontologists to study the Bone Valley land mammals favored a Pliocene age for this fauna (Sellards 1916; Simpson 1929, 1930, 1933; Stirton 1936). Among the 14 taxa of Bone Valley land mammals listed by Simpson (1930), the majority are late Hemphillian (early Pliocene) in age. Simpson strongly disagreed with Kellogg's (1924) contention that most Bone Valley marine mammals were late Miocene or older.

From the more complete stratigraphic data now available, it is clear that both Kellogg and Simpson were correct, at least in part. Over the past 25 years paleontologists have begun to achieve a clearer understanding of the complex stratigraphic relationships of the various vertebrate faunas derived from the Bone Valley Formation. A dramatic improvement in our understanding of Bone Valley faunas can be traced directly to the recovery of key *in situ* quarry samples of early Barstovian, late Barstovian, early Clarendonian, and late Hemphillian land mammals. Many of these same faunas contain associated marine mammals or can be confidently correlated with nearby strata that possess marine mammals. Beginning in the late 1960s and 1970s with the work of David Webb and several of his students, especially John Waldrop, important collections of land mammals were recovered from known stratigraphic levels in the Bone Valley Formation. Since the 1970s detailed stratigraphic work on Bone Valley vertebrate faunas has been carried out by field crews from the Florida Museum of Natural History and by Donald Crissinger, a mining geologist with the Mobil Chemical Company. During the 1980s, paleontologists collecting for the Smithsonian Institution, principally Frank Garcia and Daryl Domning, sampled the rich marine mammal fauna derived from the lower Bone Valley Formation. As a result of their efforts, the Smithsonian has accumulated a large collection of Bone Valley dugongs, long-beaked dolphins, and "cetotheres."

Microfossils (foraminifera, ostracodes, and calcareous nannoplankton) and identifiable macroinvertebrate fossils are virtually absent from the Bone Valley Formation, and the sediments are not suitable for paleomagnetic analysis or radioisotopic dating. Therefore, the ages of the various Bone Valley vertebrate faunas are based primarily on correlations to the North American Land Mammal biochronology (Tedford et al. 1987), with supplementary data from studies of eustatic sea level changes (Haq et al. 1987). The three major vertebrate faunas from the Bone Valley Formation that have produced marine mammals are each represented by one or more *in situ* localities containing biochronologically diagnostic species of land mammals.

I closely follow the definitions for the Barstovian, Clarendonian, and Hemphillian proposed by Tedford et al. (1987), to facilitate correlations with other North American vertebrate faunas of similar age. The definitions of the Blancan and earliest Irvingtonian follow Lundelius et al. (1987). The correlations of the various terrestrial vertebrate faunas from the Bone Valley Formation were determined by biochronological comparisons of *in situ* samples of land mammals, particularly the equids, with well-dated vertebrate faunas from the western United States (Webb and Crissinger 1983; Webb and Hulbert 1986; Hulbert 1988b).

Hulbert (1988b: table 10) listed all fossil equid species known from Barstovian, Clarendonian, and Hemphillian sites in the Bone Valley region and elsewhere in Florida. He specified several *in situ* local faunas and a composite equid assemblage for each of the major Bone Valley vertebrate faunas. Marine mammals occur in most of the Bone Valley faunas listed by Hulbert (1988a), as well as in many additional Bone Valley sites, particularly those of early Clarendonian and late Hemphillian age. Most of the phosphate mines in the Bone Valley region that have produced diverse vertebrate faunas are shown in Fig. 3.

Webb and Hulbert (1986) recognized four distinct vertebrate faunas from the Bone Valley Formation of central Florida. Marine mammals are known from three of these faunas (see Fig. 4): (1) the Bradley Fauna of late Barstovian age (middle Miocene, early Serravallian, 13.5–11.5 Ma), (2) the Agricola Fauna of early Clarendonian age (late middle Miocene, late Serravallian, 11.5–10.5 Ma), and (3) the Palmetto Fauna of late Hemphillian age (early Pliocene, early Zanclian, 5.2–4.5 Ma). The approximate correlation of the Bone Valley vertebrate faunas to the standard European ages is provided to facilitate eventual correlation with Miocene and Pliocene marine mammal faunas from Europe. The chronology of the standard European ages and their correlation with the Cenozoic time scale follows Berggren et al. (1985) and Harland et al. (1990).

Late Barstovian equids reported from the Bradley Fauna include *Megahippus* sp., "*Merychippus*" *californicus*, *Pliohippus mirabilis*, *Protohippus perditus*, *Calippus proplacidus*, and *Cormohipparion sphenodus* (Hulbert 1988b: table 10). *Hypohippus chico* (MacFadden 1982) may also belong to the Bradley Fauna, although no specimens of this large browsing horse have been found *in situ*. Other late Barstovian land mammals reported from the Bradley Fauna include the dromomerycid *Procranioceras* cf. *P. skinneri* and

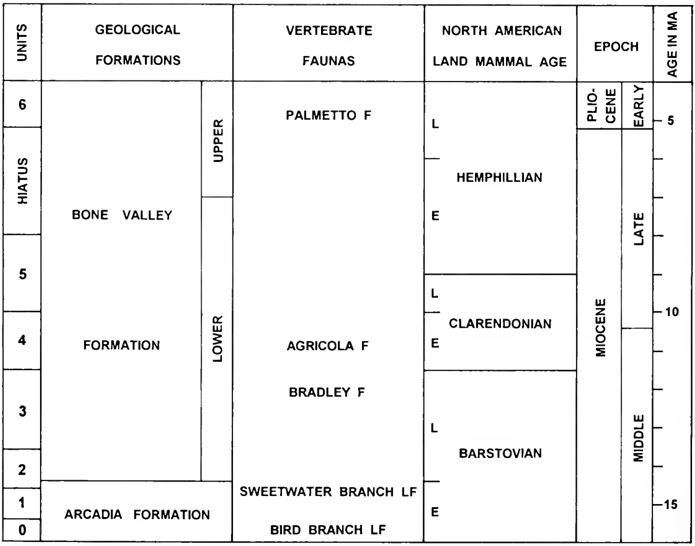

Figure 4. Stratigraphy and chronology of the geologic units and vertebrate faunas in the Bone Valley region of central Florida. The numbered units (units 0–6) are named and defined by Crissinger (1977) and Webb and Crissinger (1983). The chronology and subdivisions of the North American land mammal ages follow Tedford et al. (1987). The vertebrate faunas and geological formations are discussed in the text.

an early species of gomphothere, *Gomphotherium* cf. *G. calvertense* (see Webb and Crissinger 1983). Western faunas of similar age are the late Barstovian Cold Spring Fauna of Texas and the Devil's Gulch Fauna of Nebraska (Webb and Hulbert 1986; Hulbert 1988b).

The richest *in situ* land mammal samples of the Agricola Fauna include the Gray Zone Site in the Phosphoria Mine and the Agricola Road LF (Hulbert 1988b) in the Hookers Prairie Mine. These and several other sites constituting the Agricola Fauna (sites 3–5 in Hulbert 1988b: table 10) are early Clarendonian on the basis of the associated equid assemblage, which includes *Hypohippus affinis*, *Protohippus supremus*, *Calippus martini*, *Pseudhipparion curtivallum*, *Cormohipparion ingenuum*, and *Cormohipparion occidentale*. The amphicyonid *Pliocyon robustus*, collected in association with *Calippus martini* in the Brewster Mine (Berta and Galiano 1984), probably belongs to the Agricola Fauna as well. Numerous other early Clarendonian land mammals from the Gray Zone and Agricola Road faunas are currently under study by R. C. Hulbert, Jr., and S. D. Webb. Western vertebrate faunas that correlate with the Agricola Fauna include the Lapara Creek Fauna from the Gulf Coastal Plain of Texas, the type Clarendon Fauna from western Texas, the Minnechaduza Fauna in Nebraska, and the Ricardo Fauna in California (Tedford et al. 1987).

The richest *in situ* land mammal sample of the Palmetto Fauna has been collected from the Whidden Creek LF (new name) in the Gardinier Mine. This and several other sites (e.g., the TRO Quarry in the Payne Creek Mine) have yielded characteristic late Hemphillian taxa, including four genera of Eurasian immigrant carnivores: the large ursid *Agriotherium*, the sabercat *Megantereon* (Berta and Galiano 1983), small cats of the extant genus *Felis* (MacFadden and Galiano 1981), and the extinct wolverine *Plesiogulo* (Harrison 1981). The Bone Valley artiodactyls *Hexameryx* and *Kyptoceras* are confined to the late Hemphillian (Webb 1973, 1981), while the gomphotheriid proboscidean *Rhynchotherium* first appears at this time. Three species of horses from the Palmetto Fauna are restricted to the late Hemphillian, including *Astrohippus stocki*, *Dinohippus mexicanus*, and *Pseudhipparion simpsoni* (MacFadden 1986; Webb and Hulbert 1986; Hulbert 1988b).

According to Brooks (1974) and Waldrop and Wilson (1990), the stratigraphic section in the Payne Creek Mine about 4 km southwest the TRO Quarry is composed of a tan phosphatic sandy limestone that occurs between two phosphate pebble units typical of the upper Bone Valley Formation. On the basis of lithology and invertebrate fossils, these authors referred the sandy limestone to the Tamiami Formation, a unit found primarily in southwestern Florida. A partial mandible of *Ninoziphius platyrostris* from this locality was embedded in the sandy limestone of the Tamiami Formation. The pebble phosphate bed overlying the Tamiami Formation contained several land mammals typical of the late Hemphillian Palmetto Fauna (Brooks 1974; Waldrop and Wilson 1990), including the equids *Neohipparion eurystyle* and *Pseudhipparion simpsoni*, as well as two rostral fragments of *Goniodelphis hudsoni*. This site not only confirms the early Pliocene age of *Ninoziphius* and *Goniodelphis* but also establishes the correlation between the upper Bone Valley Formation and a portion of the Tamiami Formation, a unit that produces a rich marine mammal fauna but few land mammals.

According to Tedford et al. (1987:192), "the Upper Bone Valley Fauna of peninsular Florida appears to be one of the latest Hemphillian assemblages known and contains the earliest representatives of such common Blancan and younger taxa as *Megantereon*, *Borophagus*, *Mylohyus*, and odocoileine deer." To this list of typical Blancan mammals from the Palmetto Fauna should be added the leporids *Hypolagus ringoldensis* and *Nekrolagus progressus* (see White 1987, 1991) and the small sigmodontine rodent *Calomys* (*Bensonomys*), although the latter genus does occur in several other late Hemphillian faunas (Baskin 1978; Lindsay and Jacobs 1985). Despite the occurrence of several characteristic Blancan taxa in the Palmetto Fauna, most of the genera in this assemblage are typical of the late Hemphillian and became extinct by the Blancan, including *Agriotherium*, *Plesiogulo*, the large sabercat *Machairodus*, the giant procyonid *Arctonasua* (Baskin 1982), the rhinoceros *Teleoceras*, the horses *Astrohippus*, *Dinohippus*, *Neohipparion*, and *Pseudhipparion*, the protoceratid *Kyptoceras*, and the antilocaprid *Hexameryx*.

A combination of sea-level data and land mammal biochronology limits the age of the Palmetto Fauna to a rather restricted interval. The Palmetto Fauna could not have been deposited during the Messinian (between 6.7 and 5.2 Ma) when sea levels were as much as 50 m lower than at present. The land mammals are late Hemphillian in age and thus are older than 4.5 Ma, the generally accepted boundary between the Hemphillian and Blancan NALMA (Lindsay et al. 1984; Tedford et al. 1987). The combination of high sea level and the late Hemphillian age of the land mammals restricts the age of the Palmetto Fauna to between 5.2 and 4.5 Ma.

A maximum age for the Bone Valley Formation is provided by two *in situ* vertebrate faunas, the Bird Branch LF (new name), collected high in the Arcadia Formation, and the Sweetwater Branch LF (Hulbert and MacFadden 1991), derived either from the top of the Arcadia Formation or the basal unit of the Bone Valley Formation. The Bird Branch LF from the Nichols Mine, discovered by Donald Crissinger in 1985, is the oldest vertebrate fauna currently known from the Bone Valley region. Hulbert and MacFadden (1991) identified the equid "*Merychippus*" cf. "*M.*" *isonesus* from the Bird Branch LF, which also has an early species of the murid rodent *Copemys*, one of the genera defining the Barstovian NALMA (Tedford et al. 1987). These and other taxa from the Bird Branch LF indicate an early Barstovian age (early middle Miocene, Langhian, 16.5–15.5 Ma). The Bird Branch LF appears to correlate with the early Barstovian Willacoochee Creek Fauna from Gadsden County in the Florida Panhandle (Bryant 1991; Bryant et al. 1992). The Willacoochee Creek Fauna was derived from the Torreya Formation, corroborating the correlation of the upper part of the Arcadia Formation with the Torreya Formation (Scott 1988). The only marine mammal fossils in the Bird Branch LF are fragmentary sirenian ribs.

The Sweetwater Branch LF from the Phosphoria Mine was collected in 1985 by Rick Carter and James Pendergraft. This fauna was derived from a clay lens overlying the indurated dolostone of the Arcadia Formation. Scott (1988) regarded these basal clays as part of his Bone Valley Member, whereas Crissinger (1977) and Webb and Crissinger (1983) placed them in the Hawthorn Group (= Arcadia Formation of present usage). Whether the Sweetwater Branch LF was derived from the top of the Arcadia Formation or the base of the Bone Valley Formation, it provides a minimum and a maximum age, respectively, for these two units. From the presence of three equids, including "*Parahippus*," *Merychippus* cf. *M. brevidontus*, and "*Merychippus*" *goorisi*, Hulbert and MacFadden (1991) regarded the Sweetwater Branch LF as early Barstovian (early middle Miocene, Langhian, 15.5–14.5 Ma), slightly younger than the Bird Branch LF (Fig. 2) and correlative with the early Barstovian Burkeville Fauna of Texas and the Lower Snake Creek Fauna of Nebraska. No marine mammals occur in the Sweetwater Branch LF.

The absence of Blancan (4.5–1.9 Ma) faunas from the Bone Valley region suggests that the earliest Pliocene (latest Hemphillian) Palmetto Fauna provides a minimum age for the Bone Valley Formation of approximately 4.5 Ma. An early Pleistocene (early Irvingtonian, 1.5–1.0 Ma) vertebrate fauna from the Bone Valley region, the Pool Branch LF (Webb 1974), was derived from beds overlying the typical phosphatic gravels of the upper Bone Valley Formation.

Sea Level Changes in Florida During the Miocene and Pliocene

Additional data on the age of the Bone Valley Formation are provided by comparisons with worldwide sea level curves (e.g., Haq et al. 1987). Many vertebrate assemblages in the Bone Valley Formation contain a mixture of marine, estuarine, freshwater, and terrestrial taxa, suggesting deposition in shallow, nearshore marine waters. The richest marine mammal localities occur in strictly marine strata that probably were deposited somewhat farther offshore, although most likely in water less than 10 m deep.

Most of the Bone Valley vertebrate faunas discussed here occur between 25 and 50 m in elevation above present sea level. The elevation at which a site was collected has been used to provide a general indication of sea level at the time of deposition (± 10 m) for Florida vertebrate faunas containing a mixture of terrestrial and marine taxa (Webb and Tessman 1968; MacFadden and Webb 1982). This hypothesis is based on the assumption that the central portion of the Florida peninsula has been tectonically stable since the Miocene.

During the middle Miocene, between about 15 and 10.5 Ma, worldwide sea levels were relatively high, generally 50 m or more above present sea level (Haq et al. 1987). Two of the Bone Valley vertebrate faunas, the Bradley and Agricola faunas, were deposited during this interval, as was the Occidental Fauna in northern Florida. In the early late Miocene, between 10.5 and 9.0 Ma (corresponding to the late early and late Clarendonian), sea level dropped sharply (Haq et al. 1987). The following period of low sea level probably would have been a time of erosion and nondeposition on the Florida peninsula, and indeed there are no vertebrate faunas of this age known from Florida.

Following this hiatus, there was a return to higher sea levels at the end of the Clarendonian (about 9 Ma) and into the early Hemphillian. This period is represented by the Archer and Gainesville Creeks faunas (Fig. 2) of northern peninsular Florida (Webb and Hulbert 1986). Both of these faunas contain marine mammals and lie at elevations of 25 to 50 m above present sea level. Land mammals equivalent in age to the Archer Fauna are also known from the Bone Valley region (Webb and Hulbert 1986). Sea level curves indicate that during the latest Clarendonian and early Hemphillian (9–7 Ma) sea level was generally near or below present levels (Haq et al. 1987). However, Blackwelder (1981) has shown that the marine Eastover Formation of Virginia, which is approximately the same age as the Archer and Gainesville Creeks faunas, was also deposited during a marine transgression reaching 50 m above present sea level.

