Vertebrate Paleobiology and Paleoanthropology Series

Darin A. Croft
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Methods in Paleoecology

Reconstructing Cenozoic Terrestrial Environments and Ecological Communities

Springer

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Cover illustration: Montage of modern terrestrial habitats and Cenozoic terrestrial fossil localities, illustrating a small portion of the diversity seen in both. A primary goal of many paleoecological studies is reconstructing ancient habitats: using data from modern environments and ecological communities to envision how a landscape would have appeared thousands to millions of years ago. From left to right: Contamana, Peru (middle Eocene); western Nebraska, USA; Los Queñes, central Chile (late Eocene); Cordillera de Sama, southern Bolivia; Cerdas, Bolivia (middle Miocene); Uvita, Costa Rica. Photo credits: D. Croft.

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Foreword

The past has always fascinated people once we became self-aware. In early days, it was the study of written history that engaged the best minds, but the ideas of prehistory, that humans had a history going beyond this, did not really take shape until after the work of T. H. Huxley. Darwin speculated on the subject, but at the time when he was working there was no fossil record for apes or humans other than the few dryopithecine specimens in France and the Neanderthal skull from Gibraltar. Huxley could also draw on paleontological studies in the 19th century and the work of Charles Lyell, who wrote extensively on the burial and 'imbedding' of plant and animal remains as well as the geological processes producing them. Similarly, the descriptions by William Buckland and Boyd Dawkins of British cave sites generally included comments on the preservation of animal remains and the processes by which they entered the caves. None of these 19th century authors commented directly on paleoecology, but Darwin's (1881) book *The Formation of Vegetable Mould Through the Action of Worms: With Observations on Their Habits* is a classic (and delightful) description of what happens to bones after burial, a taphonomic consideration essential to interpreting paleoecology.

As fossils accumulated in the 19th and 20th centuries, the prehistory of life began to fill out. It was mostly concerned with what kinds of animals and plants were present in the past, and how they were related to each other and to modern biota. Early works on the Carboniferous floras or the London Clay mainly consisted of taxonomic descriptions, but they also included interpretations of the type of environment the plants were living in, and although the word 'paleoecology' was not used, they were in fact paleoecological descriptions of past environments. In the case of plants, it is reasonably straightforward inferring the vegetation type from the species present, even as far back as the Eocene, and the plants growing in the London Basin at this time can easily be interpreted as tropical forest. However, most sites with fossil animals do not have fossil floras preserved, and many interpretations of paleoecology are based on species identifications of the preserved animals.

Once people started thinking about paleoecology, it was recognized that it has two aspects, the physical world and the biological world. The former consists of properties of the Earth and climate, and the latter the properties of the plants and animals. The paleoecology of a fossil site is therefore based on the geological attributes of the site, its inferred climate, and the animals and plants occupying the space and time of the site. As paleontology developed as a science, questions began to be asked about how fossils came to be preserved and what kind of environment they represented. Pei (1938) in *Le rôle des animaux et des causes naturelles dans la cassure des os* described marks on bones that he related, sometimes mistakenly in the light of present knowledge, to the agents that produced them and the ways in which the agents altered the composition of bone assemblages. This was the starting point for numerous taphonomic studies in the 20th and 21st centuries that have laid the groundwork for paleoecology.

At this stage, the interpretations of paleoecology were based on identifications of the animal species (and plants where available) present at a site. This was, and continues to be, a major source of evidence for paleoecology for general paleontologists, for it is the most straightforward approach to reconstructing past environments. It depends on James Hutton's principle of uniformitarianism that changes in the past came about by the same processes that operate today. If a large species of deer is present at a fossil site, this 'indicates' that woodland was present, as most deer today live in woodland; if an alcelaphine antelope is present, this 'indicates' grassland, as alcelaphines today feed on grass; and so on. Sometimes paleontologists take account of relative abundances of these indicator species, and sometimes the numbers of species indicating the same environment, but that is usually as far as it goes. Only in the past 50 years or so has paleoecology come of age and used established ecological principles in trying to reconstruct past communities of animals, but whereas ecology can be studied by direct observation, paleoecology is based on inferences about the past, assuming that processes in the past were the same as they are today.

