

Historical Perspectives

Annalisa Berta

(Born 23 July 1952)

Annalisa Berta received a Bachelor of Arts (*magna cum laude*) from the University of Washington in 1974 where she was elected to Phi Beta Kappa. She earned a Ph.D. from the University of California at Berkeley in 1979. She is Professor Emerita in the Department of Biology at San Diego State University (SDSU) and a Research Associate at the San Diego Natural History Museum, the Los Angeles County Museum of Natural History, and the Smithsonian Institution. She is an evolutionary biologist who for the last 30 years has

been studying the anatomy, evolution, and systematics of fossil and living marine mammals with funding from the National Science Foundation. She has taught a popular course on the evolution and ecology of marine mammals at SDSU for more than 30 years. Berta has made research trips to Australia, Europe, Japan, Mexico, and New Zealand and led educational trips to Baja California and Belize to view marine mammals in the wild. She is a Past President of the Society of Vertebrate Paleontology and former Associate

Editor of *Marine Mammal Science* and Senior Editor of the *Journal of Vertebrate Paleontology*. She was a Fulbright Fellow to Italy in 2011, and was elected a Fellow of the American Association for the Advancement of Science in 2015 for “Distinguished Research on the Fossil Record and Evolutionary Biology of Marine Mammals.” She was honored for her many contributions to the study of fossil cetaceans and pinnipeds by having an extinct baleen whale named for her—*Balaenoptera berta*. She has published more than 100 scientific papers and several books for the specialist as well as nonscientist, including *Return to the Sea: The Life and Evolutionary Times of Marine Mammals* (University of California Press, 2012), *Marine Mammals: Evolutionary Biology* (3rd ed.) with J. L. Sumich and K. M. Kovacs (Elsevier, 2015), *Whales, Dolphins and Porpoises: A Natural History and Species Guide* (University of Chicago Press, 2015), and *The Rise of Marine Mammals: 50 Million Years of Evolution* (Johns Hopkins University Press, forthcoming 2017).



Experiences, Future Directions, and Lessons Learned in Marine Mammal Evolutionary Biology

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Introduction

The review that follows is a summary of the role that evolutionary biology has played in my career in marine mammal science focused on experiences, future directions, and lessons learned. It is a highly personal account that highlights both triumphs and challenges in my research on fossil and extant marine mammals undertaken in collaboration with colleagues and students (my academic children). I hope that my perspective and advice inspires students and early career scientists passionate about pursuing research on the evolutionary biology of marine mammals. There is still much to learn based on the continued discovery of fossil marine mammals incorporated with the comparative study of the biology of extant species. New techniques of study, including 3D imaging, morphometrics, and genomic analyses, have enriched our understanding of marine mammal biology and evolution and provided exciting new research directions. Perhaps most importantly, I want to encourage international collaborations with colleagues and students in other disciplines such as developmental biology, ecology, genetics, and geology. I have found that an integrated approach to marine mammal evolutionary biology offers new, diverse, and wide-ranging perspectives.

Background

My interest in paleontology developed more than 50 years ago in 1964 when I participated in summer paleontology excavations at Camp Hancock run by the Oregon Museum of Science and Industry in central Oregon. This experience—uncovering the teeth and bones of fossil mammals such as horses, tapirs, and carnivores more than 40 million years old—fueled my lifelong passion and interest in deciphering the history of life.

I was trained as a vertebrate paleontologist at the University of California at Berkeley under the skillful mentorship of William A. Clemens. Bill's expertise was the evolution and paleobiology of early mammals, but he encouraged his students to pursue topics of curiosity and interest to them. I became fascinated with South American carnivores having learned of my office mate

Larry Marshall's exciting adventures collecting and studying fossil mammals in Argentina. With Larry's help and the tutelage of carnivore expert, the late Richard "Dick" Tedford, Curator of Fossil Mammals at the American Museum of Natural History in New York, I learned carnivore anatomy and systematics and spent two months in Argentina studying specimens in museum collections for my dissertation on the evolution and biogeography of large South American canids (Berta, 1988). I spent a one-year teaching stint as a sabbatical replacement in the Department of Geology at Hobart and William Smith Colleges in upstate New York. I next accepted an academic position teaching in the Department of Geology at Radford University in Virginia, although I was very concerned about the heavy teaching load. Serendipity interceded. At the last minute, I was offered and happily accepted instead a postdoctoral (postdoc) position at the Florida Natural History Museum in Gainesville. I mostly pursued research on the anatomy and evolution of terrestrial fossil carnivores, working with Bruce MacFadden, Ron Wolff, and David Webb, but after the description of a new fossil sea otter from Florida—my first marine mammal publication with co-author and fellow vertebrate paleontologist Gary Morgan (Berta & Morgan, 1985)—I was hooked on the study of these magnificent mammals of the sea.