Marine mammals occur at five sites constituting the Manatee Fauna (new name) of late Miocene age, located along southwestern Florida's Gulf coast. The late early Hemphillian age (8–7 Ma) of the associated land mammals from the Manatee Fauna sites, as well as their location near or slightly above present sea level, suggests they were deposited just prior to the Messinian (6.7–5.2 Ma). No Florida vertebrate faunas of Messinian age (equivalent to the early phase of the late Hemphillian) are known, probably because this time of low sea level would have been a time of erosion and nondeposition.

Beginning in the early Pliocene and continuing into the late Pliocene (between about 5.2 and 3.0 Ma) there was a return to high sea levels (Haq et al. 1987; Harland et al. 1990). The latest Hemphillian Palmetto Fauna dates early in this interval (between 5.2 and 4.5 Ma). Blancan marine mammals from the Tamiami Formation date to the later portion (between 3.5 and 3.0 Ma). Sea levels during the late Pliocene and throughout the Pleistocene fluctuated widely following the onset of major continental glaciation in the late Pliocene, about 2.5 Ma. Several Florida sites containing marine mammals were deposited during interglacial high sea levels in the late Pliocene (late Blancan, 2.5–1.9 Ma) and latest Pliocene/early Pleistocene (early Irvingtonian, 1.9–1.0 Ma).

TABLE 1. Marine mammals from the early Clarendonian Agricola Fauna, Bone Valley Formation, Polk County, central Florida.

- Cetacea
  - Odontoceti
    - Platanistidae
      - *Pomatodelphis bobengi* (Case, 1934), new combination
      - *Pomatodelphis inaequalis* Allen, 1921
    - Ziphiidae
      - genus and species undetermined
    - Physeteridae
      - *Scaldicetus* sp.
    - Odontoceti incertae sedis[a]
      - *Delphinodon* cf. *D. mento* (Cope, 1868)
      - *Hadrodelphis* sp.
      - aff. *Lophocetus* sp.
      - genus and species undetermined[b]
  - Mysticeti
    - Cetotheriidae[c]
      - ?*Isocetus* sp.
      - ?*Mesocetus* sp.
      - unidentified genus
- Sirenia
  - Dugongidae
    - *Metaxytherium floridanum* Hay, 1922
    - *Dioplotherium allisoni* (Kilmer, 1965)[d]

[a] There are numerous additional taxa of small and medium-sized odontocetes in the Bone Valley Formation, most of which are represented by isolated teeth or periotics lacking stratigraphic data. Only teeth of *Delphinodon* and *Hadrodelphis* can be identified with some confidence as originating from the middle Miocene.

[b] This taxon was originally described as *Megalodelphis magnidens* Kellogg, 1944, but Morgan (1986) showed that the holotype belonged to the crocodilian *Gavialosuchus americanus* Sellards, 1915. Kellogg's (1944) referred specimen of *M. magnidens* and several other fossils from middle Miocene sediments in the Bone Valley Formation do represent a very large, long-beaked odontocete that is currently undescribed.

[c] On the basis of skulls, dentaries, and isolated auditory bullae, there appear to be at least three genera and four species of cetotheres in the Agricola Fauna.

[d] The stratigraphic provenience of this specimen is uncertain, although Don Crissinger (pers. comm.) thought it may have come from Unit 5.

BONE VALLEY MARINE MAMMAL FAUNAS

Bradley Fauna

The late Barstovian Bradley Fauna is represented by only a few sites in the Bone Valley Formation, including the Red Zone Site in the Phosphoria Mine, the Page 1 LF in the Kingsford Mine, and several small sites in the Nichols Mine (Fig. 3). The Bradley Fauna is the least common of the three typical Bone Valley faunas, as judged from the rarity in this region of Barstovian terrestrial mammals. Only three taxa of marine mammals, the sirenian *Metaxytherium floridanum*, the long-beaked dolphin *Pomatodelphis inaequalis*, and a "cetothere" are known from localities that have produced late Barstovian land mammals. Although based on limited material, the marine mammal assemblages of the Bradley Fauna do not appear to differ significantly from those of the slightly younger early Clarendonian Agricola Fauna. The marine mammals of the Bradley Fauna are the least diverse of the Bone Valley faunas primarily because of the overall paucity of vertebrates of this age. Several odontocetes represented in the Bone Valley Formation only by isolated teeth lacking stratigraphic provenience, including *Delphinodon* cf. *D. mento* and *Hadrodelphis*, may be representatives of the Bradley Fauna. These two genera are also known from the Calvert Formation of Chesapeake Bay.

Agricola Fauna

The early Clarendonian Agricola Fauna has produced well-preserved skulls and articulated skeletons of marine mammals from phosphate mines located in the northern half of the Bone Valley phosphate-mining district, south of County Road 640 and north of County Road 630, in a roughly rectangular area bounded by the towns of Pierce and Homeland on the northwest and northeast, respectively, and Bradley and Fort Meade on the southwest and southeast (Fig. 3). The most productive mines for the Agricola Fauna are the Phosphoria Mine of the International Minerals and Chemical (IMC) Corporation, the Hookers Prairie Mine, formerly belonging to W. R. Grace and Company, the Silver City Mine, formerly belonging to the Swift Agricultural Chemical Corporation, and the Fort Meade Mine of the Mobil Chemical Company.

The Phosphoria and Hookers Prairie mines have yielded the best-preserved fossils of marine mammals in the entire Bone Valley region. Numerous skulls and articulated skeletons of *Metaxytherium floridanum* (see Domning 1988), more than ten complete skulls of *Pomatodelphis*, and several nearly intact "cetothere" skulls and mandibles have been collected from the lower Bone Valley Formation in the past 20 years. The lower vertebrates associated with this marine mammal assemblage are almost always marine, primarily sharks, rays, and bony fish. The preservation of delicate skulls and articulated skeletons suggests deposition in quiet water, perhaps in a protected marine embayment.

The Agricola Fauna contains at least 14 species of marine mammals, including 12 cetaceans and two sirenians (Table 1). Domning (1988:395) characterized *M. floridanum* from the Bone Valley Formation as "the most abundantly fossilized sirenian in the New World (and perhaps the entire world)." The second most abundant marine mammal in the Agricola Fauna is *Pomatodelphis inaequalis*. Skulls and partial rostra and mandibles of this long-beaked dolphin are commonly collected from the same strata that produce the sirenians, but articulated skeletons of *Pomatodelphis* are rare in the Bone Valley region. The larger species of *Pomatodelphis*, *P. bobengi*, although less common than *P. inaequalis*, is represented by three nearly complete skulls. Next in abundance are several taxa of small to medium-sized "cetotheriid" mysticetes. "Cetothere" fossils collected from Unit 4 in the Bone Valley Formation include two skulls with articulated skeletons, several additional skulls and mandibles, and numerous isolated auditory bullae and periotics. The Bone Valley "cetotheres" are seriously in need of revision, but preliminary analysis of the available material suggests at least three genera and four species.

The rarer members of the early Clarendonian marine mammal fauna include one and possibly two additional sirenians, the giant long-beaked dolphin originally described by Kellogg (1944) as *Megalodelphis magnidens* (represented by several rostral and mandibular fragments), a ziphiid, the physeterid *Scaldicetus* (represented by a mandible with 16 teeth; MOSI, uncatalogued); and several taxa of enigmatic odontocetes, including *Delphinodon* cf. *D. mento*, *Hadrodelphis*, and a species (represented by a pair of mandibles with teeth and associated partial skull) that appears related to *Lophocetus*. The dugongid sirenian *Dioplotherium allisoni* is represented in the Bone Valley region by a single tusk fragment (possibly derived from Unit 5 in the lower Bone Valley Formation; Domning, pers. comm.). The chronological range of this species is not well understood, but specimens referred to it have been reported from the early Miocene of Brazil (Toledo and Domning 1991) and the early to middle Miocene of California (Domning 1978). An additional undescribed small dugongid is present in the Bone Valley region (Domning, pers. comm.) and is either Barstovian or Clarendonian in age. No pinnipeds have been recovered from the Agricola Fauna.

TABLE 2. Marine mammals from the latest Hemphillian (early Pliocene) Palmetto Fauna, Bone Valley Formation, Polk County, central Florida.

- Cetacea
  - Odontoceti
    - Pontoporiidae
      - genus and species undetermined
    - Iniidae
      - *Goniodelphis hudsoni* Allen, 1941
    - Delphinidae
      - genus and species undetermined
    - Ziphiidae
      - *Mesoplodon* sp.
      - *Ninoziphius platyrostris* Muizon, 1983
    - Physeteridae
      - *Kogiopsis floridana* Kellogg, 1929
      - *Physeterula* sp.
    - Odontoceti incertae sedis[a]
  - Mysticeti
    - Balaenopteridae
      - *Balaenoptera floridana* Kellogg, 1944
      - *Balaenoptera* sp.
- Carnivora
  - Mustelidae
    - *Enhydritherium terraenovae* Berta and Morgan, 1985
  - Odobenidae
    - *Trichecodon huxleyi* Lankester, 1865
  - Phocidae
    - *Callophoca obscura* van Beneden, 1877
    - *Phocanella pumila* van Beneden, 1877
    - undetermined small phocine
- Sirenia
  - Dugongidae
    - *Corystosiren varguezi* Domning, 1990

[a] There are numerous additional taxa of small and medium-sized odontocetes in the Bone Valley Formation, most of which are represented by isolated teeth or periotics lacking stratigraphic provenience. The only small odontocete from the Palmetto Fauna that can be confidently identified from isolated teeth is *Goniodelphis hudsoni*.

Another diagnostic vertebrate often found in association with cetaceans and sirenians in the Agricola Fauna is the long-snouted estuarine crocodile *Gavialosuchus americanus* (see Morgan 1986). Many of the marine mammals, as well as *Gavialosuchus*, are found in the correlative early Clarendonian vertebrate fauna from the Statenville Formation in the Occidental Phosphate Mine of Hamilton County, northernmost peninsular Florida (Morgan 1989).

Palmetto Fauna

Four phosphate mines in southwestern Polk County, including the Fort Green, Palmetto, and Payne Creek mines of the Agrico Chemical Company and the Gardinier (= Cargill) Mine, have produced the most diverse and abundant assemblages of the late Hemphillian Palmetto Fauna (Fig. 3).

The marine mammal assemblage from the Palmetto Fauna comprises 15 species, including nine cetaceans, four pinnipeds, a sea otter, and a dugong (Table 2). Marine mammals are rarer in the

Palmetto Fauna than in the Agricola Fauna, and most of the fossils are more fragmentary, suggesting deposition in higher-energy environments that rarely preserve articulated skeletons or skulls. The frequent association of marine and land mammals in the Palmetto Fauna also suggests a nearshore marine depositional environment, perhaps near the mouth or delta of a large river.

The most common marine mammals in the Palmetto Fauna are cetaceans, including the small balaenopterid mysticete *Balaenoptera floridana*, sperm whales of the genus *Physeterula* (or possibly *Kogiopsis floridana*), and the iniid "river" dolphin *Goniodelphis hudsoni*. Most other cetaceans from the Palmetto Fauna, including a pontoporiid, a delphinid, and the ziphiids *Mesoplodon* sp. and *Ninoziphius platyrostris*, are represented by only one or a few specimens lacking stratigraphic data. Right whales are unknown from the Palmetto Fauna, although auditory bullae of a small balaenid occur in both the older late Miocene Manatee Fauna and the younger late Pliocene Bee Ridge Fauna (new name).

Pinnipeds known from the Palmetto Fauna include the odobenid *Trichecodon huxleyi* and the phocids *Callophoca obscura*, *Phocanella pumila*, and a small undetermined species. Although not as diverse as the pinnipeds of the correlative Lee Creek LF in North Carolina (at least six species; Ray 1976), the Palmetto Fauna has a pinniped fauna considerably larger than that of any other Florida site. *T. huxleyi* and *C. obscura* are also known from several late Pliocene (Blancan) faunas in southwestern Florida. The Palmetto Fauna also contains the rare dugongid *Corystosiren varguezi* (see Domning 1990) and the largest known sample of the giant otter *Enhydritherium terraenovae* (see Berta and Morgan 1985).

In addition to marine mammals, the Palmetto Fauna contains a diverse assemblage of other marine and estuarine vertebrates, including sharks (Tessman 1968), rays, bony fish, sea turtles (Dodd and Morgan 1992), and birds (Brodkorb 1955; Becker 1987).

OTHER FLORIDA MIOCENE AND PLIOCENE MARINE MAMMAL FAUNAS

Figure 2 summarizes the stratigraphic relationships and chronology of Florida Neogene faunas and sites from which marine mammals are known. The Parachucla Formation, exposed along the Suwannee River near White Springs in Columbia and Hamilton counties in northernmost peninsular Florida (Huddlestun 1988; Morgan 1989; see Fig. 1, site 6), has produced several complete skulls and skeletons of three genera of dugongids, including *Crenatosiren* (= "*Halitherium*") *olseni*, *Dioplotherium manigaulti*, and *Metaxytherium* sp. (Reinhart 1976; Morgan and Pratt 1983; Domning 1989a,b, 1991). The Parachucla Formation has been regarded as very early Miocene (Aquitanian) on the basis of planktonic foraminifera from supposedly correlative strata in Georgia (Huddlestun 1988). Land mammals constituting the White Springs LF, derived from these same strata of the Parachucla Formation, are early Arikareean, probably between 25 and 23 Ma (Morgan 1989). The land mammals indicate that at least a portion of this unit may be latest Oligocene (Chattian), as the Oligocene–Miocene boundary is placed at 23.3 Ma (Harland et al. 1990). No cetaceans are presently known from Florida Oligocene or earliest Miocene deposits.

There is a gap of about 5 million years in the Florida marine mammal record between the latest Oligocene/earliest Miocene White Springs LF and the next youngest faunas of late early Miocene age. The rarity of marine mammals in Florida during most of the early Miocene (between 23 and 18 Ma) is puzzling since this was a time of generally high worldwide sea levels (Haq et al. 1987). The late early Miocene (late Hemingfordian, late Burdigalian, 18–17 Ma) Midway Fauna was collected from a series of fuller's earth mines in the vicinity of Midway and Quincy in Gadsden County in the Florida panhandle (Simpson 1929, 1932; Tedford and Hunter 1984; Bryant et al. 1992). The Midway Fauna (Fig. 1, site 3) has produced several articulated skeletons of the dugongid sirenian *Hesperosiren crataegensis*, rostral fragments of *Pomatodelphis*, and auditory bullae of a "cetothere," as well as a rather diverse sample of equids and other land mammals indicating a late Hemingfordian age (Tedford and Hunter 1984). The Midway Fauna and the slightly younger Willacoochee Creek Fauna of early Barstovian age (Langhian, 16–15 Ma) both were derived from the Dogtown Member in the upper Torreya Formation (MacFadden et al. 1991; Bryant et al. 1992). The Willacoochee Creek Fauna (Fig. 1, site 2), also principally collected from fuller's earth mines in Gadsden County, is very similar to the Midway Fauna in its marine mammals. The Willacoochee marine mammals are represented primarily by isolated fossils, including cranial fragments of *Hesperosiren crataegensis*, partial rostra and mandibles of *Pomatodelphis* sp., auditory bullae of a "cetothere," and the tooth of a large odontocete similar to *Delphinodon mento*. This tooth was referred to ?*Squalodon* by Bryant (1991); however, it is too small for any species of *Squalodon* from the Calvert Formation and also differs from that genus in several morphological details. Teeth referred to *D. mento*, a species originally described from the Calvert Formation, are also known from the lower Bone Valley Formation. From the presence of the rodent *Copemys* and several other diagnostic land mammal taxa, the Willacoochee Creek Fauna is early Barstovian in age (Bryant et al. 1992). The localities that have produced the Midway and Willacoochee Creek faunas are mostly >75 m in elevation, indicating high sea level at the time of their deposition.

Several marine mammal faunas of middle Miocene age (late Barstovian and early Clarendonian) are known from phosphatic sands of the Statenville Formation in northernmost Florida and southernmost Georgia. Outcrops of the Statenville Formation at the type locality in Statenville, Echols County, Georgia, contain sirenian ribs and several species of sharks, as well as late Barstovian land mammals (Voorhies 1974). Sediments of the Statenville Formation along the upper Suwannee River in Hamilton County, Florida, and Echols County, Georgia (Fig. 1, site 4), of late Barstovian age (early Serravallian, 13.5–11.5 Ma), have produced two taxa of marine mammals, a nearly complete skeleton of the sirenian *Metaxytherium* sp. (Domning 1989b) and a rostral fragment of a large odontocete similar to "*Megalodelphis magnidens*."