Ecological communities consist of groups of animals and plants that coexist at one place and time and form an interacting unit. The place may range from a few meters, such as an area of forest floor, to several kilometers, for example the ecology of a forest unit. The time may be days, years, or even centuries. Paleoecology attempts to reconstruct these past ecologies by means of the fossil record, and in this case, the place means an excavation area, a stratigraphic level, or a fossil locality, taking into account the possibilities of intrusive or transported species. The time unit is the best estimate of the period over which the fossils were assembled, which may be measured in thousands of years. Stable isotopes, phytoliths, and fossil soils may provide direct insights into the paleoecology, but the evidence may be spatially limited to the immediate extent of the site. Similarly, fossil assemblages are often biased by taphonomic processes, which may exclude rare species or may bring about the mixing of faunas from two or more sources.

Based on these principles, Shotwell (1955) set out several criteria by which fossil mammal 'communities' differ from the communities from which they were derived. Selection may be indicated by biases in bone density, by which some bones are more likely to be preserved than others, biases in body size (modern faunas are approximately 80% small mammals and 20% large mammals), biases in state of preservation (mammals living close to the fossil site may be better preserved than those from far away), and biases from predator selection. These potential sources of error in reconstructing past communities provided the stimulus for taphonomic work in the second half of the 20th century, but at the same time it steered paleontologists toward considering community paleoecology.

Building on many discussions, Judy Van Couvering (now Judith Harris) and I tried out several different approaches to using entire faunas to reconstruct paleoecology. We devised two methods based on weighted averages ordination of entire fossil faunas, but these had two drawbacks. Firstly, they assumed that the faunas provided good representations of past communities, i.e., that they were not biased. I tried to estimate potential bias by experimentally altering living faunas either by rarefaction, for example eliminating species below a certain size limit from faunas of known habitat, or by mixing faunas from known habitats in different proportions. Secondly, both methods are based on interpreting past ecological preferences of fossil species from known preferences of the same or related species. Reliance on species equivalence between present and past is always going to be questionable for mammals. For invertebrates and plants, which had established their evolutionary niches by the beginning of the Tertiary, it is possible to reconstruct past communities in this way, setting out the interrelationships between all members of the community, but mammals lack a long evolutionary history, and modern families of mammal have rather fluid habitat preferences. Mammals have radiated quickly and are still diversifying, making it difficult to reconstruct their paleoecology on the basis of uniformitarianism. I then came across a new method of ecological analysis called species diversity, which I thought could be applied, not just to a few species, but to an entire mammal community. Instead of the taxonomic identifications of the species, the method

depended on analyzing key features in the anatomy of the species in a community: their body sizes, using regressions of body parts against size in modern mammals; their types of locomotion, based on the morphology of their limbs; and their diet, based on their tooth morphology. In theory, it should be possible to extend this method to all animals, particularly including amphibians and birds, but here the fossil record lets us down, for it is unusual to find other vertebrates, to say nothing of invertebrates, preserved alongside mammals.

The principle of ecological diversity is based on the observations made by many naturalists, including Darwin and Wallace. Species of mammals and birds living in similar environments but on different continents evolve similar adaptations because they occupy similar ecological niches. Thus, the distributions of mammalian body sizes in tropical forests are similar on different continents even though the species, genera and even families are all different; there are anteaters in South America that have evolved feeding adaptations similar to those of anteaters in Africa even though they are not related phylogenetically; there are species of hedgehog, flying squirrel, and carnivore which are unrelated but which have evolved similar limb structure in parallel from different ancestral stocks. (Although Darwin observed this phenomenon, he was more concerned with showing the phylogenetic connectivity of faunas and floras *within* continents as opposed to similarities *between* continents.) These similarities come about because mammals adapt in similar ways to similar environments by convergent evolution, independently of phylogeny, so that by analyzing by multivariate analysis the range of adaptations present in all members of a fossil mammal fauna and comparing it with analyses of modern faunas from known habitats, an indication of the environment to which they are adapted can be obtained free of taxonomic bias.