Lest I leave you with the impression that I fell easily into a faculty position, it was many job applications later (and a file drawer full of rejection letters) that I accepted a one-year faculty appointment in the Department of Biology at San Diego State University (SDSU) in southern California. I was fortunate enough to extend this temporary appointment and make SDSU my academic home from 1982 to the present. I was initially hired as a full-time lecturer, a position I held for seven years until my official appointment as a tenure-track faculty member thanks to the encouragement and efforts of colleagues Richard Estes and J. David Archibald. I was hired to teach Human Anatomy to nursing and pre-professional undergraduates, but my interests and enthusiasm were elsewhere. Given my fascination and that of students with marine mammals and the rich San Diego community of marine mammalogists

(e.g., Sam Ridgway, Paul Ponganis, Gerry Kooyman, Ann Bowles, Brent Stewart, Stephen Leatherwood, Bill Perrin, Aleta Hohn, Tom Deméré, and Jim Sumich), I developed and taught a course that soon became my favorite, the Evolution and Ecology of Marine Mammals, and I continue to teach this course once a year to this day. For the first few years, I taught this course with Jim Sumich, a physiologist working on gray whales, an experience that led to our collaboration on a marine mammal textbook, *Marine Mammals: Evolutionary Biology*, now in its third edition. My familiarity and training in paleontology led me to the San Diego Museum of Natural History where I began my study of fossil marine mammals that were largely acquired and curated by vertebrate paleontologist Tom Deméré, thus beginning a research collaboration that has continued for more than 30 years (e.g., Deméré & Berta, 2001, 2002, 2005, 2008; Deméré et al., 2005, 2008). As I have often remarked about our connection, I provided eager graduate students looking for thesis projects and Tom provided fossil marine mammal expertise and access to the marine mammal collection. Initially, I began my research on fossil pinnipeds with a study of the cranial and dental remains of a fossil fur seal (*Callorhinus gilmorei*), named after Ray Gilmore, long-time whale biologist at the San Diego Natural History Museum, that led to a publication (Berta & Deméré, 1986).

Fossils and Collections-Based Research

My background on carnivore systematics set me up for a serendipitous encounter with Clayton Ray, a vertebrate paleontologist and curator in the Department of Paleobiology at the Smithsonian in the mid-1980s. Clayton showed me a beautifully preserved skeleton of a fossil marine carnivore in his office and enlisted my help to sort out its evolutionary relationship to terrestrial carnivores. This fortuitous meeting led to our description of a skeleton of the oldest known fossil pinniped, *Enaliarctos mealsi* (Berta et al., 1989; Berta & Ray, 1990; Berta & Wyss, 1990). Later, with Clayton's encouragement and funding from the National Science Foundation (NSF), I began working on the vast collection of well-preserved fossil pinnipeds housed in the Smithsonian's Department of Vertebrate Paleontology, amassed by the prodigious amateur fossil collector Douglas Emlong. Beginning in 1991, publications followed on the description and systematics of early fossil pinnipeds *Enaliarctos*, *Pteronarctos*, and *Pinnarctidion* in the Emlong collection (Berta, 1991, 1994a, 1994b). I continued to study fossil pinnipeds in the Emlong collection; and later, with Tom Deméré,

published several papers describing their anatomy and evolution (e.g., Deméré & Berta, 2001, 2002).