Land mammals from the Statenville Formation in the Occidental Phosphate Mine in Hamilton County (Fig. 1, site 5) constitute the Occidental Fauna (Morgan 1989) of early Clarendonian age (late middle Miocene, late Serravallian, 11.5–10.5 Ma). Thanks to the diligent collecting efforts of Eric and Craig Taylor over the past five years, a fauna of at least 11 species of marine mammals, including two sirenians, eight cetaceans, and a pinniped, is now known from the Occidental Mine. Of the sirenians, *Dioplotherium manigaulti* is known only from a single premaxilla with a tusk (Domning 1989a), while the more common *Metaxytherium floridanum* is represented by a partial articulated skeleton, several incomplete skulls, and a complete mandible. *Pomatodelphis inaequalis* is known primarily from rostral and mandibular fragments. The remainder of the odontocete fauna, including *Scaldicetus* and at least three additional unidentified taxa, are represented only by isolated teeth. At least two species of "cetotheres" are present, on the basis of partial crania and auditory bullae. A single phalanx represents the earliest Florida record of the Phocidae. The land mammal fauna from the Occidental Mine, particularly the equids, is very similar to the early Clarendonian Agricola Fauna from the lower Bone Valley Formation.

Marine mammals of late Miocene (latest Clarendonian/early Hemphillian) age occur in unnamed sediments of the Hawthorn Group exposed in creeks in the vicinity of Gainesville, Alachua

County, northern Florida. Ten taxa of marine mammals have been identified from the Gainesville Creeks Fauna (Fig. 1, site 7). *Metaxytherium floridanum* is known from a nearly complete articulated skeleton with beautifully preserved skull and mandibles (Domning 1988). Several partial skulls and rostra of *Pomatodelphis inaequalis* and *P. bobengi* have been found in the Gainesville Creeks Fauna. At least two sizes of "cetotheres" are known from auditory bullae, periotics, and partial mandibles. *Scaldicetus* and a minimum of four additional odontocetes are represented by isolated teeth. Two of these odontocetes, *Delphinodon* cf. *D. mento* and *Hadrodelphis* sp., also occur in the Bone Valley Formation. The Gainesville Creeks marine mammal fauna belongs to the *Metaxytherium–Pomatodelphis*–"cetothere" assemblage that is typical of the lower Bone Valley Formation and the Occidental Fauna. The most probable age of the marine mammals from the Gainesville Creeks Fauna is early Hemphillian (late Miocene, middle Tortonian, 9–8 Ma), on the basis of the rather diverse equid fauna of this age identified from several creeks in Gainesville, most notably Coffrin Creek (Hulbert 1988b). The equids from Coffrin Creek compare closely in age with those of the Archer Fauna, a diverse land mammal assemblage derived from a well-known series of local faunas located about 20 to 30 km west and southwest of Gainesville in Alachua and Levy counties, including the latest Clarendonian Love Bone Bed and early Hemphillian McGehee Farm (Webb et al. 1981; Webb and Hulbert 1986; Hulbert 1988b). Domning (1988) reported *Metaxytherium floridanum* from both the Love Bone Bed (Fig. 1, site 9) and McGehee Farm (Fig. 1, site 8), and an auditory bulla and a humerus of *Pomatodelphis* are known from the latter fauna.

Scattered and mostly fragmentary remains of marine mammals occur in a series of sites of late early Hemphillian age (late Miocene, late Tortonian, 8–7 Ma) located along the Gulf coast in Hillsborough, Manatee, and Sarasota counties. Where these faunas have been collected *in situ*, the sediments resemble the pebble phosphates of the upper Bone Valley Formation (Webb and Tessman 1968; MacFadden 1986). These late early Hemphillian sites, here collectively named the Manatee Fauna (Fig. 1, sites 15–18, 20), include Leisey 1C in Hillsborough County (Hulbert 1988b; Hulbert and Morgan 1989), Braden River, Manatee Dam, and Port Manatee in Manatee County (Webb and Tessman 1968; Hulbert 1988b), and Lockwood Meadows in Sarasota County (MacFadden 1986; Hulbert 1988b). All of these localities are less than 20 km from the present Gulf coast and are below 5 m in elevation.

The marine mammals of the Manatee Fauna comprise eight species: a partial skeleton and isolated teeth of *Metaxytherium floridanum*, isolated teeth of the sperm whale *Physeterula*, periotics and isolated teeth of two small odontocetes, and auditory bullae representing four taxa of mysticetes, including a "cetothere," a small balaenid, and a small and medium-sized balaenopterid. The Manatee Fauna records several first and last occurrences of marine mammal taxa in the Florida fossil record, including the oldest balaenids and balaenopterids and the youngest *Metaxytherium* (Domning 1988) and "cetotheres." From its equids, the Manatee Fauna is equivalent in age to the better-known late early Hemphillian Withlacoochee River 4A (Fig. 1, site 11) and Moss Acres Racetrack (Fig. 1, site 10) local faunas from Marion County, northern Florida (Hulbert 1988b: table 10). The Withlacoochee River 4A and Moss Acres sites also contain the earliest records of the giant otter *Enhydritherium terraenovae* (Berta and Morgan 1985; Lambert 1990).

The Tamiami Formation is a widespread marine unit exposed in southwestern Florida in Sarasota, Charlotte, Lee, and Collier counties. The only marine mammals previously reported from the Tamiami Formation are a partial skeleton of a large species of *Balaenoptera*, a partial skeleton of a smaller species of *Balaenoptera* (similar in size to *B. floridana* from the Bone Valley Formation), and a periotic and teeth of a small delphinid, all from the Hickey Creek LF in Lee County (Morgan and Pratt 1983; Fig. 1, site 22). An articulated skeleton and several partial skulls and mandibles of balaenopterids have been collected from the Tamiami Formation in the APAC (= Macasphalt = Warren Brothers) and Richardson Road (= Quality Aggregates) shell pits, located 1 km apart in northern Sarasota County. The marine mammal assemblage from the Tamiami Formation in the APAC and Richardson Road pits (Unit 11 of Petuch 1982), here named the Bee Ridge Fauna (Fig. 1, site 19), includes at least ten species: periotics and teeth of two small unidentified odontocetes, teeth of *Physeterula*, auditory bullae of a small balaenid, several partial mandibles of *Megaptera*, several partial skulls and mandibles and numerous isolated auditory bullae and periotics of a small and a medium-sized species of *Balaenoptera*, associated vertebrae and ribs of a small unidentified dugongid, and two species of pinnipeds, including several tusks of the odobenid *Trichecodon huxleyi* and a mandible, isolated teeth, and postcranial elements of the large phocid *Callophoca obscura*. *Trichecodon* has been identified from several other localities in southern Florida, including De Soto Lakes in Sarasota County, where a complete tusk was found (Ray 1960).

The Tamiami Formation ranges in age from late Miocene to late Pliocene (e.g., Hunter 1968; Peck et al. 1979a,b; Allmon and Scott 1992), although marine mammals are known only from the Pliocene portion of the unit. The interdigitation of the Tamiami Formation with pebble phosphates of the upper Bone Valley Formation in the Payne Creek Mine in Polk County (Brooks 1974; Waldrop and Wilson 1990) suggests that portions of these two formations are equivalent in age. The marine mammal assemblage from the Tamiami Formation, especially the Bee Ridge Fauna, is similar to that discussed above from the early Pliocene Palmetto Fauna. In particular, these two faunas are similar in the abundance of balaenopterids, the presence of the pinnipeds *Trichecodon* and *Callophoca*, the absence of "cetotheres," and the rarity of sirenians. However, many invertebrate paleontologists (e.g., Ward 1992; Zullo 1992; Zullo and Harris 1992) consider all of the shell beds in the APAC and Richardson Road shell pits to be late Pliocene. The Bee Ridge Fauna probably correlates to the early part of the late Pliocene (early Blancan, early Piacenzian, 3.5–3.0 Ma), about a million years younger than the Palmetto Fauna.

Exposures of the marine Jackson Bluff Formation at Alum Bluff in Liberty County in the Florida panhandle (Fig. 1, site 1) have produced several dentary fragments and auditory bullae of a small balaenopterid similar to *Balaenoptera floridana*. The Jackson Bluff Formation has been correlated with the Tamiami Formation on the basis of molluscan (Ward 1992) and barnacle (Zullo 1992) faunas and is probably early late Pliocene (early Piacenzian) as well.

Marine mammals are generally rare in Florida's latest Pliocene geologic units, although several important specimens have been collected from the Pinecrest Beds, Caloosahatchee Formation, and Nashua Formation. Teeth and postcranial elements of the phocid *Callophoca obscura* were recovered by Steve Emslie and his field crews from *in situ* strata of the Pinecrest Beds in the Richardson Road Shell Pit (Emslie 1992a; Fig. 1, site 19). Although these seal remains were derived from a stratigraphically higher unit (Unit 3 or 4 of Petuch 1982) than the beds in this same pit in which the Bee Ridge Fauna occurs, both units are generally placed in the Tamiami Formation. Correlative Pinecrest strata in the nearby Macasphalt Shell Pit have produced a rich late Blancan fauna (late Pliocene, late Piacenzian, 2.5–1.9 Ma) of land mammals (Morgan and Ridgway 1987; Jones et al. 1991) and birds (Emslie 1992b).

A complete skull of a new species of dugongid sirenian that may be referable to the extant genus *Dugong* (Domning, pers. comm.) was recently collected from the Caloosahatchee Formation in the Forsberg Shell Pit near Punta Gorda, Charlotte County (Fig. 1, site

21). This specimen represents the youngest record of the family Dugongidae from Florida. An earliest Irvingtonian (latest Pliocene, late Piacenzian, 1.9–1.6 Ma) land mammal fauna also occurs in the Caloosahatchee Formation in the Forsberg Shell Pit (Morgan and Hulbert 1994).

Two balaenopterid dentaries have been collected from commercial shell pits in the Nashua Formation in central Florida. One represents a small species similar in size to *Balaenoptera acutorostrata* from the Meade Sand Pit in Seminole County (Fig. 1, site 12), the other a much larger species tentatively referred to *Megaptera* from the F and W Mine in Orange County (Fig. 1, site 13). The F and W Mine also has produced an auditory bulla of the right whale *Eubalaena*, the oldest record of this genus in Florida. Huddlestun (1988) considered the Nashua Formation to be late Pliocene to early Pleistocene on the basis of its planktonic foraminifera. He correlated the Nashua Formation with the Caloosahatchee Formation, suggesting a latest Pliocene age.

The Pleistocene record of marine mammals in Florida is poor, despite the fairly widespread occurrence of marine Pleistocene geologic units in the southern half of the peninsula. Species of cetaceans identified from the Florida Pleistocene include *Eubalaena glacialis*, *Eschrichtius robustus*, *Megaptera novaeangliae*, *Pseudorca crassidens*, and *Globicephala macrorhynchus* [originally described as *G. baereckeii* Sellards, 1916, but I concur with Ray (1957) that the fossil species is almost certainly a synonym of *G. macrorhynchus*]. The fossils of at least two of these species, *E. robustus* and *G. macrorhynchus*, may be derived from Holocene, not Pleistocene, deposits. The gray whale, *Eschrichtius robustus*, no longer occurs in the Atlantic Ocean. However, there are numerous late Pleistocene and Holocene records of this species from the western north Atlantic (Mead and Mitchell 1984), including partial skulls from two localities in Florida, Jacksonville Beach in Duval County (UF 99000) and Jupiter Island in Martin County (UF 69000). The oldest Florida records of the West Indian monk seal, *Monachus tropicalis*, are from the Leisey Shell Pit in Hillsborough County and the Rigby Shell Pit in Sarasota County, both of which are early Pleistocene (early Irvingtonian) in age. The earliest verified record of the manatee, *Trichechus manatus*, in Florida is also from the Leisey Shell Pit.

COMPARISON AND CORRELATION OF MAMMAL FAUNAS FROM THE BONE VALLEY FORMATION AND CHESAPEAKE GROUP

There are few similarities between the mammalian faunas of the Bone Valley Formation of central Florida and those of the Chesapeake Group (including the Calvert, Choptank, St. Mary's, Eastover, and Yorktown formations) of the middle Atlantic coastal plain. The formations in the Chesapeake Group have abundant cetaceans and frequent pinnipeds, whereas sirenians and land mammals are rare. The Bone Valley Formation has a more limited cetacean fauna and few pinnipeds, but sirenians are common (particularly in the older units) and there is a diverse land mammal fauna. The more tropical latitude of the Florida peninsula and the predominantly nearshore marine depositional environments in the Bone Valley Formation probably account for some of these differences. The less diverse cetacean fauna of the Bone Valley Formation may also be related to the fairly limited outcrop area of this unit in central Florida and the ephemeral nature of exposures resulting from the phosphate mining process and rapid subsequent land reclamation. In contrast, the formations of the Chesapeake Group are widely distributed on the coastal plain in Maryland, Virginia, and North Carolina and often occur in thick, natural exposures, especially around Chesapeake Bay. Fortunately, there is enough overlap between the three major vertebrate faunas of the Bone Valley Formation and the faunas of the Chesapeake Group in both marine and land mammals to permit preliminary comparisons.

The co-occurrence of diverse land and marine mammal faunas in the Bone Valley Formation provides a strong basis for correlation with the Chesapeake Group and the North American land mammal biochronology. Although land mammals do occur in the Chesapeake Group, they generally consist of isolated fragmentary specimens often lacking precise stratigraphic data. The Calvert and Choptank formations have produced a fairly diverse Barstovian land mammal fauna (Gazin and Collins 1950; Tedford and Hunter 1984; Wright and Eshelman 1987). Tedford and Hunter (1984) combined the land mammals from the upper portion of the Calvert Formation and the Choptank Formation into the Chesapeake Bay Fauna of early late Barstovian age (about 14.5–13.5 Ma). Wright and Eshelman (1987) noted that the Tayassuidae from the upper Calvert Formation are typical of faunas from the early phase of the late Barstovian in western North America, but that "*Prosthennops*" *niobrarensis* from the Choptank Formation is more indicative of a latest Barstovian age. Two early Barstovian vertebrate faunas derived from the Arcadia Formation in the Bone Valley region, the Bird Branch LF and the Sweetwater Branch LF (Hulbert and MacFadden 1991), are probably equivalent in age to a portion of the Calvert Formation but, by the land mammal biochronology, are somewhat older than the Chesapeake Bay Fauna. Neither of the Bone Valley early Barstovian sites has produced identifiable specimens of marine mammals.

The late Barstovian Bradley Fauna (13.5–11.5 Ma), the oldest vertebrate fauna from the Bone Valley Formation that contains identifiable marine mammals, appears to be similar in age to the Choptank Formation (Webb and Hulbert 1986; Wright and Eshelman 1987; Hulbert 1988b). The Bradley Fauna has a rich sample of late Barstovian equids (Hulbert 1988b) but lacks tayassuids, while both the Choptank Formation and the Bradley Fauna contain specimens of an early species of *Gomphotherium*, cf. *G. calvertense*. The absence from the Bradley Fauna of certain cetacean groups, including eurhinodelphids and squalodonts, seems to strengthen correlation of this fauna with the Choptank Formation rather than with the slightly older Calvert Formation.

The early Clarendonian Agricola Fauna appears to correlate with the St. Mary's Formation, although they have very few taxa of land or marine mammals in common. A glauconite K/Ar date of 12.3 Ma has been obtained from the base of the St. Mary's Formation (Blackwelder 1981; Tedford and Hunter 1984), suggesting a late Barstovian correlation. Tedford and Hunter (1984) placed the top of the St. Mary's Formation at approximately 10 Ma, corresponding to the end of the early Clarendonian. A jaw of the horse *Cormohipparion* from the St. Mary's Formation seems to support a late Barstovian/early Clarendonian age assignment, although very few other diagnostic land mammals have been reported from this unit (Blackwelder 1981; Tedford and Hunter 1984). The land mammals from the Agricola Fauna clearly indicate an early Clarendonian age (11.5–10.5 Ma).

Several late Miocene marine mammal faunas from Florida, including the latest Clarendonian and early Hemphillian (9–8 Ma) Archer Fauna derived from the Alachua Formation, the early Hemphillian Gainesville Creeks Fauna derived from the Hawthorn Group, and the late early Hemphillian (8–7 Ma) Manatee Fauna, are probably correlative with the Eastover Formation of the Atlantic coastal plain. Glauconite K/Ar dates from near the base (8.9 Ma) and the top (6.6 Ma) of the Cobham Bay Member of the Eastover Formation, the uppermost member of this unit, indicate a late Miocene age (Tedford and Hunter 1984). This interval corresponds to the Hemphillian NALMA (Tedford et al. 1987), although diagnostic Hemphillian land mammals have not yet been reported from the Eastover. The base of the Eastover Formation may be as old as 11 Ma (Andrews 1986; Whitmore this volume), and therefore the lower portion of this unit may be the same age as the early Clarendonian Agricola Fauna.