This taxon-free approach is based on the summation of all adaptations present in entire floras and faunas, but ecological diversity relied on subjective interpretations of mammalian skeletal anatomy. Quantitative methods based on ecomorphology have been devised to relate measurements of anatomy directly with bodily function. Ecomorphology is a time-consuming method, however, and it can realistically be applied only to segments of faunas. In addition, while some morphologies are directly related to equivalent behaviors in one group, the same behavior may have different anatomical traits in a different group of mammals. For example, running bovids have different adaptations of the femur from leaping bovids, and these differences can readily be identified in fossil bovids, but the same anatomical features are different in equids. In other words, ecomorphology is not always a taxon-free approach to paleoecology, for it may depend on identifying the phylogenetic position of the groups before they can be analyzed. On the other hand, some dental ecomorphologies such as microwear and mesowear on teeth may cross phylogenetic boundaries.

Ecomorphological criteria applied to large databases of mammals in the northern hemisphere may indicate environmental and climate change. For example, molar hypsodonty distinguishing grazing from browsing herbivores is used as a proxy for changing vegetation patterns in Europe. The change from browser-dominated faunas in the early Miocene to grazer-dominated faunas today indicates loss of forest browse and increase in grasslands, and this has been linked with decreases in temperature and precipitation. This is a good indication of how the herbivore communities have evolved through time, but it does not provide any insights into how the interrelationships within the herbivore/carnivore communities changed.

Another method of paleoecology is now based on physiological constraints of mammals in relation to their ecological place in communities. This grew out of a seminal paper by Olson (1966), who distinguished pelycosaur-therapsid communities on the basis of physiological adaptations, for example between terrestrial and water-based food chains. These principles were applied to mammals by Damuth (1982), who investigated community structure by analysis of body size in relation to species abundances. He found that there are energetic and metabolic limits to present-day mammalian communities; for example, very large mammals have limited numbers of species, and insectivores could not survive above a certain weight limit. These ideas were developed by Chistophe Soligo and me (Soligo and Andrews 2005) by linking the physiological constraints with ecological diversity variants. We were able to show

that there are limits to species numbers based on metabolic and size constraints and that all modern communities conform to these limits. Assuming the same constraints apply to fossil mammals, fossil faunas could be analyzed by the same criteria, and those that were outside those limits were not true communities.

The present volume describes and extends many of these historical topics in a timely fashion, describing techniques applied to individual mammal species, species richness, analyses of sediments and plants (in the broadest sense of the word), and community analysis. The significance of body size, functional morphology of limb structure, and tooth structure all have chapters. Dietary inferences are made from microwear and mesowear, and growth patterns of teeth record ecological pressures on individuals and communities. Trace fossils contribute both to biological aspects of paleoecology, by identifying the agents that produced them, and the physical aspects by their effects on the sediment in which they are preserved. Physical evidence of paleoecology is based on analyses of fossil soils, biomarkers, and minerals preserved in sediment, isotopes, phytoliths, pollen, and trace fossils, for they all contribute to understanding paleoecology in addition to plant macrofossils. Geometric morphometrics is a form of shape analysis that is here applied to ecomorphological data, and ecometrics is applied to the distribution of functional traits. Finally, there are chapters on ecometrics and community structure analysis, which shows the striking similarities in communities sharing similar habitats. These contributions bring paleoecology up to date and show that the subject is alive and kicking.

London, UK

Peter Andrews
Natural History Museum

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Preface

The field of paleontology has changed dramatically and rapidly over the past several decades. Although discovering, naming, and determining the evolutionary relationships of extinct species are still a priority for paleontologists, understanding the biology of extinct species (paleobiology) and reconstructing the environments in which they lived have become increasingly prominent goals of such investigations. This is partly due to new technologies (e.g., microtomographic imaging, laser surface scanning), greater computational abilities, and innovative analytical methods (e.g., texture analysis in tooth wear, morphometrics, novel isotopic analyses), but it also results from an increased emphasis on the interconnectedness of organisms and their environment: the field of paleoecology. This greater emphasis on paleoecological studies, in turn, has resulted in a proliferation of techniques for understanding how extinct species lived, moved, and what they ate, the habitats in which they lived, and the climatic regime that affected them and their environment. These advances have revolutionized our understanding of the paleobiology and paleoecology of past organisms. They have also enabled us to better document the timing and context of adaptations and to more confidently reconstruct the evolutionary history of life.