At this time, I began working with a former SDSU Master of Science (MS) student Andre Wyss on pinniped systematics. We published the first comprehensive morphology-based phylogeny of pinnipeds that included evidence for a single common origin for pinnipeds (i.e., monophyly) (Berta & Wyss, 1994). This paper was published in *Proceedings of the San Diego Society of Natural History* that incorporated papers presented at a symposium on marine mammal evolution held at the 51st Annual Meeting of the Society of Vertebrate Paleontology in San Diego in 1991. This special issue, edited by Tom Deméré and me, included 15 papers on marine mammal evolution, systematics, faunas, and biostratigraphy in honor of the U.S. Geological Survey/Smithsonian vertebrate paleontologist Frank C. Whitmore's contributions to the systematics and biogeography of fossil cetaceans. As a vertebrate paleontologist, I regularly attended a single meeting a year, the annual meeting of the Society of Vertebrate Paleontology, but after attending my first Marine Mammal Biennial Meeting in 1989 in Miami, Florida, I became an enthusiastic participant at those meetings as well. Andre Wyss and I were invited plenary speakers, presenting talks on a monophyletic origin of pinnipeds—a new and much debated idea at that time. At that conference, I recognized the importance of presenting research on marine mammal evolution to a different audience; and ever since then, I have continued to attend Marine Mammal Society biennial meetings with graduate students.

In the late 1980s, my first MS student, Sharon Messenger, was co-advised by J. David Archibald since I was not yet in a tenure-track position. Sharon's MS thesis provided one of the first comprehensive morphology-based phylogenetic studies of cetaceans that was later combined with molecular data (Messenger & McGuire, 1998). Sharon completed a Ph.D. in the Bull and Hillis labs at the University of Texas at Austin, and she is employed as a research scientist for the California Department of Public Health. In the mid-1990s, after my tenure-track appointment at SDSU and as a result of student interest in marine mammals, I began to attract MS students to my lab. Although my second graduate student, Peter Adam, did not finish his MS degree, we published several papers while he was at SDSU on the evolution of feeding and locomotion in pinnipeds analyzed in a phylogenetic context (Berta & Adam, 2001; Adam & Berta, 2002; Deméré et al., 2003). Peter completed a Ph.D. in the Van Valkenburgh lab at the University of California at Los Angeles and is currently employed as an assistant professor in

the Department of Biology at Northwest Missouri State University in Maryville.

At about this same time, I also began collaborating with Ted Cranford, a functional anatomist with CT scanning expertise and a student of preeminent marine mammalogist Ken Norris. Beginning in the late 1990s and continuing to the present, Ted, Tom, and I mentored more than 25 SDSU graduate students' MS theses on the anatomy, evolution, and systematics of fossil as well as living marine mammals, especially pinnipeds and whales. Next, I highlight some of this research organized topically.

Systematics and Anatomy Research and Lots of Graduate Students

Early on, I recognized the importance of a phylogenetic framework for understanding species relationships. I trace this back to my time at University of California at Berkeley as a graduate student in the late 1970s when I learned about a then new method for inferring evolutionary relationships—phylogenetic systematics or cladistics. Methods for inferring phylogenies greatly improved in the 1980s and 1990s with the availability of DNA sequence data, the application of statistical methods, and improved computer programs. Although my expertise is in morphology, one of my SDSU colleagues, Tod Reeder, was a molecular systematist, and he agreed to co-advise several marine mammal molecular studies undertaken by my next few graduate students. These analyses would not have been possible without the generous loan of tissue samples from the Southwest Marine Fisheries Science Center with the assistance of Kelly Robertson and Andy Dizon. Amanda Rychel's MS thesis project on mysticete phylogeny, among the first using a broad taxonomic sampling, used mitochondrial and nuclear DNA data (Rychel et al., 2004, 2005; see Figure 4). Amanda completed a Ph.D. and postdoc in the Swalla lab at the University of Washington. She is currently employed as a research scientist at Petrometrica in Somerville, Massachusetts. Carrie Fyler completed a MS thesis on the molecular phylogeny and biogeography of monk seals (Fyler et al., 2005). Carrie earned a Ph.D. in the Caira lab at the University of Connecticut and is currently teaching at Montclair Kimberly Academy in Montclair, New Jersey. Later studies that I undertook with colleagues (e.g., John Gatesy, Tom Deméré, Eric Ekdale, Giovanni Bianucci, and Sarah Kienle) incorporated both molecular and morphological data in combined phylogenetic analyses. In my opinion, combined analyses using multiple datasets are the most informative in terms of reconstructing evolutionary histories, although separate data partitions (e.g., morphology vs DNA

sequences or second vs third codon position) also should be performed as they are often very instructive—especially with regard to identifying potential conflicts in the data.