The basal Yorktown Formation at the Lee Creek Mine in North Carolina contains an extremely rich fauna of cetaceans and pinnipeds, as well as occasional fragmentary specimens of land mammals. Similarities between the marine mammals from Lee Creek and the Palmetto Fauna include the presence of the pinnipeds *Trichecodon huxleyi*, *Callophoca obscura*, and *Phocanella pumila*, the ziphiid *Ninoziphius platyrostris*, an undescribed pontoporiid, and the predominance of balaenopterid mysticetes. Although the land mammals of the Lee Creek LF are not diverse, the presence of the canid *Osteoborus* (= *Borophagus*) *dudleyi*, the equid *Pseudhipparion simpsoni*, and the protoceratid *Kyptoceras amatorum* (Tedford and Hunter 1984; R. E. Eshelman, F. C. Whitmore, Jr., and C. E. Ray, pers. comm.) all strongly suggest correlation with the better-known late Hemphillian Palmetto Fauna from the Bone Valley Formation.

A glauconite K/Ar date of 4.4 Ma has been obtained from the Yorktown Formation in Virginia, and the biochronology of planktonic foraminifera and ostracodes associated with the Lee Creek LF indicate an early Pliocene age (zone N19/20) for this unit (Gibson 1983; Hazel 1983; Snyder et al. 1983). These ages agree closely with the age range proposed here for the Palmetto Fauna (5.2–4.5 Ma) based on the land mammal biochronology. Both the Lee Creek LF and the Palmetto Fauna were deposited during periods of high sea level and thus are post-Messinian (younger than 5.2 Ma) but are older than 4.5 Ma, the age of the Hemphillian/Blancan boundary (Lindsay et al. 1984; Tedford and Hunter 1984; Tedford et al. 1987). According to Tedford and Hunter (1984:139), "the Lee Creek Local Fauna and its equivalent in the upper part of the Bone Valley Formation are among the latest Hemphillian faunas known."

SYSTEMATICS

The following accounts of the marine mammals currently known from the Bone Valley Formation emphasize taxa not previously reported (e.g., ziphiids), species for which significant new material has been collected (e.g., *Enhydritherium terraenovae*), and taxonomic changes. Species that have been reviewed recently, such as the sirenian *Metaxytherium floridanum* (see Domning 1988), or taxa for which no additional diagnostic material has been recovered since the original description, are only briefly discussed. The Bone Valley pinnipeds are currently under study by C. E. Ray and I. Koretsky and thus are not covered in detail. The synonymies list only the literature in which specimens from the Bone Valley Formation are described or figured. Likewise, I cite only holotypes and referred specimens described from the Bone Valley Formation and describe the morphology only of taxa not previously reported from it.

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Family Platanistidae Gray, 1863

Pomatodelphis Allen, 1921

Pomatodelphis Allen, 1921:148.
Schizodelphis Gervais, 1861 (in part). Allen, 1921:145. Case, 1934:105.

Discussion.—Allen (1921) described the genus *Pomatodelphis*, with *P. inaequalis* from the Bone Valley Formation as the type species. In this same paper, he described another new species of long-beaked dolphin, *Schizodelphis depressus*. Case (1934) later described a second species of *Schizodelphis* from the Bone Valley Formation, *S. bobengi*. However, Muizon (1988a) demonstrated that typical members of the genus *Schizodelphis* from the Miocene of France belong to the family Eurhinodelphidae. Neither of the two nominal species from the Bone Valley Formation previously referred to *Schizodelphis* are eurhinodelphids. Representative eurhinodelphids, such as the genera *Eurhinodelphis* and *Rhabdosteus* from the Calvert Formation, lack teeth on the distal extremity of the rostrum, possess mandibles that are much shorter than the rostrum, and have dissimilar rostra and mandibles that are not noticeably flattened dorsoventrally. In contrast, the rostrum and mandibles of *S. depressus* and *S. bobengi* have teeth all the way to their distal extremities, are the same length, and are dorsoventrally flattened mirror images of one another. Therefore, the two species of *Schizodelphis* described from the Bone Valley Formation appear to have been incorrectly referred to that genus. Both of these species closely resemble *Pomatodelphis* in the morphology of the rostrum, mandibles, periotic, and supraorbital process of the frontal, and are here transferred to that genus. As discussed below, *S. depressus* is a synonym of *P. inaequalis*. *Pomatodelphis* is referred to the Platanistidae (Muizon 1987).

All Bone Valley skulls referred to *Pomatodelphis* have the same general morphology characterized by a greatly elongated rostrum that is strongly flattened dorsoventrally. The anterior two-thirds of the rostrum and mandibles are extremely similar in external form, appearing to be almost mirror images of one another. The species of *Pomatodelphis* are also similar in the structure of the supraorbital process of the frontal and the periotic. Although only two species of *Pomatodelphis* are recognized here, the smaller *P. inaequalis* and the larger *P. bobengi*, available Bone Valley specimens actually present a bewildering array of sizes. The skulls of *Pomatodelphis* differ in size and proportions of the rostrum. A small, narrow-beaked form with tiny teeth is tentatively referred to *P. inaequalis*, while specimens referred to *P. bobengi* have a comparatively shorter and broader beak, larger teeth, and reach over a meter in skull length. Furthermore, although the braincase of "*Megalodelphis magnidens*" is unknown, the rostrum and mandibles of this enormous long-beaked odontocete are elongated, dorsoventrally flattened, and mirror images of one another, as in *Pomatodelphis*.

Pomatodelphis inaequalis Allen, 1921

Platanistidae, genus and species indet. Sellards, 1915:102, fig. 31.
Pomatodelphis inaequalis Allen, 1921:148, pls. 10, 11, figs. 7–12. Kellogg, 1959:7, fig. 1, pls. 1–6.
Schizodelphis depressus Allen, 1921:145, pl. 9, figs. 1–5.

Holotype.—MCZ 15750, fragment of right maxilla with 13 alveoli (Allen 1921: pl. 11, fig. 10).

Type locality.—Amalgamated Phosphate Company Mine, Brewster, Polk County, Florida. Collected by Anton Schneider.

Referred specimens.—FGS 5834 (recatalogued as UF/FGS 568), partial skull and rostrum (Allen 1921: pl. 10, figs. 7, 8; pl. 11, figs. 11, 12) from the Phosphate Mining Company, Mulberry, Polk County, Florida. FGS 828, fragment of rostrum (holotype of *Schizodelphis depressus* Allen, 1921: pl. 9, figs. 1, 2), Dominion Phosphate Company Mine, 5 miles south of Bartow, Polk County, Florida (this specimen was later transferred to the Smithsonian Institution and recatalogued as USNM 16758). FGS 5885 (recatalogued as UF/FGS 1298), fragment of rostrum [originally referred to *S. depressus* (Allen, 1921: pl. 9, figs. 3, 4)] from the Amalgamated Phosphate Company Mine, Brewster, Polk County, Florida. MCZ 4433, nearly complete skull from the Homeland Mine, near Homeland, Polk County, Florida (Kellogg 1959: pls. 1–4, pl. 5, figs. 1, 2). USNM 20738, incomplete rostrum from the Noralyn Mine, 3 miles south of Bartow, Polk County, Florida (Kellogg 1959: pl. 5, fig. 3).

The following specimens of *Pomatodelphis inaequalis* were collected during the past 15 years from the IMC Phosphoria Mine, Polk County, Florida. UF 27502, partial braincase and posterior portion of rostrum with associated right periotic; UF 50000, nearly complete skull; UF 54000, complete braincase and posterior portion of rostrum with associated left periotic; UF 58078, associated partial rostrum and mandibles; UF 61938, complete braincase and posterior portion of rostrum; UF 115691, nearly complete skull and associated mandibles; USNM 299695, complete braincase and partial rostrum; USNM 360056, nearly complete skull.

Age and stratigraphic occurrence.—*Pomatodelphis inaequalis* is the second most abundant marine mammal in the Bone Valley Formation after the dugong *Metaxytherium floridanum*. Both of these species occur in the fine-grained marine unit of the lower Bone Valley Formation (Unit 4 of Webb and Crissinger 1983) and are common taxa of the early Clarendonian Agricola Fauna. Fragmentary specimens of *P. inaequalis* also have been found in the late Barstovian Bradley Fauna. No specimens of *Pomatodelphis* have been recovered in the Bone Valley region from the late Hemphillian Palmetto Fauna. Specimens referable to this species are also known from the early Clarendonian Occidental Fauna in the Statenville Formation in Hamilton County and the early Hemphillian Gainesville Creeks Fauna in Alachua County.

Discussion.—Both Allen (1921) and Kellogg (1959) described *Pomatodelphis inaequalis* in considerable detail, but neither author made thorough comparisons of this species with *Schizodelphis depressus*, which was described from only two rostral fragments. Recent study of numerous skulls, rostra, and mandibles of long-beaked dolphins collected *in situ* from the lower Bone Valley Formation indicates that the characters proposed by Allen (1921) as supposedly separating *P. inaequalis* and *S. depressus*, including the presence or absence of pits in the maxillae to receive the posterior mandibular teeth, are quite variable. I consider these two names synonyms. Allen (1921) proposed *S. depressus* (p. 145) and *P. inaequalis* (p. 148) in the same paper, with the former having page priority. The holotypes of both species consist of rostral fragments, but Kellogg (1959) referred a complete skull from the Bone Valley Formation to *P. inaequalis*. Because *P. inaequalis* is the better known and more thoroughly described of the two species, I select it as the senior synonym.

Examination of the large sample of well-preserved skulls and mandibles of long-beaked dolphins from the Bone Valley Formation reveals a significant amount of variation in overall size, especially in the breadth of the rostrum and size of the teeth and alveoli. There appear to be two different sizes present among the smaller long-beaked dolphins here referred to *Pomatodelphis inaequalis*. The more common of the two forms is larger and has a broader rostrum (examples are MCZ 4433, UF 27502, UF 54000, UF 115691, UF/FGS 568, and USNM 299695). The holotypes of both *P. inaequalis* and *Schizodelphis depressus* belong to this larger form, as do all other published specimens, with one exception. The second form is smaller and has a noticeably narrower rostrum. This small form is best represented by a nearly complete skull (UF 50000), as well as by several partial rostra and mandibles, including UF 132953 from the Hookers Prairie Mine and a specimen Allen (1921) referred to *S. depressus* (FGS 5885 = UF/FGS 1298). Until a more thorough study is undertaken, it would be unwise to describe any new taxa of long-beaked dolphins from the Bone Valley Formation. However, it seems likely that the small, narrow-beaked form represents an undescribed species of *Pomatodelphis*.

Pomatodelphis bobengi (Case, 1934), new combination

Schizodelphis bobengi Case, 1934:106, pls. 1–2.

Pomatodelphis inaequalis Allen, 1921 (in part). Kellogg, 1959:22, pl. 6, figs. 1–4.

Holotype.—UMMP 15117, partial skull and associated mandibles.

Type locality.—International Agricultural Corporation Mine, Mulberry, Polk County, Florida. Collected by M. L. Bobeng in December 1932.

Referred specimens.—USNM 6683, anterior extremity of rostrum, and USNM 6684, anterior extremity of mandibular symphysis, from a phosphate mine at Christina, about 6.5 miles south of Lakeland, Polk County, Florida [these two specimens were referred to *Pomatodelphis inaequalis* by Kellogg (1959: pl. 6, figs. 1–4)]. UF 111800, nearly complete crushed braincase and posterior portion of rostrum with intact right and left periotics from the Phosphoria Mine, Polk County, Florida. USNM 323775, nearly complete skull and associated mandibles from the Phosphoria Mine, Polk County, Florida. MOSI, uncatalogued, complete skull, Tiger Bay Mine, Polk County, Florida.

Age and stratigraphic occurrence.—*Pomatodelphis bobengi* is not nearly as common as the smaller *P. inaequalis* and is restricted to the early Clarendonian Agricola Fauna. Three fairly complete skulls of *P. bobengi* have been collected *in situ* from the lower Bone Valley Formation.

Discussion.—Justification for transferring this species to *Pomatodelphis* was presented above. *P. bobengi* can be separated from *P. inaequalis* by its greater size (the three nearly complete skulls average about a meter in length), comparatively shorter and broader rostrum, and larger teeth. The holotype skull and a referred skull (UF 111800) of *P. bobengi* both have associated right and left periotics that, except for their larger size, are very similar to periotics associated with Bone Valley skulls of *P. inaequalis* (Fig. 5) and to the periotic associated with a referred skull of *P. inaequalis* from the Choptank Formation in Maryland (Muizon 1987). UF 111800 not only has both periotics but also possesses a greatly enlarged supraorbital process of the frontal, a feature characteristic of the genus *Pomatodelphis* (see Kellogg 1959; Muizon 1987).

Family Pontoporiidae (Gill, 1871)

Genus and Species Undetermined

Referred specimens.—UF 135926, left periotic, Palmetto Mine, Polk County, Florida. UF 135935, left periotic, Payne Creek Mine, Polk County, Florida.

Age and stratigraphic occurrence.—Both pontoporiid periotics from the Bone Valley Formation were collected from spoil piles in mines that have produced land mammals representative of the late Hemphillian Palmetto Fauna.

Description.—Except for their larger size, the two periotics from the Bone Valley Formation are very similar to periotics of the modern La Plata river dolphin, *Pontoporia blainvillei*, from South America (Fig. 6). The periotics of both taxa are characterized by their extremely small anterior and posterior processes, particularly the former. The anterior process barely projects beyond the cochlear portion of the periotic. Because of the reduced anterior and posterior processes, the cochlear region appears to be comparatively larger in *Pontoporia* and the fossils than in most other odontocetes. The Bone Valley periotics have a somewhat larger cochlear region that is slightly more squarish than that of *P. blainvillei*. The strong similarity between the Bone Valley periotics and those of modern *Pontoporia* suggests that the fossils should be referred to the family Pontoporiidae. Periotics similar to those from the Bone Valley Formation are also known from the early Pliocene Lee Creek LF (F. C. Whitmore, Jr., pers. comm.). Barnes (1985) compared the periotics of *Pontoporia* and the late Miocene and Pliocene pontoporiid *Parapontoporia sternbergi* from the Pacific coast of California and Mexico. The periotic of *Parapontoporia* differs from that of *Pontoporia* and the Bone Valley pontoporiid in

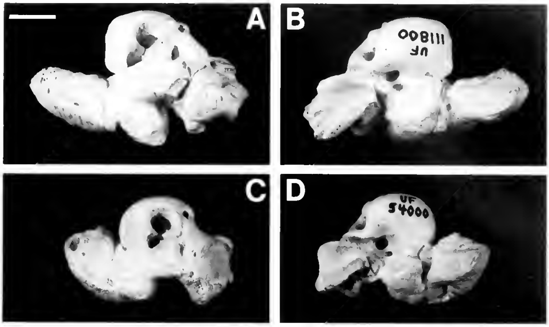

Figure 5. Left periotics of *Pomatodelphis* from the Phosphoria Mine, Polk County, Florida, early Clarendonian. *Pomatodelphis bobengi*, UF 111800; A, dorsal view; B, ventral view. *Pomatodelphis inaequalis*, UF 54000; C, dorsal view; D, ventral view. Scale equals 10 mm.

having a relatively smaller cochlear portion and a much larger anterior process.

A fragment of the fused right and left mandibles (UF 95685) of a very small odontocete from the Gardinier Mine (Fig. 7) was compared to mandibles of *Pontoporia*, *Parapontoporia*, and the two genera of long-beaked odontocetes from the Bone Valley Formation, *Pomatodelphis* and *Goniodelphis*. The preserved portion of the mandibles is slightly less than 80 mm long, 12.5 mm in maximum width, and has empty alveoli for approximately 20 teeth on each side. The individual alveoli are indistinct, and the teeth were rooted in a narrow, deep alveolar groove. The interalveolar region is flat and considerably higher than the lateral alveolar margin. The mandibles are elliptical in cross-section, being very slightly flattened laterally. The ventral surface is nearly featureless, except for two shallow, narrow grooves located on the anterior 15 mm of the preserved fragment that extend anteriorly from the mental foramina just lateral to the midline.

UF 95685 differs from mandibles of *Pomatodelphis* and *Goniodelphis* in several important features, including very small size. In contrast to the possible pontoporiid, the mandibles of *Pomatodelphis* are strongly flattened dorsoventrally, possess deep longitudinal grooves on either side of the midline, and have larger teeth that are more widely spaced. Compared to the tiny Bone Valley odontocete, the mandibles of *Goniodelphis* are more laterally compressed, have large anteroposteriorly elongated alveoli, and have a very narrow, ridgelike interalveolar region. The Bone Valley fossil also exhibits several differences from *Pontoporia blainvillei*. The mandibles of *Pontoporia* are flattened dorsoventrally and have narrow, deep, longitudinal grooves on the ventral surface just lateral to the midline that extend from the posterior edge of the symphysis almost to the anterior tip. The Bone Valley mandibles are not dorsoventrally flattened and there is no evidence of deep, elongated grooves on the ventral surface. Furthermore, although the interalveolar region in *Pontoporia* is narrow compared to that of most other small odontocetes, it is comparatively broader than in the Bone Valley fossil, even though the latter specimen is somewhat larger. Like *Pontoporia*, and unlike the Bone Valley fossil, the mandibles of *Parapontoporia* are dorsoventrally flattened and have well developed longitudinal grooves lateral to the midline on the ventral surface.