Keeping up with the rapidly changing field of paleoecology is a formidable task for professionals and students alike. Equally challenging is integrating the many techniques developed by specialists in different disciplines to create a coherent picture of an ancient environment and the animals that inhabited it. To this end, we convened a three-day conference in Cleveland, Ohio, in September 2015 to bring together a diversity of early- and mid-career researchers with strong interests in paleobiology and paleoecology. (Conference participates are designated by '#' in the contributors list.) The principal goals of this conference were to: (1) summarize and synthesize currently available tools for paleoecological investigations; (2) facilitate new research collaborations; and (3) create a plan for publishing a volume that would be a 'how to' guide on paleoenvironmental reconstruction for researchers and students. We focused on terrestrial ecosystems and limited the scope to the Cenozoic Era, since communities and habitats from this interval can generally be reconstructed with greater confidence than those from more ancient ones. Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities is the product of that conference.

Our Cleveland conference was generously supported by the Cleveland Museum of Natural History (CMNH), an anonymous donor to the CMNH, Case Western Reserve University's Institute for the Science of Origins, and Bob Jackson. All chapters were reviewed by at least three external referees in addition to the editors, and we thank all of the reviewers for taking time to provide valuable feedback. We are grateful to Peter Andrews for crafting an insightful and historically illuminating foreword to this volume. Thanks to Caitlin Schwarz for editorial assistance. We are also indebted to the editors of Springer's Vertebrate Paleobiology and Paleoanthropology Book Series, Eric Delson and Eric Sargis, for their help and guidance in bringing this volume to fruition.

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Chapter 1
Introduction to Paleoecological Reconstruction

Darin A. Croft, Denise F. Su, and Scott W. Simpson

Abstract Ancient terrestrial ecosystems cannot be observed directly, but a wide variety of approaches and techniques have been developed that provide indirect evidence of many aspects of ecosystem functioning. By integrating multiple lines of evidence about the climate, vegetational structure, and fauna of a given location at a particular time, a relatively complete paleoecological picture of a fossil locality can be generated. This volume reviews some of the most commonly used techniques for paleobiological and paleoecological analysis; in this chapter, we briefly introduce these approaches and the insights they can provide. They include techniques for: inferring attributes of particular mammal species and/or individuals (body mass, locomotor adaptations, diet, life history variables); interpreting ancient soils (paleosols), trace fossils (ichnofossils), organic biomolecules, and plant remains of various types (pollen, phytoliths, macrofossils); analyzing isotopic and geometric morphometric data to answer a range of ecological and environmental questions; and seeking patterns in data across broad taxonomic, geographic, and/or temporal scales (ecomorphology, ecometrics, and ecological diversity analysis).

Keywords Ecosystems • Ecometrics • Paleobiology • Paleoecology • Paleoenvironment

Although many aspects of modern ecological communities are not yet understood, describing the animals, plants, and climate of a particular point on the globe – at least in broad strokes – is relatively straightforward. For example, we have a pretty good idea of the number and types of birds, mammals, amphibians, and other animals that inhabit Great Smoky Mountains National Park in the eastern United States. We know that the area is covered by temperate deciduous forest, has a mean annual temperature of about 13°C, and generally receives 140–220 cm of precipitation per year. Similar data are readily available for such sites as the Iberá Wetlands in northeast Argentina, Krau Wildlife Reserve in Malaysia, and Kruger National Park in South Africa. As a result, much of the research that goes on in these areas focuses on clarifying details of these ecosystems, such as documenting inconspicuous and/or unrecognized species, unraveling the complex relationships among organisms and between them and their environment, and predicting how small and large-scale human activities many affect these areas in the future.

Understanding ecosystems of the ancient past requires a different strategy. Since it isn't possible to directly observe extinct organisms or measure rainfall or ambient temperature in the past, such ecosystems must be reconstructed from the physical evidence and chemical signatures left in the geological record by their biotic (plants and animals) and abiotic (rain, temperature) components. Instead of starting from the big picture and drilling down to the details, a paleoecologist must start with the details – such as fossil teeth and bones, phytoliths, or soil carbonates – and work up. This bottom-up approach is also necessitated by the nature of the fossil record itself, which preserves only a subset of the plants and animals that comprised an ancient ecosystem. The many methods that are available for reconstructing particular aspects of ancient ecosystems are all based on certain assumptions and generate some degree of error. Therefore, maximal confidence comes from combining analyses of entire faunal and floral assemblages with geological, geochemical, and other types of contextual data. Integrated paleoecological studies like these provide a historical

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perspective on the evolution of Earth's ecosystems that permits macroecological analyses of patterns of climate change, the evolution of lineage and guild-level adaptations, and large scale biogeographic patterns.