My next cohort of graduate students (2001 to 2007) included Lisa Cooper, Liliana Fajardo, Megan McKenna, Breda Walsh, and Michael McGowen; followed a few years later by Morgan Churchill, Rachel Racicot, and Mandy Keogh. By this time, I had realized the significance of not only collecting morphological/molecular data and obtaining phylogenies, but also using these trees to understand how various traits (e.g., hyperphalangy, feeding, and locomotion) evolved. Lisa Cooper completed a MS in 2004. Her research evaluated the phylogenetic and functional significance of the forelimb in mysticetes. In addition to forelimb osteology, the soft tissue anatomy of several extant species were examined using dissection and histology (Cooper et al., 2007a, 2007b). Lisa completed a Ph.D. in the Thewissen lab at Kent State University in Ohio and a postdoc in the Sears lab at the University of Illinois at Champaign-Urbana. Lisa is currently an assistant professor in the Department of Anatomy and Neurobiology at Northeastern Ohio Medical University in Rootstown. Michael “Rocky” McGowen completed a MS in 2005. He mapped characters related to feeding morphology, behavior, and diet onto a phylogeny of mysticetes (Gatesy et al., 2013). Rocky earned a Ph.D. in the Gatesy lab at the University of California at Riverside, and he completed postdocs at Wayne State University in Detroit, Michigan, and at the University of London. He recently accepted a position as Marine Mammal Curator at the Smithsonian. Liliana Fajardo-Mellor completed a MS in 2005. Her research was a comprehensive morphological study of phocoenids, including extant species and a few well-known fossil species. She also considered the origin and diversification of phocoenids through time (Fajardo-Mellor et al., 2006). Liliana completed a Ph.D. in the Department of Anatomy and Cell Biology at the Brody School of Medicine at East Carolina University in Greenville, North Carolina. She is currently a staff scientist at Centro Nacional de Investigaciones Oncológicas in Madrid, Spain. Breda Walsh completed a MS degree in 2006 in record time—2.5 years! Her research was a comparative morphologic study of growth patterns in mysticetes based on determination of ontogenetic stages of cranial ossification among extant species and several fossil species. Relative age determinations were based on sequence of cranial suture closure (Walsh & Berta, 2011). Breda is employed at a research lab at University of California at San Diego. Mandy Keogh came to my lab after having worked as a technician with Sam Ridgway, then director of the

Navy Marine Mammal Program. Mandy completed a MS in 2006. Her research involved comparative histological examination of the corpus callosum morphometry (i.e., relative size and fiber density) in representative odontocetes considered in both phylogenetic and functional contexts. Mandy completed a Ph.D. at the University of Alaska, Fairbanks, and is now employed as a wildlife physiologist at Alaska Fish and Game in Juneau.

Rachel Racicot came to my lab from the renowned CT lab at the University of Texas at Austin. I was eager to have her in the lab since she brought with her expertise in CT scanning. She completed a MS thesis in 2007 on the anatomy of the pterygoid sinuses in phocoenids considered in a phylogenetic context (Racicot & Berta, 2013). Her results reinforced the functional role that sinuses play in concert with head anatomy for biosonar sound production. Rachel completed a Ph.D. at Yale University. She is currently a postdoc at the Los Angeles County Museum of Natural History. Morgan Churchill's MS research completed in 2007 was a comprehensive morphological study of balaenoid phylogeny, including extant species and well-known fossil taxa. He also evaluated the origin and diversification of balaenoids through time in the context of a

phylogenetic framework (Churchill et al., 2012). Morgan completed a Ph.D. in the Clementz lab at the University of Wyoming. After a two-year postdoc in the Department of Anatomy at New York Institute of Technology in Westbury, he recently accepted a position as assistant professor in the Department of Biology at the University of Wisconsin at Oshkosh.

At this time, I also became interested in dissecting marine mammals to learn more about their anatomies. This work was enhanced by the assistance of Ted Cranford who provided a dissecting table, tools, and a wealth of anatomical knowledge and experience. Judy St. Leger (Sea World), Joy Reidenberg, Larry Witmer, Eric Ekdale, and Tom Deméré, together with graduate students, joined several dissections and provided much needed advice and assistance. We began this research focus by dissecting the head of a killer whale (*Orcinus orca*), followed by a fetal fin whale (*Balaenoptera physalus*) (Figure 1) and an adult fin whale (Figure 2). We also participated with National Oceanic and Atmospheric Administration scientists led by Susan Chivers in the dissection of a stranded subadult fin whale off the San Diego coast. Our most recent dissection of the head of a neonate gray whale involved a



Figure 1. Fetal fin whale dissection in 2006 (from left: Janet Boehm, Anders Galatius, the author, Rachel Racicot, Morgan Churchill, and Tom Deméré)

large number of graduate students and resulted in thematic publication of a series of articles in *The Anatomical Record* (e.g., Berta et al., 2015; Ekdale et al., 2015; Kienle et al., 2015; Young et al., 2015).