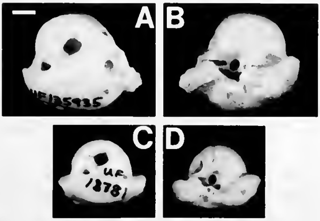

Figure 6. Undescribed pontoporiid, left periotic, UF 135935, Payne Creek Mine, Polk County, Florida, late Hemphillian; A, dorsal view; B, ventral view. *Pontoporia blainvillei*, left periotic, UF 18781 (mammalogy), La Plata River, Uruguay, modern; C, dorsal view; D, ventral view. Scale equals 5 mm.

Discussion.—The similarity of the two Bone Valley periotics to the periotic of *Pontoporia blainvillei* seems to confirm that a member of the family Pontoporiidae was present in Florida during the early Pliocene. These two specimens and similar periotics from the Lee Creek Mine in North Carolina (F. C. Whitmore, Jr., pers. comm.) represent the first records of this South American odontocete family from the Atlantic coast of North America. The affinities of the mandible fragment (UF 95685) from the Bone Valley Formation are more problematic, as it differs from *Pontoporia* in several important morphological characters.

Family Iniidae Flower, 1867

Goniodelphis Allen, 1941

Goniodelphis hudsoni Allen, 1941

Goniodelphis hudsoni Allen, 1941:4, pls. 1–3. Kellogg, 1944:434, pl. 1, figs. 1–2, pl. 2, fig. 1.

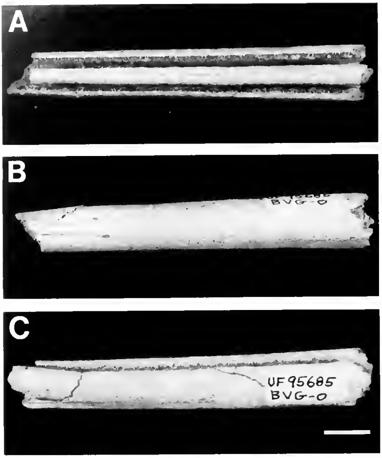

Figure 7. Small unidentified odontocete, fragment of fused right and left mandibles, UF 95685, Gardinier Mine, Polk County, Florida, late Hemphillian; A, dorsal view; B, ventral view; C, left lateral view. Scale equals 10 mm.

Holotype.—MCZ 3920, partial skull lacking the braincase and anterior portion of the rostrum (Allen 1941: pls. 1–3). Collected by H. L. Hudson.

Type locality.—American Agricultural Chemical Company Mine, Pierce, Polk County, Florida.

Referred specimens.—MCZ 17881, large portion of fused left and right mandibles (Kellogg 1944: pl. 1, figs. 1, 2), and MCZ 17879, partial right mandible (Kellogg 1944: pl. 2, fig. 1), collected from the type locality. UF 55921, UF 57349, and UF 57350, rostral fragments from the Fort Green Mine, dragline 13, Polk County, Florida. UF 121944, UF 135908, and UF 135909, rostral fragments, and UF 135906 and UF 135907, mandible fragments, from the Whidden Creek LF, Gardinier Mine, Polk County, Florida. UF 135910 and UF 135911, rostral fragments, from the Payne Creek Mine, Polk County, Florida.

Age and stratigraphic occurrence.—Allen (1941:4) gave the age of the type skull of *Goniodelphis hudsoni* as "probably early Pliocene." In his discussion of this species, Kellogg (1944:434) noted that "the type and ankylosed mandibular rami presumably were derived from the pebble phosphate deposits, which belong to the lower Pliocene Bone Valley Formation; the short portion of the right mandibular ramus is thought to have been removed from the laminated blue clays, immediately below the pebble phosphate, which are tentatively referred to the middle Miocene Hawthorn Formation." Kellogg's wording suggests that he was uncertain of the stratigraphic provenience of these specimens. Several cetacean taxa, including *G. hudsoni*, that Kellogg (1944) thought were derived from the laminated blue clays of the lower Bone Valley Formation are now known to be restricted to the pebble phosphate deposits of the upper Bone Valley Formation.

Over the past ten years a small sample of rostral and mandibular fragments of *Goniodelphis hudsoni* has been collected from the Bone Valley Formation in direct association with late Hemphillian faunas. Five rostral and mandibular fragments of *G. hudsoni* were collected in 1990 from the Whidden Creek LF in the Gardinier Mine, here assigned to the late Hemphillian Palmetto Fauna. Several specimens of *G. hudsoni* were collected from spoil piles in the Fort Green Mine (Number 13 Dragline), a site that also produced a rich sample of land mammals characteristic of the Palmetto Fauna.

Discussion.—Despite the recent discovery of much additional material of *Goniodelphis hudsoni*, the type skull described by Allen (1941) and the nearly complete set of mandibles described by Kellogg (1944) are still the most complete specimens known of this species. Muizon (1988b) tentatively referred *Goniodelphis* to the Iniidae, although he noted that a definite allocation was not possible without a braincase. The occurrence of *G. hudsoni* in the Palmetto Fauna, a vertebrate assemblage that contains many freshwater taxa, suggests the possibility that this species may have frequented freshwater habitats, as does its living relative, the Amazon dolphin or boutu, *Inia geoffrensis*.

Family Kentriodontidae (Slijper, 1936)

Hadrodelphis Kellogg, 1966

Hadrodelphis sp.

Referred specimen.—UF 97037, tooth, Gardinier Mine, Number 7 Dragline, Polk County, Florida.

Age and stratigraphic occurrence.—The Bone Valley tooth was collected from a spoil pile and thus lacks stratigraphic context. Although the great majority of land mammals from the Gardinier Mine belong to the late Hemphillian Palmetto Fauna, several horse teeth collected from this mine are early Clarendonian. *Hadrodelphis calvertense* Kellogg, 1966, is known from the middle Miocene Calvert and Choptank formations in Maryland (Kellogg 1966; Dawson 1992). A second tooth of *Hadrodelphis* (UF 58517) has been identified from the early Hemphillian (late Miocene) Gainesville Creeks Fauna from Alachua County. The probable age of the Florida *Hadrodelphis* teeth is Clarendonian or Hemphillian, although a Barstovian age is possible.

Discussion.—The two Florida teeth here referred to *Hadrodelphis* are very similar to one another and to specimens of *H. calvertense* from the Calvert Formation. The enamel crown of *Hadrodelphis* teeth is bulbous and subconical, and its apex curves inward, overhanging a broad internal basal shelf (Kellogg 1966). The entire crown is covered by irregular, finely striated enamel. The two Florida specimens possess the characteristic shape and enamel ornamentation of the Calvert *Hadrodelphis* teeth. From previously undescribed skulls, Dawson (1992) regarded *Hadrodelphis* as a primitive member of the Kentriodontidae.

Family Delphinidae (Gray, 1821)

Genus and Species Undetermined

Referred specimen.—UF 58052, anterior portion of right mandible including symphysis and four teeth, Palmetto Mine, Polk County, Florida.

Age and stratigraphic occurrence.—This mandible lacks stratigraphic context. It was collected from a spoil pile in the Palmetto Mine, which has produced the typical sample of land mammals constituting the late Hemphillian Palmetto Fauna (Webb and Hulbert 1986).

Description.—The Bone Valley mandible fragment (Fig. 8) is

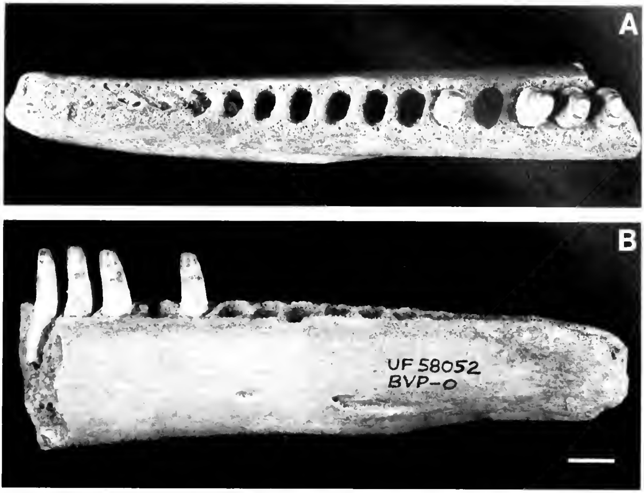

Figure 8. Undescribed delphinid, anterior portion of right mandible, UF 58052, Palmetto Mine, Polk County, Florida. late Hemphillian; A, dorsal view; B, right lateral view. Scale equals 10 mm.

131 mm long. There are alveoli for 16 teeth, of which numbers 12 and 14–16 are preserved. The most anterior 20 mm of the symphysis appears to have been edentulous, although this region may have possessed several tiny symphyseal teeth as in some modern delphinids. The most characteristic features of this mandible are the long symphysis (79.8 mm) and teeth that are strongly compressed anteroposteriorly. Not only the tooth crowns but also the roots are noticeably flattened. Each of the four teeth preserved in UF 58052 has a smooth enamel crown that is flattened apically by occlusal wear from the upper teeth. The two most posterior teeth also have distinct wear facets on their posterior surface.

The strongly flattened tooth crowns and roots of the Bone Valley specimen are unlike any teeth of modern odontocetes, most of whose teeth are round in cross-section. However, the closest match in both dental and mandible morphology is found among certain members of the Delphinidae. The Bone Valley fossil is tentatively referred to this family pending discovery of more diagnostic material.

Family Ziphiidae Gray, 1865

Mesoplodon Gervais, 1850

Mesoplodon sp.

Referred specimen.—UF 24171, partial rostrum, Payne Creek Mine, Polk County, Florida.

Age and stratigraphic occurrence.—The single specimen of *Mesoplodon* from the Bone Valley Formation was collected in 1977 from a spoil pile in the northeast corner of the Payne Creek Mine. One of the richer *in situ* samples of the late Hemphillian Palmetto Fauna, the TRO Quarry, was excavated from the same region of the Payne Creek Mine. The preservation of the *Mesoplodon* rostrum is consistent with other specimens collected from the TRO Quarry, indicating an early Pliocene age.

Description.—The rostrum (Fig. 9) is edentulous, ruling out referral to *Ninoziphius*. This specimen was compared to the extant species *Ziphius cavirostris* and to most living members of the genus *Mesoplodon*, as well as to the extinct species *M. longirostris*. The fossil differs from *Ziphius* and resembles *Mesoplodon* in having the rostrum elliptical to somewhat laterally flattened in cross-section. The rostrum tends to be dorsoventrally flattened in *Ziphius*. Posteriorly, the intermaxillary region and maxillaries form a deep, rounded concavity in *Ziphius*, whereas in *Mesoplodon* this area varies from slightly concave to noticeably convex. The fossil is missing the region posterior to the maxillary foramina, but the posterior portion of the intermaxillary region is slightly convex. The mesorostral ossification, although highly variable, tends to be better developed in *Mesoplodon* than in *Ziphius*. The Bone Valley specimen is well ossified mesorostrally. In all characters examined the Bone Valley fossil is similar to *Mesoplodon*.

UF 24171 is most similar to *Mesoplodon europaeus* among living species, although there are several differences. Both the fossil and *M. europaeus* have a prominent mesorostral ossification, a feature that tends to be somewhat variable in species of *Mesoplodon*. Nonetheless, this ossification is flattened posteriorly in the fossil and has a more prominent convexity in *M. europaeus*. The fossil is somewhat worn, but its maxillae are narrower posteri-

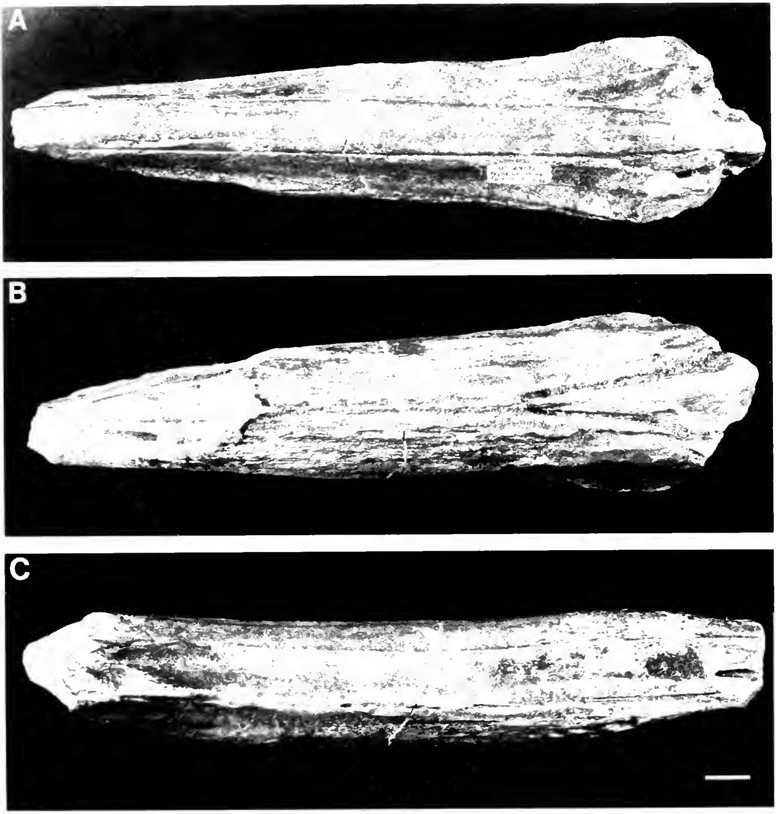

Figure 9. *Mesoplodon* sp., partial rostrum, UF 24171, Payne Creek Mine, Polk County, Florida, late Hemphillian; A, dorsal view; B, ventral view, C, right lateral view. Scale equals 20 mm.

orly and the lateral maxillary ridges are weaker than in the modern species. Finally, the Bone Valley specimen is narrower anteriorly than rostra of *M. europaeus*.

The extinct Miocene and Pliocene species *Mesoplodon longirostris* is the only fossil ziphiid previously reported from Florida (Whitmore et al. 1986). The Bone Valley rostrum was compared directly to the single Florida specimen of *M. longirostris* (USNM 336180) and to the figures and descriptions of this rostrum in Whitmore et al. (1986). Compared to *M. longirostris*, the Bone Valley rostrum is broader, has more prominent maxillary ridges, and has a wider and more dorsally exposed mesorostral ossification.

Discussion.—The first record of a fossil ziphiid from Florida was of a rostrum of *Mesoplodon longirostris* (Cuvier, 1823) dredged from a depth of 650 m in the Atlantic Ocean about 35 km east of Miami (Whitmore et al. 1986). On the basis of microfossils from associated phosphorites this specimen is probably early middle Miocene in age. The rarity of ziphiid fossils in Florida probably results from a combination of the lack of geologic units that sample deep-water, offshore environments and the pelagic habits of most beaked whales.

Ninoziphius Muizon, 1983

Ninoziphius platyrostris Muizon, 1983

Ninoziphius platyrostris Muizon, 1983:85, figs. a–d.

Referred specimens.—UF 132931, partial fused right and left mandibles, Phosphoria Mine, Polk County, Florida. UF 135912, three associated mandibular fragments, Payne Creek Mine, Polk County, Florida. UF 135913, partial fused right and left mandibles, Kingsford Mine, Polk County, Florida. USNM 323768, partial fused right and left mandibles, Fort Green Mine, Number 13 Dragline, Polk County, Florida.

Age and stratigraphic occurrence.—Only one specimen of *Ninoziphius platyrostris*, UF 135912, from the Bone Valley region has been collected *in situ*. This specimen, from the Payne Creek Mine, was partially embedded in a tan phosphatic sandy limestone referred to the Tamiami Formation by Brooks (1974) and Waldrop and Wilson (1990) from its lithology and invertebrate fossils. According to these authors, this sandy limestone was deposited between two phosphate pebble units typical of the upper Bone Valley Formation. The pebble phosphate bed overlying the Tamiami Formation contained several land mammals typical of the late Hemphillian Palmetto Fauna, as well as two rostral fragments of *Goniodelphis hudsoni*. USNM 323768 was collected from a spoil pile in the Fort Green Mine. Although this fossil lacks stratigraphic provenience, spoil piles in this region of the Fort Green Mine produced a diverse sample of land mammals characteristic of the Palmetto Fauna. *N. platyrostris* was originally described by Muizon (1983) from the early Pliocene Pisco Formation in Peru and has since been identified from the Yorktown Formation at the Lee Creek Mine, North Carolina (F. C. Whitmore, Jr., pers. comm.). The Pisco Formation, Yorktown Formation, and upper Bone Valley Formation are all early Pliocene.