The goal of this volume is to review some of the most common techniques that are used to reconstruct ancient terrestrial environments and ecosystems in order to illustrate the myriad sources of data and types of analyses that can inform such an effort. The chapter authors are experts in fields that span chemistry, geology, and biology. They describe approaches that provide varying levels of resolution about the environmental conditions and the plants and animals that existed thousands to millions of years ago. They also provide glimpses into the future of paleoenvironmental reconstruction by discussing potential ways that these approaches may be refined.

While many of the techniques discussed in this volume can be applied to any part of the fossil record, we focus here on examples from Cenozoic terrestrial localities. Mammals are among the most conspicuous elements of modern ecological communities, and extinct mammals have long been a prime source of information about the ancient habitats in which they lived. This is primarily due to the fact that their teeth and skeletons withstand fossilization far better than those of most other organisms. Thus, most terrestrial paleontological sites from the past 66 million years yield mammal fossils, often in abundance. The first five chapters of this volume discuss techniques used to elucidate the paleoecology of particular mammal species or individuals by studying the structure or attributes of their remains. Although understanding the ecologies and adaptations of the mammals themselves is often the ultimate goal of such studies, these data can also be integrated into studies of the broader mammal community in order to characterize the paleoenvironment in which they lived, a topic addressed near the end of this volume.

Three attributes describe much of an animal's ecological niche: body mass, locomotor style, and diet. The next four chapters address these topics in turn. Chapter 2, by Samantha Hopkins (2018), discusses how one goes about determining the size (body mass) of an extinct species through analyses of their skeleton. Body size is probably the most immediately recognizable aspect of any mammal, and it can easily be quantified in a living individual by measuring its body mass. Measuring body mass is much less straightforward when one is dealing with fossil remains – which are often fragmentary – particularly for mammals with a body form quite unlike any species alive today. Body mass estimates have traditionally relied on regression equations, and although the mathematics involved is relatively simple, many important considerations must be taken into account to obtain reasonably accurate estimates. More complex methods have been developed in recent years, but whether these are widely applicable remains to be seen.

The limbs are the load-bearing structures of most mammals, and thus there is a reasonably tight correlation between their structure and body mass. However, limb bone morphology is also tightly linked to function. Chapter 3, by Rachel Dunn (2018), describes the process whereby a functional morphologist deduces limb function in an extinct species by reconstructing the sizes and positions of muscles based on their bony attachments. This chapter provides a solid theoretical grounding for comparative anatomical studies, whether one uses traditional descriptive approaches or more computationally-intensive investigative techniques such as three-dimensional morphometrics. As noted in this chapter, a species' evolutionary (phylogenetic) relationships can strongly influence many aspects of its anatomy and physiology, including its limb structure. For this reason, the influence of phylogeny in paleoecological studies is a recurring theme throughout this volume. It is likely that correcting for underlying phylogenetic biases in data will become increasingly important and feasible as the structure of the tree of life is ascertained with greater confidence and precision.

Chapters 4 and 5 both tackle the subject of determining what an extinct species ate, but they do so from different perspectives. Chapter 4, by Alistair Evans and Silvia Pineda-Munoz (2018), describes a mechanical and material properties approach to that question that strives to determine the types of foods a tooth (or dentition) is optimally structured to process. In other words, for what type of diet have the teeth been shaped by natural selection? This is a "long-view" strategy for determining the average diet to which a species is adapted that parallels methods used to reconstruct locomotor style, and certain aspects of tooth form, most notably hypsodonty, can be (and have been) applied quite broadly across space and time to deduce large-scale environmental and climatic patterns. But not all aspects of tooth form are dictated at birth. Teeth undergo wear through interactions with one another as well as with consumed foods. How one reads that wear record is described in Chap. 5 by Jeremy Green and Darin Croft (2018), who focus on mesowear and microwear analyses. Mesowear and microwear can be thought of *a posteriori* strategies, as they strive to correlate tooth wear (macroscopic and microscopic, respectively) with the foods an individual animal consumed prior to its death. Thus, they represent direct evidence of behavior, though they do so at different time scales. (The analogous approach for limb function might be analyzing the distribution of internal trabeculae in limb bones, but a standardized, broadly-applicable technique for interpreting such data has not yet been developed.) The techniques for inferring diet described in Chaps. 4 and 5 are

complementary and, when combined, can assess diet variation among individuals and populations in addition to species.