My interest in morphometrics took a leap forward when Anders Galatius, then a Ph.D. student at the University of Copenhagen in Denmark, came to study in my lab in 2006 to gain some experience in phylogenetics. I was also a member of Galatius's Ph.D. Committee. Anders brought with him a 3D portable digitizer (MicroScribe) and a background in geometric morphometrics for use in his investigation of the ontogeny of skull variation in porpoises. While in California, he visited a number of museums and collected porpoise skull measurements that he incorporated into his Ph.D. which led to a publication (Galatius et al., 2011).

Given his CT expertise, Ted Cranford was a key resource and co-chaired several MS theses during my tenure at SDSU. Megan McKenna's 2005 MS thesis research involved the first detailed morphological description of the melon among various lineages of odontocetes derived from CT images. Melon structure and function was also considered in an evolutionary context (McKenna et al., 2012). Megan completed a Ph.D. in Biological Oceanography from the University of California

at San Diego (Scripps Institute of Oceanography). She is now employed as an acoustics biologist for the National Park Service in Fort Collins, Colorado. Celia Barroso's MS thesis involved investigation of the anatomy and evolution of mandibular shape across the odontocetes using x-ray CT and geometric morphometrics. Her results provided the first solid evidence that lower jaws and associated soft tissues allow whales to reduce low-frequency noise and focus on certain frequencies such as those from returning echos (Barroso et al., 2012). Celia is employed by an environmental consulting firm in the Los Angeles area. Most recently, William Ary's MS thesis (2017 in progress), with Petr Krysl and Ted Cranford providing guidance, used vibrational analysis, finite element modeling, and geometric morphometrics to quantify the relationship between shape and function in cetacean ear bones. He then mapped that variation onto a phylogeny to see how shape varies within and between groups.

My next cohort of graduate students (2007 to 2010) included Alex Sanchez, Josh Yonas, Celia Barroso, and Cassie Johnston. Alex Sanchez completed a MS in 2007. His thesis investigated forelimb osteology and muscular anatomy of representative odontocetes in an evolutionary context. Alex is currently teaching part-time at



Figure 2. Adult fin whale baleen rack at the Berta lab in 2011 (from left: the author, Will Ary, Sarah Kienle, Nick Zellmer, Eric Ekdale, Jessica Martin, and Joe El Adli)

Mira Costa College in southern California. Josh Yonas completed a MS thesis in Fall 2008 on the anatomy and evolution of aquatic locomotion in walruses (*Odobenus rosmarus*). He investigated fore- and hindlimb osteology and myology in the walrus using dissection, x-ray, and MRI imaging. The evolution of locomotion in fossil and modern walruses and other pinnipeds was also considered. Josh graduated from Vet School in Pomona and is currently a veterinarian in West Seattle, Washington. Cassie Johnston completed a MS in 2009. Her research examined the comparative anatomy and evolutionary history of suction feeding in cetaceans with an emphasis on the gray whale (Johnston et al., 2010; Johnston & Berta, 2011). Cassie is employed by an environmental consulting firm in the Los Angeles area. In 2009, Heather Liwanag, then at the University of California at Santa Cruz in Terrie Williams' lab, contacted me for advice on pinniped phylogenetics and invited me to be on her Ph.D. Committee. Her dissertation investigated changes in the morphology and physiology of fur in pinnipeds associated with the transition from terrestrial to aquatic living. Her study, conducted in an evolutionary context, confirmed that fur was an ancestral otariid character lost several times in the evolution of sea lions (Liwanag et al., 2012a, 2012b). Heather is currently an assistant professor in the Department of Biological Sciences at California Polytechnic University in San Luis Obispo.