Description.—The large number of alveoli in the Bone Valley mandibles rules out referral to *Mesoplodon* or *Ziphius*. The Bone Valley specimens, all consisting of fragments of the fused right and left mandibles, compare well to fossils identified as *Ninoziphius platyrostris* (e.g., USNM 317793, 362103) from the Lee Creek Mine (F. C. Whitmore, Jr., pers. comm.). Like the referred material from Lee Creek, the region between the tooth rows in the Bone Valley *Ninoziphius* mandibles is broad, gently concave, and elevated compared to the lateral alveolar margin (Fig. 10). The alveoli are round, very closely spaced, and lack a complete wall separating them from adjoining alveoli. Because the alveoli are partially coalesced, the alveolar region resembles a deep longitudinal groove. One of the Bone Valley specimens (UF 135912) preserves the anterior tip of the mandibles, revealing two large, rounded, anteriorly directed teeth. The Bone Valley *Ninoziphius* mandibles conform very closely with the description of the type mandible of *N. platyrostris* from Peru (Muizon 1983), particularly in the presence of two large teeth at the anterior tip and a deep alveolar groove with only rudimentary bony partitions between the teeth.

Ziphiidae

Genus and Species Undetermined

Referred specimen.—UF 28714, right periotic, Gray Zone Site, Phosphoria Mine, Polk County, Florida.

Age and stratigraphic occurrence.—The Gray Zone Site in the Phosphoria Mine has produced one of the richest *in situ* samples of land mammals representing the early Clarendonian Agricola Fauna from the lower Bone Valley Formation (Webb and Hulbert 1986; Hulbert 1988b).

Discussion.—UF 28714 was compared with periotics of the modern ziphiids *Ziphius cavirostris* and *Mesoplodon europaeus*. The Bone Valley fossil is considerably smaller than periotics of either of the two modern species but is otherwise quite similar (Fig. 11). All three taxa have a large, bulbous anterior process that is separated from the cochlear portion by a deep groove that extends onto the dorsal surface of the periotic. The anterior process is about equal in size to the cochlear portion in the two modern genera, while in UF 28714 the anterior process is not as inflated and thus is somewhat smaller than the cochlear region. The Bone Valley periotic also compares closely in size and morphological characters with a ziphiid periotic (USNM 310833) from the Lee Creek Mine, North Carolina (F. C. Whitmore, Jr., pers. comm.).

Family PHYSETERIDAE Gray, 1821

Scaldicetus sp.

?*Hoplocetus*, species indet. Kellogg, 1944:451, figs. 3, 4.

Referred specimens.—MCZ 17886, two teeth from the American Agricultural Chemical Company Mine, Pierce, Polk County, Florida. MOSI, uncatalogued, mandible with 16 teeth from the Fort Meade Mine, Polk County, Florida. UF 96251, tooth, and USNM 454332, two teeth, Hookers Prairie Mine, Polk County, Florida.

Age and stratigraphic occurrence.—Kellogg (1944) presumed that the two teeth he tentatively referred to *Hoplocetus* (= *Scaldicetus*) were derived from the pebble phosphate deposits of the Bone Valley Formation and were early Pliocene in age. Specimens of *Scaldicetus* have been collected *in situ* from the lower Bone Valley Formation at the Mobil Fort Meade Mine and the Hookers Prairie Mine. The Fort Meade Mine has produced a fauna of sirenians and long-beaked dolphins typical of the lower Bone Valley Formation. The early Clarendonian Agricola Road LF was collected from correlative strata in the same general area of the Hookers Prairie Mine where the three sperm whale teeth were found. Thus, *Scaldicetus* appears to be restricted to middle Miocene (Barstovian and Clarendonian) faunas in the Bone Valley region.

Discussion.—Isolated sperm whale teeth are difficult to identify, as noted by Kellogg (1944). Large physeterid teeth from the Lee Creek Mine in North Carolina are typically separated into two types. Teeth with bulbous roots and heavily striated enamel crowns are apparently derived from the middle Miocene Pungo River Formation. Such teeth have been assigned to the genus *Scaldicetus* du Bus, 1867. Teeth that lack an enamel crown and are cylindrical or have flattened roots are apparently derived from the Pliocene Yorktown Formation. Such teeth from Belgium have been placed in the genus *Physeterula* van Beneden, 1877. The Bone Valley sperm whale teeth with an inflated root and distinct crenulated enamel crown are tentatively placed in *Scaldicetus*, though this may represent a form genus.

Kogiopsis Kellogg, 1929

Kogiopsis floridana Kellogg, 1929

Kogiopsis floridana Kellogg, 1929:2, figs. 1–3.

Holotype.—AMNH 20470, symphyseal portion of lower jaws with eleven teeth collected by William D. Matthew in 1924.

Type locality.—American Cyanamid Company Pit at Brewster, Polk County, Florida.

Age and stratigraphic occurrence.—The age of *Kogiopsis*

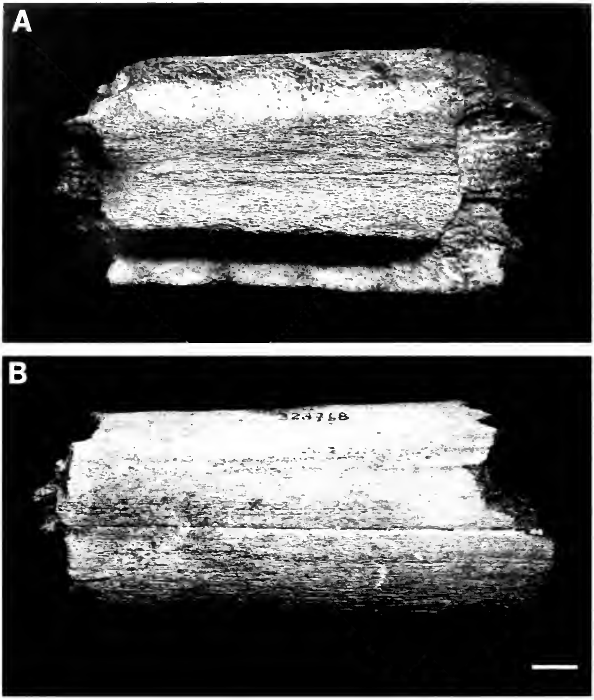

Figure 10. *Ninoziphius platyrostris*, fragment of fused right and left mandibles, USNM 323768, Fort Green Mine, Polk County, Florida, late Hemphillian; A, dorsal view; B, ventral view. Scale equals 10 mm.

floridana is unclear as the only known specimen of this species lacks stratigraphic provenience. Physeterid teeth similar to those of *Kogiopsis* are most typically found in association with the late Hemphillian Palmetto Fauna.

Discussion.—No specimens clearly identifiable as *Kogiopsis floridana* have been collected from the Bone Valley Formation since the original description of this species by Kellogg (1929). Bone Valley physeterid teeth that lack enamel crowns and have a generally cylindrical shape are tentatively referred to *Physeterula* (Table 2). Sperm whale teeth from the Bone Valley Formation with this morphology and similar teeth from the Lee Creek Mine both resemble teeth of *P. dubusii* from Belgium (F. C. Whitmore, Jr., pers. comm.). However, as noted by Kellogg (1929), the teeth of *Kogiopsis* are similar to those of *Physeterula*. It is highly probable that some teeth of *K. floridana* are included within the large sample of isolated physeterid teeth from the Bone Valley Formation. Isolated physeterid periotics, all of which lack stratigraphic provenience, are also fairly common in the Bone Valley region. Some of these periotics may pertain to *Kogiopsis* as well.

Suborder Odontoceti, *Incertae Sedis*

Delphinodon cf. *D. mento* (Cope 1868)

Referred specimens.—UF 131984, tooth, West Palmetto Mine, Polk County, Florida. UF 135797, tooth (cast), Noralyn Mine, Polk County, Florida. USNM 256525, tooth, Fort Green Mine, Polk County, Florida.

Age and stratigraphic occurrence.—All three teeth were collected from spoil piles and thus lack stratigraphic context.

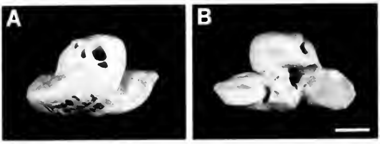

Figure 11. Ziphiid, genus and species undetermined, right periotic, UF 28714, Gray Zone Site, Phosphoria Mine, Polk County, Florida, early Clarendonian; A, dorsal view; B, ventral view. Scale equals 10 mm.

Delphinodon mento was originally described from the middle Miocene Calvert Formation in Maryland. The Bone Valley *D. mento* teeth are probably derived from the middle Miocene lower Bone Valley Formation and belong to either the late Barstovian Bradley Fauna or the early Clarendonian Agricola Fauna. Two other teeth tentatively identified as *D. mento* are known from elsewhere in Florida. One tooth (UF 116824, cast) is from the Willacoochee Creek Fauna of early Barstovian age from the Torreya Formation in Gadsden County, and a second tooth (UF 22604) is from the Devils Millhopper LF of middle or late Miocene age from Gainesville, Alachua County.

Discussion.—The Florida specimens were compared to a cast of one of the type teeth of *Delphinodon mento* and to a sample of isolated teeth of this species in the USNM collection, all from the Calvert Formation. The Bone Valley teeth are similar to *D. mento* in size and their conical to somewhat laterally flattened shape with a posteriorly oriented tip. The enamel is heavily striated, especially at the base of the crown, where there are also several large cuspules on the anterior and posterior edges. Isolated teeth of *D. mento* have been identified from the Calvert Formation and the correlative Pungo River Formation at the Lee Creek Mine in North Carolina. Although it is unwise to place too much emphasis on isolated odontocete teeth, the Florida specimens are very similar to teeth of the large species of *Delphinodon*, *D. mento*.

Suborder Odontoceti, *Incertae Sedis*

Genus and Species Undetermined

Genus and species indet. Sellards, 1915:102, fig. 32.

Diaphorocetus mediatlanticus (Cope, 1895) (in part). Allen, 1921:154, pl. 9, fig. 6, pl. 12, figs. 13, 14.

Schizodelphis bobengi Case, 1934:110 (in part).

Megalodelphis magnidens Kellogg, 1944:445, pl. 3, fig. 1 (in part).

Odontoceti, genus and species indet., Morgan, 1986:415.

Referred specimens.—MCZ 17880, partial rostrum from the American Agricultural Chemical Company Mine, Pierce, Polk County, Florida (Kellogg 1944: pl. 3, fig. 1). USNM 10922, associated rostrum and mandible from the Prairie Pebble Phosphate Company Mine, Mulberry, Polk County, Florida (Sellards 1915: fig. 32; Allen 1921: pl. 12, fig. 13). Sellards noted that the specimen was in the collection of the Prairie Pebble Phosphate Company, whereas Allen (1921) recorded it as lost. Sometime prior to 1934 this fossil was obtained by the U. S. National Museum, as Case (1934:110) referred USNM 10922 to "*S.* [*Schizodelphis*] *bobengi*, fide Kellogg in correspondence." UF 102692, fragment of mandibles, Phosphoria Mine, Polk County, Florida. UF 117367, rostral fragment, Hookers Prairie Mine, Polk County, Florida.

Age and stratigraphic occurrence.—The few known specimens of this large long-beaked odontocete (originally described as *Megalodelphis magnidens*) from the Bone Valley Formation lack stratigraphic data. The occurrence of two recently collected fossils in the Phosphoria Mine and Hookers Prairie Mine suggests that this species is probably derived from the middle Miocene lower Bone Valley Formation. A mandibular fragment (UF 95642) of this same large odontocete was collected from the middle Miocene (late Barstovian) Statenville Formation along the upper Suwannee River in Hamilton County, just south of the Georgia line.

Discussion.—The rostral fragment (MCZ 17880) and associated partial rostrum and mandibles (USNM 10922) referred to *Megalodelphis magnidens* by Kellogg (1944) clearly belong to some type of very large long-beaked odontocete. However, Kellogg (1944) selected a third specimen, a partial mandible with four teeth (MCZ 17883), as the holotype of *M. magnidens*. The type specimen has since been shown by Morgan (1986) to belong to the long-snouted crocodile *Gavialosuchus americanus* (Sellards, 1915), a fairly common species in the early Clarendonian Agricola Fauna. It seems inexplicable why Kellogg chose a partial mandible as the type, as USNM 10922 consists of an associated portion of the rostrum and mandibles containing at least ten teeth. Allen (1921) referred this same specimen to the sperm whale *Diaphorocetus mediatlanticus*, whereas Case (1934:110) placed it in *Schizodelphis bobengi*, supposedly on Kellogg's authority. Kellogg (1944:454) later stated that USNM 10922 "seems to be allied to if not identical with *Megalodelphis magnidens*," although he did not list this fossil as a referred specimen in the formal description of *M. magnidens*. Instead he mentioned USNM 10922 in his discussion of Bone Valley physeterids.

The giant long-beaked dolphin from the Bone Valley Formation is thus now without a name. Only fragmentary specimens of the rostrum and mandibles and isolated teeth are known of this taxon, described by Kellogg (1944:445) as "the largest known long-beaked porpoise, either extinct or living." Kellogg (1944) noted that the dorsoventrally compressed and elongated rostrum and mandibles of this large odontocete are similar in shape to those of *Pomatodelphis*. However, the rostrum of "*Megalodelphis*" is considerably broader and the teeth are much larger than in either species of *Pomatodelphis*. It would be ill-advised to propose a new name for this species until a skull or braincase is found.

Suborder Mysticeti Flower, 1864

Family "Cetotheriidae" Cabrera, 1926

Age and stratigraphic occurrence.—Kellogg (1944) tentatively identified two genera of "cetotheres," ?*Mesocetus* and ?*Isocetus*, from the Bone Valley region on the basis of isolated auditory bullae. According to Kellogg (1944:454–455), the specimens of ?*Mesocetus* were derived from "laminated blue clays immediately below the pebble phosphate, which are tentatively referred to the Hawthorn formation," whereas the bullae of ?*Isocetus* were (p. 457) "presumably from the laminated blue clays." Kellogg's indecisiveness with regard to the stratigraphic provenience of the ?*Isocetus* specimens suggests they were collected from spoil piles. The "laminated blue clays" of Kellogg are almost certainly the same as the fine-grained marine Unit 4 of the lower Bone Valley Formation that produces abundant well-preserved marine mammals. Careful stratigraphic collections accumulated from the Bone Valley Formation over the past 20 years confirm that "cetotheres" are restricted to the middle Miocene Bradley and Agricola faunas. The most abundant and complete "cetothere" fossils occur in the early Clarendonian Agricola Fauna.

Discussion.—A detailed analysis of the Bone Valley "cetotheres" is beyond the scope of this study. Furthermore, their identification and phylogenetic relationships are questionable, as a thorough systematic review of the entire group of small to medium-sized Miocene mysticetes typically placed in the family

"Cetotheriidae" is needed. The monophyly of this group has been questioned by several authors, hence the use of quotes.

Three nearly complete skulls of "cetotheres," as well as several partial skulls and complete dentaries, are known from the lower Bone Valley Formation, and most were collected *in situ*. Isolated "cetothere" auditory bullae and periotics are also fairly common, although most of these lack stratigraphic data. On the basis of morphological differences in isolated auditory bullae, there are at least three genera and four species of "cetotheres" in the Bone Valley Formation. The two Bone Valley bullae Kellogg (1944) assigned to ?*Mesocetus* (MCZ 17885) were characterized by their small size (<60 mm in maximum length), angular or squarish outline in dorsal and ventral views, and having a broad, deep, longitudinal furrow on the ventral and medial surfaces. Several additional auditory bullae similar in size and morphology to those identified as ?*Mesocetus* by Kellogg (1944) are known from the Bone Valley Formation (e.g., UF 28951, 132982, 132983; see Figs. 12A–D). The assignment of these bullae to *Mesocetus* is by no means certain, as Kellogg (1944) noted that the Bone Valley specimens differ from bullae of the type species, *M. longirostris* from Belgium. Several bullae from the Bone Valley region (e.g., UF 132922; see Figs. 12E–F) are similar to the specimens referred to ?*Mesocetus* by Kellogg but much larger, probably representing a closely related species.

Kellogg (1944) reported the "cetothere" ?*Isocetus* from the Bone Valley region on the basis of two isolated auditory bullae (MCZ 17884). These bullae are considerably larger (73–74 mm long) than those of ?*Mesocetus*, are more globose in shape, and lack the ventral furrow. Slightly smaller, but otherwise very similar, bullae (Figs. 13A–C) were found in association with a "cetothere" skull, mandibles, and partial skeleton (UF 130000) collected *in situ* from the lower Bone Valley Formation in the Agrico Fort Green Mine.

A fourth type of "cetothere" bulla from the Bone Valley Formation is intermediate in size (65–70 mm long) between the two types reported by Kellogg (1944). These bullae are more elongated and dorsoventrally flattened than the Bone Valley specimens referred to ?*Isocetus* or ?*Mesocetus*. One of these narrow, elongated bullae was found in association with a partial "cetothere" skull (USNM 299777) collected *in situ* from the lower Bone Valley Formation in the Phosphoria Mine. Another similar bulla (UF 28518) was collected in association with late Barstovian land mammals in the Red Zone Site in the Phosphoria Mine. A third bulla of this same type (UF/FGS 5472, see Figs. 13 D–F) was collected in 1952 from the American Agricultural Chemical Company Mine in Pierce, Polk County, the same mine that produced Kellogg's specimens of ?*Isocetus* and ?*Mesocetus*.