In 2010, with NSF funding, Tom Deméré and I were able to hire Eric Ekdale as a postdoctoral researcher for our research on the evolution and feeding anatomy of baleen whales. Eric was a recent Ph.D. from the University of Texas at Austin (and former SDSU MS student), specializing in evolution of the mammalian ear using CT imagery. Eric was instrumental in helping Tom and I organize the Sixth Triennial Conference on Secondary Adaptations of Tetrapods to Life in Water held in San Diego in June 2011. This interdisciplinary meeting held every three years brought together an international contingent of more than 50 scientists who study the evolution of mammals, birds, other reptiles, and amphibians that are secondarily adapted to life in the water. A highlight of the San Diego Meeting was a Marine Tetrapod Osteology Workshop held at the Natural History Museum. Since his arrival in San Diego, Eric, currently a lecturer at SDSU and a research scientist at the San Diego Natural History Museum, has been involved in mentoring graduate students as well as working with Tom, Ted, and me on various mysticete anatomy projects (Ekdale et al., 2011; Berta et al., 2014, 2016).

My next cohort of graduate students (2011 to 2014) included Jessica Martin, Samantha Young,

William Ary, Reagan Furbish, and Sarah Kienle. Jessica Martin came with a background and interests in geology, having worked as an undergraduate in Jonathan Geisler's lab, then at George Southern University. She completed a MS in Fall 2012. Her MS thesis investigated the evolutionary history of balaenopterid whales (rorquals) using morphology and divergence dating. She described a new fossil balaenopterid from the Pliocene San Diego Formation and incorporated this new taxon into a phylogenetic analysis. Jessica is employed as an instructor in the Department of Biology at the University of Great Falls in Great Falls, Montana. Sarah Kienle completed a MS in 2013. Her research was a comparative analysis of the four feeding types—(1) suction feeding, (2) grip and tear feeding, (3) pierce feeding, and (4) filter feeding—employed by extant phocids (seals) using 3D morphometrics (landmark data collected using MicroScribe) and comparative phylogenetic analyses. Quantitative feeding characters were used to examine type(s) of feeding in stem phocids to understand the evolutionary origins of each feeding strategy (Kienle & Berta, 2016, in review). Sarah is a Ph.D. student in the Costa and Mehta labs in the Department of Ecology and Evolutionary Biology at the University of California at Santa Cruz. Samantha Young completed a MS thesis in Fall 2011. Her project examined the anatomy (including SEM ultrastructure and morphometrics) and evolution of baleen. She also investigated baleen (bristle morphology) and its correlation with prey type. She is employed in the Education Department at the San Diego Zoo's Institute for Conservation Research. Reagan Furbish completed a MS thesis in 2014. She examined the controversial placement of the extinct pinniped, *Allodesmus*, on the pinniped phylogenetic tree. Her total evidence analysis of pinnipeds incorporated both morphological data and DNA evidence and suggested that *Allodesmus* together with otariids and odobenids is an otarioid pinniped. Based on ancestral state reconstruction of swimming patterns, she proposed that pinnipeds entered the water as hindlimb-dominated swimmers, with otarioids specializing in forelimb swimming. Reagan teaches human anatomy at several local San Diego colleges.

My last graduate students are MS students Bridget Borce and Meghan Smallcomb and Ph.D. student Agnese Lanzetti. As an undergraduate at SDSU, Meghan gained research experience working with then graduate student Sarah Kienle. Her MS thesis (in progress 2017) investigates cranial growth in the gray whale with implications for ontogeny and phylogeny. Given the large size of gray whale skulls, the MicroScribe was not appropriate; thus, skull measurements were obtained from a newly acquired 3D surface scanner (NextEngine, Inc., Santa Monica,

CA, USA), which was purchased with grant funds. Bridget Borce came to my lab after having been an SDSU undergraduate student in the Department of Geology. Given her interest in working on fossils, she undertook a MS thesis project (in progress 2017) on the systematics and biogeography of the extinct river dolphin *Parapontoporia*, hypothesized as a close relative of the recently extinct Chinese river dolphin (*Lipotes vexillifer*). Agnese Lanzetti came to my lab in 2014 with BS and MS degrees in Geology from the University of Pisa in Italy. For her dissertation, Agnese is investigating the transition from teeth to baleen in fetal baleen whales with implications for mysticete evolution. To understand skull growth, she is employing CT images of fetal baleen whales obtained from museum specimens (Berta et al., 2016; Lanzetti, in prep.). To this day, I continue to remain active in research, working on various projects with graduate students and colleagues (Berta et al., in review).