Family Balaenopteridae Gray, 1864

Balaenoptera Lacépède, 1804

Balaenoptera floridana Kellogg, 1944

Balaenoptera floridana Kellogg, 1944:459, figs. 5–10, pl. 6. Deméré, 1986:294.

Holotype.—MCZ 17882, complete right mandible.

Type locality.—American Agricultural Chemical Company Mine, Pierce, Polk County, Florida.

Referred specimens.—UF 103712, posterior portion of left mandible with intact coronoid process, Gardinier Mine, Polk County, Florida. UF 136061, posterior portion of left mandible with intact coronoid and condyle, Whidden Creek LF, Gardinier Mine, Polk County, Florida. UF 135785, cast of anterior tip of left mandible, TRO Quarry, Payne Creek Mine, Polk County, Florida.

Age and stratigraphic occurrence.—According to Kellogg (1944), the type specimen of *Balaenoptera floridana* was collected from pebble phosphates in the upper Bone Valley Formation of Pliocene age. Subsequent mandibles collected *in situ* from the Bone Valley Formation confirm that *B. floridana* is derived from the early Pliocene Palmetto Fauna. Two additional mandibles of *B. floridana* have been collected from the late Pliocene Tamiami Formation in the APAC Shell Pit, Sarasota County.

Description.—Measurements of the type mandible of *Balaenoptera floridana* from the Bone Valley Formation are total length (outside curvature), 226 cm; total length (straight line), 212 cm (Kellogg 1944). One of the mandibles from the APAC Pit tentatively referred to *B. floridana* is nearly complete (UF 25704). Measurements of this mandible (as preserved) are total length (outside curvature), 194 cm; total length (straight line), 186 cm (see Deméré 1986 for definition of measurements). Damage to the posterior end of UF 25704 probably accounts for the shorter total length of this specimen.

Discussion.—Mandibles, cranial fragments, auditory bullae, and periotics of at least two species of small to medium-sized balaenopterids occur in the early Pliocene Palmetto Fauna. However, no complete or even partial balaenopterid skulls are known from the Bone Valley Formation, nor have bullae or periotics been collected in direct association with mandibles. Therefore, it is unclear which auditory bullae belong to *B. floridana*. Among a large sample of mysticete bullae collected *in situ* from the late Hemphillian Whidden Creek LF, two species of balaenopterids appear to be represented: the smaller, more globose bullae probably are referable to *B. floridana*, whereas the somewhat larger, more elongated bullae belong to the unidentified balaenopterid listed in Table 2. A better understanding of the balaenopterid fauna from the upper Bone Valley Formation must await the discovery of mandibles associated with skulls, periotics, and bullae.

Deméré (1986) reviewed the Neogene species of *Balaenoptera*, including a brief discussion of the holotype mandible of *B. floridana* from the Bone Valley Formation. He noted that a mandible very similar to *B. floridana* is known from the late Pliocene (Blancan) San Diego Formation in southern California, and that both of these specimens might be conspecific with *B. cuvierii* from the late Pliocene (Piacenzian) of Italy.

Order Carnivora Bowdich, 1821

Suborder Fissipedia Blumenbach, 1791

Family Mustelidae Swainson, 1835

Enhydritherium Berta and Morgan, 1985

Enhydritherium terraenovae Berta and Morgan, 1985

Enhydritherium terraenovae Berta and Morgan, 1985:810, figs. 1–3.

Type specimens.—UF 18929 (holotype), left mandible with M_1; UF 32001 (paratype), partial left mandible with M_{1-2}.

Type locality.—Palmetto Mine, 10 km southeast of Bradley, Polk County, Florida (holotype). Fort Green Mine, 10 km south of Bradley, Polk County, Florida (paratype). The holotype and paratype are from slightly different localities, although these two phosphate mines are separated by less than 2 kilometers.

Referred specimens.—Ten specimens of *Enhydritherium terraenovae* have been recovered from the Bone Valley region since this species was described (see Berta and Morgan 1985:810 for original list of referred material). UF 125000, nearly complete right mandible with P_4–M_2; UF 133943, proximal end of right tibia, Whidden Creek LF, Gardinier Mine, Polk County, Florida. UF 95693, partial left mandible with P_3–M_1; UF 95691, partial right mandible with broken M_1; UF 95692, toothless fragment of right mandible; UF 117672, left metatarsal 2, Gardinier Mine, Number 7 Dragline, Polk County, Florida. UF 95747, partial left mandible

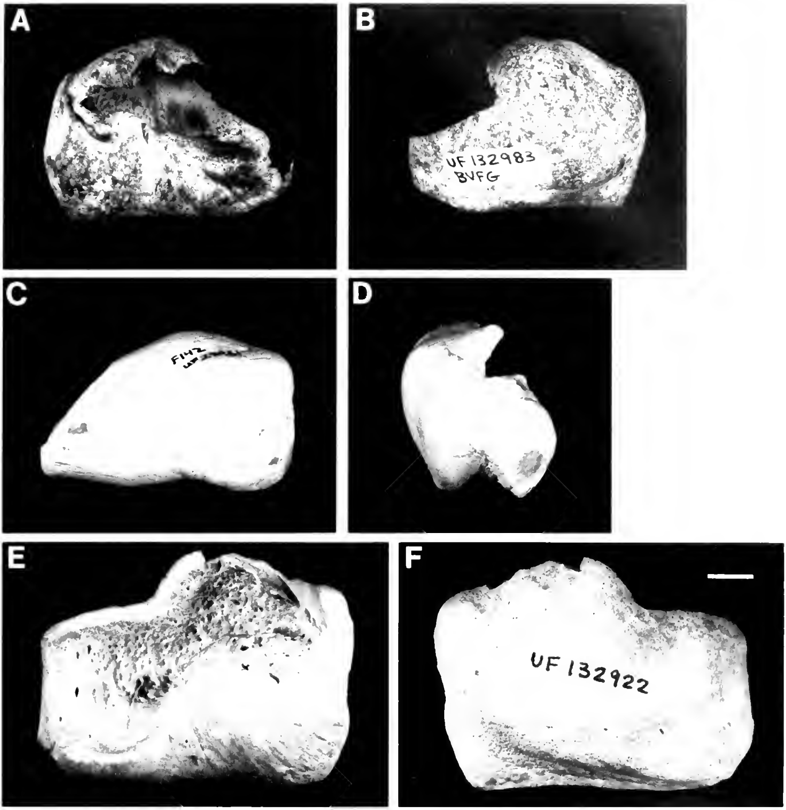

Figure 12. "Cetotherid" species 1, left auditory bulla, UF 132983, Fort Green Mine, Polk County, Florida, middle Miocene; A, dorsal view; B, ventral view. "Cetotheriid" species 1, left auditory bulla, UF 28951, Nichols Mine, Polk County, Florida, middle Miocene, C, medial view; D, posterior view. "Cetotheriid" species 2, right auditory bulla, UF 132922, Hookers Prairie Mine, Polk County, Florida, middle Miocene, E, dorsal view, F, ventral view. Scale equals 10 mm.

with M_1, northeast corner of the Payne Creek Mine (vicinity of TRO Quarry), Polk County, Florida. UF 102100, posterior half of edentulous right mandible, Kingsford Mine, Polk County, Florida. UF 124508, right M_2, Fort Green Mine, Number 13 Dragline; UF 65693, distal end of right radius, Brewster Mine, Polk County, Florida.

Age and stratigraphic occurrence.—All specimens of *Enhydritherium terraenovae* recovered from the Bone Valley Formation have been found in association with late Hemphillian land mammals, although most individual fossils were collected from spoil piles (Berta and Morgan 1985). In 1990 a nearly complete mandible and a proximal tibia of *E. terraenovae* were collected *in situ* from the Whidden Creek LF, a site that has yielded the richest sample of land mammals of the late Hemphillian Palmetto Fauna. *E. terraenovae* is also known from the somewhat older late early Hemphillian Moss Acres Racetrack and Withlacoochee River 4A

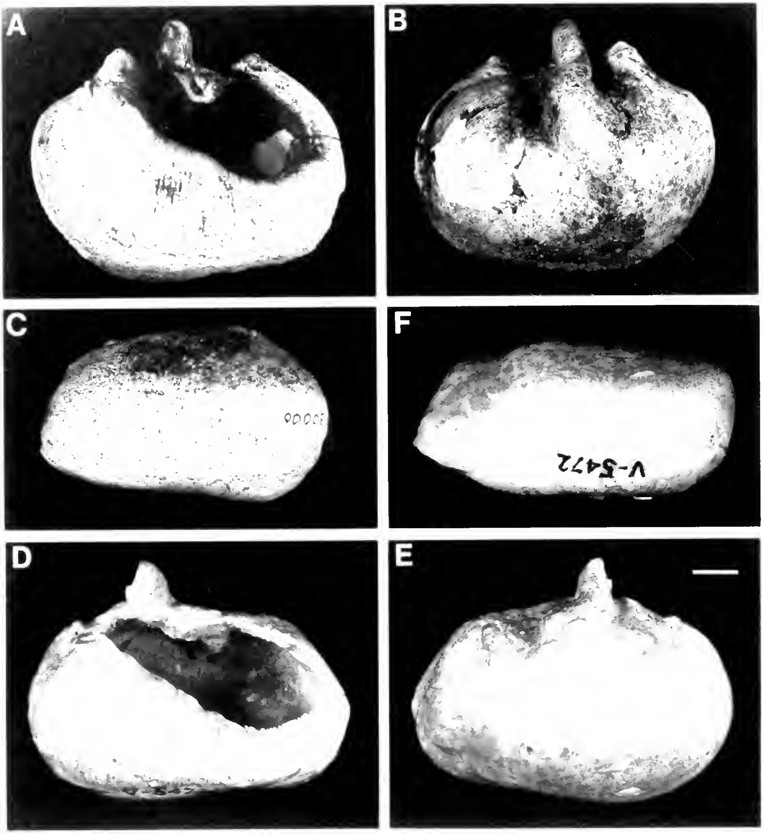

Figure 13. "Cetotheriid" species 3, left auditory bulla, UF 130000, Fort Green Mine, Polk County, Florida, middle Miocene; A, dorsal view; B, ventral view; C, medial view. "Cetotheriid" species 4, left auditory bulla, UF/FGS 5472, American Agricultural Chemical Company Mine, Pierce, Polk County, Florida, middle Miocene; D, dorsal view; E, ventral view; F, medial view. Scale equals 10 mm.

local faunas, both of which are located in Marion County in northern peninsular Florida.

Description.—Several recently discovered specimens of *Enhydritherium terraenovae* from the Bone Valley region add to the original description by Berta and Morgan (1985). The mandible from the Whidden Creek LF (UF 125000) represents the largest known individual of *E. terraenovae* (anteroposterior length of M_1 19.2 mm). The pronounced size variation in the sample of *E. terraenovae* from the Palmetto Fauna suggests that this species may have been sexually dimorphic. The dental morphology of the new specimens agrees very closely with the original description of *E. terraenovae*.

The recent discovery of a nearly complete articulated skeleton of *Enhydritherium terraenovae* from the Moss Acres Racetrack LF (UF 100000; see Lambert 1990) has made it possible to confirm the identification of several postcranial elements of this species from the Bone Valley Formation. David Lambert is currently undertaking a detailed study of the Moss Acres *Enhydritherium* skeleton. A complete right tibia from the TRO Quarry in the Payne Creek Mine (UF 40087) was tentatively referred to *E. terraenovae* by Berta and Morgan (1985). This specimen and a proximal tibia from the Whidden Creek LF (UF 133943) are very similar to the tibia from the Moss Acres skeleton, although the Bone Valley limbs are somewhat larger. A distal radius from the Brewster Mine (UF 65693) and a metatarsal 2 from the Gardinier Mine (UF 117672) also are quite similar to comparable elements of *Enhydritherium* from Moss Acres.

The distal end of a right humerus from the Gardinier Mine (UF 67973), provisionally referred to *E. terraenovae* by Berta and Morgan (1985), differs in size and several morphological features from the humerus of the Moss Acres *Enhydritherium*. The Moss Acres humerus is considerably larger than the Bone Valley specimen (distal width of humerus: Gardinier Mine, 32.0 mm; Moss Acres, 40.2 mm), whereas almost all other Bone Valley *Enhydritherium* fossils are larger. The Moss Acres humerus has a much larger entepicondylar foramen and a considerably broader flange of bone extending proximally and laterally from the ectepicondyle. These comparisons suggest the Bone Valley humerus is not referable to *Enhydritherium*.

Discussion.—The Moss Acres skeleton of *Enhydritherium terraenovae* originated from a fauna composed exclusively of terrestrial and freshwater vertebrates. The correlative Withlacoochee River LF also consists primarily of terrestrial and freshwater taxa, although several estuarine species are present. The hypothesis that *Enhydritherium* was primarily adapted to a marine existence must be revised somewhat (Berta and Morgan 1985). From the occurrence of *Enhydritherium* in predominantly marine deposits in both the Bone Valley region and at several California localities, it seems reasonable to conclude that this large otter did inhabit coastal marine environments. However, the two Florida early Hemphillian records of *Enhydritherium* from freshwater depositional environments indicate that this large otter also frequented large rivers and lakes. *E. terraenovae* has not been identified from Hemphillian faunas in the interior of North America, suggesting that this species may have been restricted to coastal plains and that it dispersed by marine routes, as proposed by Berta and Morgan (1985).

Suborder Pinnipedia Illiger, 1811

Family Odobenidae Allen, 1880

Trichecodon Lankester, 1865

Trichecodon huxleyi Lankester, 1865

Trichecodon huxleyi Lankester, 1865. Ray, 1960:129, pls. 1–2.

Referred specimens.—UF 125201, left upper tusk, Whidden Creek LF, Gardinier Mine, Polk County, Florida. UF 27504, tusk fragment, Fort Green Mine, Polk County, Florida. USNM 215201, fragment of left upper tusk, Payne Creek Mine, Polk County, Florida. USNM 25062, fragment of left upper tusk, Swift Mine, Polk County, Florida.

Age and stratigraphic occurrence.—The best-documented fossils of *Trichecodon huxleyi* in Florida are from the late Hemphillian Palmetto Fauna in the Bone Valley Formation in Polk County and from the Blancan Bee Ridge Fauna from the Tamiami Formation (Unit 11 of Petuch 1982) in the APAC and Richardson Road Shell Pits in Sarasota County. The only odobenid fossil collected *in situ* in the Bone Valley Formation is a nearly complete tusk (UF 125201) from the late Hemphillian Whidden Creek LF in the Gardinier Mine. All other Bone Valley odobenid fossils were collected from spoil piles, although two of the referred specimens are from mines (Fort Green and Payne Creek) that have produced large samples of late Hemphillian land mammals.

Discussion.—Ray (1960) reported the first fossil odobenid from Florida, a complete tusk of *Trichecodon huxleyi* (UF 3274) from De Soto Lakes in Sarasota County. Odobenid fossils are rare in the Bone Valley Formation but more frequently encountered in the Tamiami Formation in Manatee, Sarasota, and Charlotte counties along the Gulf coast. A complete right tusk (UF 61473), a partial humerus (UF 101471), and a partial skull with a tusk and several incisors (USNM 437542) have been collected in recent years from spoil piles in the APAC Shell Pit in Sarasota County. These specimens, derived from the Tamiami Formation, belong to the late Pliocene Bee Ridge Fauna. I do not describe the Florida odobenid fossils in detail as C. E. Ray and I. Koretsky are including these specimens in their analysis of the pinniped fauna from the Yorktown Formation in the Lee Creek Mine, North Carolina.

Family Phocidae Gray, 1825

Subfamily "Monachinae" Trouessart, 1904

Callophoca van Beneden, 1876

Callophoca obscura van Beneden, 1876

Referred specimens.—UF 101961, left otic region, including partial squamosal, glenoid fossa, auditory bulla, and petrosal; UF 91127, distal end of right humerus; UF 58369, proximal end of left radius; UF 117673, distal end of right tibia; UF 95686–95689, possibly associated juvenile left metatarsal 1, 2, and 5 and right metatarsal 3; UF 93380, left metatarsal 1; UF 91163, left metatarsal 4; Gardinier Mine, Numbers 7 and 9 draglines, Polk County, Florida. USNM 263605, right metatarsal 1, Payne Creek Mine (= District Grade Mine, vicinity of TRO Quarry), Polk County, Florida. UF 53947, right otic region, including partial squamosal, glenoid fossa, auditory bulla, and petrosal; UF 52423, complete right femur, Fort Green Mine, Number 13 Dragline, Polk County, Florida. UF 102002, juvenile right metacarpal 3; UF 114532, left metatarsal 2; UF 188535, left metatarsal 5; UF 118536, proximal phalanx of digit 1, left pes, Four Corners Mine, Hillsborough County, Florida.

Age and stratigraphic occurrence.—All specimens of *Callophoca obscura* from the Bone Valley region have been collected from spoil piles; however, most of these were derived from phosphate mines that have produced rich samples of the late Hemphillian Palmetto Fauna, including the Gardinier, Payne Creek, Fort Green, and Four Corners mines. Despite their lack of precise stratigraphic provenience, the *Callophoca* fossils were almost certainly derived from the upper Bone Valley Formation, as no pinnipeds have ever been collected from the lower Bone Valley Formation in association with vertebrate faunas of late Barstovian or early Clarendonian age. A small phocid phalanx from the early Clarendonian Occidental Fauna in northern Florida is the only pinniped fossil known from the state that is definitely older than Pliocene. Late Pliocene (Blancan) specimens of *Callophoca* are known from two sites in Sarasota County, the Tamiami Formation in the APAC Shell Pit and the Pinecrest Beds in the nearby Richardson Road Shell Pit.

Discussion.—C. E. Ray and I. Koretsky are describing the Bone Valley sample of *Callophoca obscura* as part of their larger review of the pinniped fauna from the Lee Creek Mine in North Carolina.

Subfamily Phocinae, Gill, 1866

Phocanella van Beneden, 1876

Phocanella pumila van Beneden, 1876

Referred specimens.—UF 114528, proximal two-thirds of left humerus, Gardinier Mine, Polk County, Florida. USNM 305299, complete right humerus, Fort Meade Mine, Polk County, Florida.

Age and stratigraphic occurrence.—Although the two Bone Valley specimens of *Phocanella* both lack stratigraphic data, they are almost certainly early Pliocene (late Hemphillian) in age. The co-occurrence of *Phocanella pumila*, *Callophoca obscura*, and *Trichecodon huxleyi* in the Bone Valley Formation invites comparison with the early Pliocene lower Yorktown Formation in the Lee Creek Mine, in which these same three pinnipeds are associated.

Discussion.—The two Bone Valley specimens listed here were identified as *Phocanella pumila* by C. E. Ray (pers. comm.).

Undetermined Genus and Species

Referred specimens.—UF 67969, distal two-thirds of left humerus; UF 101905, toothless fragment of left mandible, Gardinier Mine, Number 7 Dragline, Polk County, Florida.

Age and stratigraphic occurrence.—These two specimens of a small unidentified phocid were both collected from spoil piles in the Gardinier Mine that have produced a rich sample of late Hemphillian land mammals.

Discussion.—Both of these specimens are from very small adult phocids, but they are not complete enough for further identification. They appear to be too small to represent females of *Phocanella pumila* or *Callophoca obscura*.

Order Sirenia Illiger, 1811

Family Dugongidae Gray, 1821

Metaxytherium de Christol, 1840

Metaxytherium floridanum Hay, 1922

Genus and species indet. Matson, 1915, pl. 12, figs. A, B.

Metaxytherium floridanum Hay, 1922:1–4, pl. 1, figs. 1–5. Allen, 1923:233–238, pl. 26. Domning, 1988.

Felsinotherium floridanum Simpson, 1932:447.

Felsinotherium ossivallense Simpson, 1932:448.

Felsinotherium ossivalense [*sic*] Gregory, 1941:33–39, pls. 1–2.

Metaxytherium ossivalense [*sic*] Reinhart, 1976:199–216.

Metaxytherium calvertense Kellogg, 1966 [in part]. Reinhart, 1976:220–226, figs. 12–13.

Hesperosiren sp. [in part]. Reinhart, 1976:229–235, figs. 16–17.

Type specimen.—USNM 7221, right maxilla with M^3.

Type locality.—Pit 7 of the Prairie Pebble Phosphate Company, 1 mile west of Mulberry, Polk County, Florida.

Referred specimens.—See Domning (1988:399–400).

Age and stratigraphic occurrence.—Domning (1988) reviewed the age of *Metaxytherium floridanum* in the Bone Valley region and elsewhere in Florida. Skulls and articulated skeletons of this species have been collected *in situ* from the lower Bone Valley Formation sediments (Unit 4) that correlate with the early Clarendonian Agricola Fauna. *M. floridanum* is probably present in the late Barstovian Bradley Fauna as well, although no skulls are known from faunas of this age. *M. floridanum* is also known from several Miocene faunas in northern peninsular Florida, including the early Clarendonian Occidental Fauna and the latest Clarendonian/early Hemphillian Archer and Gainesville Creeks faunas. The youngest record of *M. floridanum* is from the late early Hemphillian Manatee Fauna (Domning 1988).

Discussion.—Domning (1988) exhaustively reviewed the taxonomy and morphology of this the most common Bone Valley marine mammal.

Corystosiren Domning, 1990

Corystosiren varguezi Domning, 1990

Hesperosiren sp. [in part]. Reinhart, 1976:229.

Corystosiren varguezi Domning, 1990:361–368, figs. 3–4.

Referred specimens.—See Domning (1990:362).

Age and stratigraphic occurrence.—The holotype of the early Pliocene *Corystosiren varguezi* is from the Yucatan Peninsula of Mexico (Domning 1990). All known specimens of *Corystosiren* from the Bone Valley region lack stratigraphic data. The Pliocene age of the type specimen and the absence of this species from Miocene sediments in the lower Bone Valley Formation led Domning (1990) to surmise that the Bone Valley *Corystosiren* belonged to the late Hemphillian Palmetto Fauna.

Discussion.—Domning (1990) reviewed this taxon.

Dioplotherium Cope, 1883

Dioplotherium allisoni (Kilmer, 1965)

Halianassa (?) *allisoni* Kilmer, 1965:58.

Dioplotherium allisoni Domning, 1978:5.

Referred specimen.—USNM 467610, upper tusk fragment (I^1) from the Nichols Mine, Polk County, Florida.

Age and stratigraphic occurrence.—*Dioplotherium allisoni* is represented in the Bone Valley region by a single tusk fragment collected by Donald Crissinger and thought by him to have possibly been derived from Unit 5 in the lower Bone Valley Formation. Land mammals collected from Unit 5 generally belong to the early Clarendonian Agricola Fauna, although this specimen could have been derived from the late Barstovian Bradley Fauna. The chronological range of this species is not well understood, but specimens referred to it have been reported from the early Miocene of Brazil (de Toledo and Domning 1989) and the middle Miocene (Barstovian) of California (Domning 1978).

Discussion.—The Bone Valley tusk fragment is flattened and bladelike, and has the diamond- or lozenge-shaped cross-section characteristic of the genus *Dioplotherium* (see Domning 1990). The presence of enamel on only the medial surface suggests referral to *D. allisoni* rather than to *D. manigaulti*, which has enamel on both the medial and lateral surfaces of I^1 (D. P. Domning, pers. comm.).

Supposed Desmostylia from the Bone Valley Formation

Reinhart (1976) reported several partial desmostylian teeth from the Bone Valley Formation of Florida, a record Barnes et al. (1985) later considered erroneous. This record, if valid, is certainly anomalous, as it represents the only known Atlantic occurrence of a mammalian order otherwise restricted to the Oligocene and Miocene of the eastern and western Pacific. It has been suggested that the Bone Valley desmostylian teeth might pertain to the Proboscidea, more specifically the Gomphotheriidae, a common group in most Bone Valley faunas. I compared the supposed Bone Valley desmostylian tooth fragments to partial gomphothere teeth from the Bone Valley Formation and to partial and complete *Desmostylus* teeth from California. The Bone Valley tooth fragments are similar to *Desmostylus* in having nearly cylindrical enamel columns that are separate for most of their length and show definite evidence of having been closely appressed to adjacent columns. In gomphotheres the cusps vary greatly in shape but are typically conical, tapering apically, and adjacent cusps are not entirely separated from one another but are broadly coalesced, especially near the base of the crown in later wear stages. On the basis of these comparisons, the Bone Valley partial teeth are referable to the Desmostylia and probably to the genus *Desmostylus*.

The Bone Valley teeth originally were discovered in a mining superintendent's private collection. Therefore, the possibility exists that they were actually collected somewhere else and then became mixed with Florida specimens. In discussing the teeth, Reinhart (1976:284) noted, "all are the typical color of the specimens from the phosphate pits of Florida, and all specimens were collected from the American Agricultural phosphate pits near Brewster, Florida." Although the color and preservation of the supposed Bone Valley *Desmostylus* teeth are not unlike that observed in certain other specimens from the Bone Valley region, they are almost identical in appearance to fragmentary *Desmostylus* teeth from the Barstovian Monocline Ridge locality in California. Many *Desmostylus* teeth from Monocline Ridge eventually end up on the commercial market (Domning, pers. comm.), casting suspicion on those supposedly from Bone Valley.

Despite intensive collecting by hundreds of people for over 80 years, not a single additional fragment of desmostylian tooth has been recovered from the Bone Valley region besides those reported by Reinhart (1976). Moreover, no desmostylians have been recorded from other Florida localities or from the numerous Miocene localities along the eastern coast of North America or around the Caribbean. The lack of any other evidence of desmostylians in the entire Atlantic basin and the questions regarding the provenience of the Bone Valley specimens lead me to conclude that the supposed Florida desmostylian teeth are probably from California.

CONCLUSIONS

Despite the substantial new information presented here, much remains to be learned about Neogene marine mammals in Florida. The most obvious gaps in the history of Florida's marine mammal fauna result from an inadequate or nonexistent fossil record from certain intervals, particularly the early Miocene (late Arikareean and Hemingfordian, 23–16 Ma), early late Miocene (late Clarendonian, 10.5–9.0 Ma), latest Miocene (early late Hemphillian, 6.7–5.2 Ma), and entire Pleistocene (Irvingtonian and Rancholabrean, 1.6 Ma–10 ka). Furthermore, most of the Miocene and Pliocene marine mammal assemblages from Florida consist of fewer than five taxa. Obviously these do not adequately sample the marine mammal faunas that inhabited Florida during those times. Only five faunas from Florida, including the late middle Miocene Agricola and Occidental faunas, the late Miocene Gainesville Creeks Fauna, the early Pliocene Palmetto Fauna, and the late Pliocene Bee Ridge Fauna, have ten or more species of marine mammals.

Most early Miocene marine mammal faunas from Florida are composed exclusively of sirenians. Several genera of archaeocete whales are known from Florida late Eocene deposits (Morgan 1978); however, the earliest Neogene record of cetaceans in the state consists of fragmentary specimens of *Pomatodelphis* and "cetotheres" from the late early Miocene (late Hemingfordian) Midway Fauna from the Torreya Formation in the eastern panhandle.

The earliest diverse marine mammal faunas known from Florida are the early Clarendonian Agricola Fauna from the Bone Valley Formation (Table 1) and the correlative Occidental Fauna from the Statenville Formation in northernmost peninsular Florida. The Agricola Fauna constitutes the typical example of the *Metaxytherium–Pomatodelphis*–"cetothere" assemblage that is characteristic of most Florida marine mammal faunas from the Barstovian, Clarendonian, and early Hemphillian.

A transition in Florida's marine mammal fauna began in the late Miocene. During the Hemphillian, between 8 and 5 Ma, there was a complete turnover of marine mammals at the generic level, resulting in the disappearance of the *Metaxytherium–Pomatodelphis*–"cetothere" assemblage in Florida by the late Hemphillian (early Pliocene). The late early Hemphillian Manatee Fauna, although not particularly diverse in marine mammals, is dervied from this transitional period. The last Florida occurrences of *Metaxytherium floridanum* and "cetotheres" are in the Manatee Fauna, as are the oldest Florida records of two families of mysticetes, the Balaenidae and Balaenopteridae. *Pomatodelphis* apparently disappeared from Florida sometime prior to the late early Hemphillian, as no specimens of this genus are known from the Manatee Fauna or younger sites.

The late Hemphillian Palmetto Fauna from the Bone Valley Formation has the most diverse marine mammal assemblage known from Florida, including at least 15 species (Table 2). The Florida marine mammal fauna underwent a second complete turnover between the early Pliocene (4.5 Ma) and the end of the Pliocene (1.6 Ma). Most marine mammal taxa from the Palmetto Fauna are unknown from younger sites in Florida, and include an undescribed pontoporiid, *Goniodelphis hudsoni*, *Ninoziphius platyrostris*, *Kogiopsis floridana*, *Enhydritherium terraenovae*, *Phocanella pumila*, an undescribed small phocid, and *Corystosiren varguezi*. Two cetacean genera present in the Palmetto Fauna, *Mesoplodon* and *Balaenoptera*, are still living, although the Bone Valley species are extinct.

The Tamiami Formation in southern Florida samples the transitional period between the early Pliocene and modern marine mammal faunas of Florida. The Tamiami Formation is in part correlative with the early Pliocene Palmetto Fauna, but the upper units of this formation are late Pliocene (3.5–1.9 Ma) in age. Taxa from the Palmetto Fauna that survived into the late Pliocene portion of the Tamiami Formation include *Balaenoptera floridana*, *Physeterula* sp., *Trichecodon huxleyi*, and *Callophoca obscura*. The Tamiami Formation records the earliest Florida occurrences of the humpback whale *Megaptera* and large species of *Balaenoptera*, which are nearly the size of the extant finback whale, *B. physalus* (see Morgan and Pratt 1983). An undescribed sirenian related to the extant genus *Dugong* occurs in the latest Pliocene (earliest Irvingtonian) Caloosahatchee Formation and is the youngest known member of the Dugongidae from Florida (Domning, pers. comm.).

It is difficult to determine when the modern Florida marine mammal fauna became established because the Quaternary record of marine mammals in the state is very incomplete. Florida currently has over 5000 km of coastline on the Atlantic Ocean and Gulf of Mexico, and a diverse fauna of marine mammals occurs in Florida waters, including at least 28 species of cetaceans, as well as the manatee *Trichechus manatus* and the recently extinct West Indian monk seal *Monachus tropicalis*. Cetaceans are poorly represented in Florida Pleistocene deposits, yet dolphins and whales are common in Florida waters and dead individuals are regularly stranded along the state's coasts (Moore 1953; Layne 1965). Only five species of Cetacea, all extant, are known from the Florida Pleistocene. Moreover, four of these species are known only from the late Pleistocene (or probably Holocene in the case of several species). *Trichechus manatus*, *Monachus tropicalis*, and the false killer whale, *Pseudorca crassidens*, all first appear in Florida during the early Pleistocene (early Irvingtonian).

ACKNOWLEDGMENTS

This project could not have been undertaken without the help of many people. I thank Annalisa Berta and Clayton E. Ray for asking me to participate in this volume. Numerous marine mammal specialists, including Lawrence G. Barnes, David J. Bohaska, Christian de Muizon, Daryl P. Domning, Irina Koretsky, James G. Mead, Charles W. Potter, Clayton E. Ray, and Frank C. Whitmore, Jr, shared their considerable expertise with me. I am especially grateful to Frank Whitmore for his help and encouragement over the past 15 years. The following curators and collection managers at the U. S. National Museum of Natural History, Smithsonian Institution, kindly permitted me to study the extensive collections of fossil and modern marine mammal specimens under their care: David J. Bohaska, James G. Mead, Charles W. Potter, Robert W. Purdy, and

Clayton E. Ray. Daryl P. Domning helped to assemble the diverse elements of the Garcia Collection during an extended visit to the Smithsonian. The manuscript benefited significantly from comments by Annalisa Berta, David J. Bohaska, Thomas A. Deméré, Daryl P. Domning, and Frank C. Whitmore, Jr. I would like to express my gratitude to the numerous avocational paleontologists whose discoveries of marine mammal fossils in the Bone Valley region over the past several decades helped make this review possible. Frank Garcia collected numerous fossil marine mammals from the Bone Valley Formation for the Smithsonian Institution, most notably skulls and skeletons of sirenians, long-beaked dolphins, and "cetotheres." He also collected a complete skull of *Pomatodelphis bobengi* and mandibles of *Goniodelphis hudsoni* and *Scaldicetus* that are now in the Museum of Science and Industry in Tampa. Rick Carter also deserves special thanks for his significant donations of Bone Valley marine mammals to the Florida Museum of Natural History. In particular, Rick has single-handedly collected the majority of Bone Valley pinniped fossils currently known. Other individuals who have made significant contributions of Miocene and Pliocene marine mammal specimens from the Bone Valley region and elsewhere in Florida to the Florida Museum of Natural History include Lelia Brayfield, William Brayfield, D. J. Bethea, Jan Brown, Robin Brown, Steven Brown, Donald Crissinger, Terry Davis, Steven Emslie, Wayne Filyaw, George Heslep, Frank Hyne, Robert Jones, Eric Kendrew, Ted Messick, James Pendergraft, Susan Pendergraft, Eric Prokopi, Dennis Price, James Ranson, William Smith, Craig Taylor, Eric Taylor, James Toomey, and John Waldrop. Significant *in situ* samples of fossil vertebrates from the Bone Valley Formation have been discovered and donated to the Florida Museum of Natural History by Rick Carter, Donald Crissinger, James Pendergraft, and John Waldrop. This is University of Florida Contribution to Paleontology 419.

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