International Collaborations

One of my most memorable experiences was a six-month sabbatical that I spent in New Zealand in 1997 hosted by Scott Baker and Gina Lento, then at the University of Auckland. I interacted with students in Scott's lab, including Marel Dalebout and Rochelle Constantine, although most of my time was spent researching and writing *Marine Mammals: Evolutionary Biology*. A highlight of my trip was a visit to the University of Otago and Ewan Fordyce's lab. Ewan took me to several of his fossil field sites as well as to a beach occupied by New Zealand sea lions (Figure 3).

Beginning in the late 1990s and early 2000s, Tom Deméré and I received NSF support for research initially on fossil pinnipeds and later on mysticete whales housed in collections in Japan. Several SDSU graduate students (i.e., Peter Adam, Amanda Rychel, Josh Yonas, and Cassie Johnston) accompanied us on various research trips to Japan (Figure 4). While in Japan, our research was facilitated by Tadasu Yamada, Yoshiro Hasegawa, and Naoki Kohno at the National Museum of Nature and Science in Tokyo, Toshiyuki Kimura at the Gunma Museum of Natural History, and Hirota Ichishima at the Fukui Prefectural Dinosaur Museum.

In the summer of 2003, Tom Deméré, Rocky McGowen, and I undertook a three-week research trip to various natural history museums in Europe to examine fossil and extant mysticetes as part of our NSF-funded research. Most of our time was spent in natural history museums in Italy with colleagues Giovanni Bianucci and Michelangelo Bisconti. In Belgium, we studied an important collection of fossil marine mammals collected by P.-J. Van Beneden from the Belgium Antwerp area



Figure 3. The author and a New Zealand sea lion on a beach near Dunedin, New Zealand, in 1997 (Photo courtesy of R. E. Fordyce)



Figure 4. Research trip to National Museum of Nature and Science in Tokyo in 1999 (from left: the author, Amanda Rychel, Yoshiro Hasegawa, and Naoki Kohno)

with the assistance of Olivier Lambert. In Berlin, we studied fossil mysticetes and discussed mysticete evolution and phylogeny with Oliver Hampe. Based on our study of baleen whales in collections in Japan, the U.S., and Europe, we published several papers (see Deméré et al., 2005, 2008).

My last sabbatical in 2011 was spent with Giovanni Bianucci in Italy on a Fulbright Fellowship. Giovanni and I and his MS student Sylvia Sorbi spent several weeks examining skeletal remains of a fossil monk seal at the Museo di Storia Naturale e del Territorio, a former monastery in the town of Calci (Figure 5). The significance of our paper was a redescription of a holotype skeleton of the best-known Mediterranean fossil pinniped and its placement in a phylogenetic framework as a monachine phocid most closely related to monk seals (Berta et al., 2015b).

Giacomo Franci, a MS student at the University of Pisa, came to my lab in the spring of 2015 to gain some morphometrics experience working on whales. For a thesis topic, he investigated skull growth in the minke whale (*Balaenoptera acutorostrata*) using a 3D laser scanner to acquire landmark measurements. He collected data from specimens at various museums in California, and his results were the basis for his thesis and a publication (Franci & Berta, in review).



Figure 5. Whale collection at the Museo di Storia Naturale e del Territorio in Calci, Italy

Interactions with the Local Marine Mammal Community

Over the years, I have been fortunate to have participated with colleagues in the San Diego marine mammal community in several events which served to enrich my understanding of the varied research undertaken by local scientists. One event hosted at Hubbs-SeaWorld on an occasional basis was S.W.I.N.E. (Scholar's Wine Imbibing Nocturnal Enclave). Over the years, I have enjoyed talks (and wine) by local and visiting distinguished marine mammalogists, including Judy St. Leger, Tom Deméré, Sam Ridgway, Heather Koopman, and Ted Cranford. Another rewarding experience was the result of my consent to serve along with Ann Bowles as co-chair of the Scientific Program for the Biennial Meeting of the Marine Mammal Society held in 2005 in San Diego. The experience of organizing such a large conference several years in the making was made easier with the assistance of my large cohort of graduate students.

Another foray into the local marine mammal community resulted from my participation with students in a symposium on "Cetacean Systematics: Approaches in Genetics, Morphology and Behavior" in the spring of 2004, which was hosted by scientists at the Southwest Fisheries Science Center and Scripps Institute of Oceanography in La Jolla, California. This led to a workshop report and later the organization of the Marine Mammalogy Taxonomy Committee chaired by Bill Perrin (and now by Patty Rosel), which provides a list, updated annually, of the current status of marine mammal species and subspecies. A forthcoming special issue of *Marine Mammal Science* on subspecies resulted from my participation in Journal Club meetings and a workshop on defining species and subspecies held prior to the 2009 Biennial Meeting in Quebec City (Rosel et al., 2017).

The Future and Lessons Learned

Phylogenetic analyses of various marine mammal groups based on morphology, fossil, and molecular data continue to be generated providing rigorous evolutionary frameworks (e.g., for cetaceans, Geisler et al., 2011; Gatesy et al., 2013; Boessenecker & Fordyce, 2015a, 2015b; for pinnipeds, Churchill et al., 2014; Boessenecker & Churchill, 2013; and for sirenians, Velez-Juarbe & Domning, 2015). These studies not only refine our understanding of evolutionary relationships among fossil and extant marine mammal species, but they also inform hypotheses of character evolution. I am especially pleased to note that the use of a phylogenetic framework has become more widely employed in marine mammal evolutionary and ecological studies, including investigations of large eyes and deep diving in pinnipeds (Debey & Pyenson, 2013), diving capacity in marine mammals (Mirceta et al., 2013), and pelage coloration in pinnipeds and cetaceans (Caro et al., 2011, 2012). The application of genomic studies to marine mammals (e.g., McGowen et al., 2014) is just beginning to address questions in population genetics and speciation, evolution and adaptation, and conservation genetics and research. What has been thus far published portends an exciting future.

Finally, I offer some advice to students and early stage career scientists alike based on what I have learned over the years advising graduate student theses and research projects:

1. *Embark on collaborative and international research.* Early in my career, I published sole-authored papers. Very quickly I came to appreciate the value of collaborative work, especially working with students both within the U.S. and elsewhere. In recognition of the importance that research publications play in the career of a scientist, one requirement was that my students submit a manuscript based on their thesis results for peer-review publication within one year of graduation. My feeling was that if the thesis research was rigorously undertaken with clearly defined objectives, methods, and results, then it should be available for other researchers to read in peer-reviewed publications. Although publication of thesis research often took a few years or more after graduation, most students met this goal.
2. *Encourage the use of new techniques and methods of analysis.* My anatomical expertise was enriched by learning new techniques, including CT imaging and 3D morphometrics (MicroScribe and laser surface scanner), that I employed in comparative studies using various phylogenetic methods. I learned a considerable amount about these tech-

niques and methods of analysis from my departmental colleagues, students in the Evolutionary Biology program area, and my mentorship of graduate student research projects.

3. *Mentor undergraduate and graduate students and postdocs.* Over the years, I have found that research experiences for undergraduates provide valuable opportunities and a good introduction into research that is helpful in career decisions. Weekly lab meetings attended by students include practice talks for upcoming professional meeting presentations and critical reviews of the current literature. Synergy in the lab was facilitated by having a cohort of students at different stages in their academic programs provide advice to each other.
4. *Promote interdisciplinary research.* Although I was trained as a paleontologist, my experience teaching at a relatively small public (i.e., non-ROI) university led me to broaden my expertise to include the anatomy and systematics of fossil and extant marine mammals so as to engage students with training and interests in both geology and biology. Looking back, accepting a faculty position at SDSU, a university that values both teaching and research, was one of the best decisions I made!
5. *Interact with local scientists and attend professional meetings with students.* I have always encouraged student attendance and participation in community events ranging from necropsies and dissections to seminars, journal clubs, and professional meetings. This is an important venue for research discussions with colleagues. It also gives students exposure to the research of other labs, facilitates collaborative work, and fosters knowledge of postdoctoral and other job opportunities.
6. *Be persistent—keep your eye on “the prize,” but don’t rule out opportunities.* Early in my career, I had my share of job disappointments. Having spent my first post-Ph.D. year teaching at a small liberal arts college with little time for research, when I accepted a postdoc appointment the following year, I knew that my focus had to expand to encompass research. I devoted as much time as possible to completing research projects and submitting publications and, in doing so, I developed a strong research focus. Recall that I accepted a position teaching human anatomy at SDSU—not marine mammals. Here again, persistence paid off, and I eventually found a way to teach a marine mammal class that led me to graduate students, grant support, and new research directions.

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