Teeth and bones are affected by internal physiological processes as well as external ecological ones, and their microscopic growth proceeds like a biological metronome, evenly marking time in variable durations ranging from days to weeks to years. Chapter 6, by Russell Hogg (2018), details how such changes can be read in the teeth and bones of extant and extinct species and applied to a variety of paleobiological and paleoecological topics such as life history traits of particular species and seasonal environmental variation. The fields of odontochronology and skeletochronology are still in their relative infancy, at least in terms of their application to non-primates, and have the potential to provide fine-scale growth and development information about individuals and populations analogous to that provided by microwear and mesowear for diet.

Teeth and bones can also be analyzed to reconstruct diet on an even finer scale by documenting the relative compositions of the stable isotopes they contain. Such analyses most often focus on oxygen and carbon isotopes, and this topic is reviewed by Penny Higgins (2018) in Chap. 7. The theoretical basis behind stable isotope analysis is that the proportions of different isotopes vary depending on the environment in which an animal lived and the plants that it ate. These isotopes are incorporated into the animal's tissues in similar proportions – though the values are altered to varying degrees by physiological processes – and can be preserved in the fossil record. Measuring these isotopes in fossil teeth and bones requires destructive sampling, but much less material is required now (typically 10+ mg for tooth or bone) than was necessary only a couple of decades ago. Moreover, newer microsampling techniques have enabled researchers to study changes in isotopic compositions within a single specimen, a strategy equivalent to sampling the composition of a mammal's tissues at different points during its life. Isotopic sampling is usually performed on fragmentary specimens that have relatively little value as comparative specimens and, as a result, this technique has been applied to a wide variety of species and sites across the globe. This, in turn, has resulted in many new insights into past climate and habitat and the development of new hypotheses to be tested by other means.

Other micro-scale sources of information are organic molecules preserved in fossil-bearing sediments, which can provide clues about past moisture, temperature, and vegetation. These "chemical fossils" represent records of past life (biomarkers), often from organisms that are not themselves preserved in the fossil record of a particular area, such as bacteria and plants. Their study lies at the intersection of biology, geology, and chemistry and comprises a relatively young (less than a century old) field of scientific research known as organic geochemistry. In Chap. 8, Melissa Berke (2018) describes a portion of the wide diversity of organic biomarkers that have been discovered thus far, how they are collected and analyzed, and the types of information they can provide about ancient terrestrial environments.

Organic biomarkers, like fossils themselves, are commonly preserved in ancient ("fossilized") soils, which are termed paleosols. As detailed by Emily Beverly and colleagues (2018) in Chap. 9, studying the macroscopic, microscopic, and chemical characteristics of these paleosols – the purview of paleopedology – can provide a wide range of complementary information about past landscapes and climatic conditions. Paleosols are the product of local conditions and thus act as archives of the paleoenvironment of a specific site over a relatively constrained period of time. They provide information about a site's climate (mean annual temperature and precipitation), vegetation, sedimentary regime, and landscape stability and can be used to assess regional variation in these variables when studied throughout a basin.

Among the more commonly encountered fossils in paleosols are ichnofossils: traces of organisms and records of their behavior, often organisms not directly preserved in the fossil record. In Chap. 10, Daniel Hembree (2018) reviews various kinds of animal-soil interactions that can result in ichnofossils, such as nests, burrows, and trails, and describes the types of interpretations that can be gleaned from them regarding habitat and environmental conditions. One of the key challenges in continental (terrestrial) ichnology is correlating ichnofossils with the organisms that made them. In recent decades, researchers have begun to build an ichnological library based on laboratory studies of traces made by living organisms, a pursuit that will undoubtedly provide new information about otherwise unrecognized inhabitants of ancient ecosystems.

Plants are closely adapted to abiotic factors such as climate and soil composition, and any ecological interpretation of a terrestrial paleontological site is incomplete without considering its predominant plant types and vegetational structure. Unfortunately, the conditions that permit the preservation of plant macrofossils such as leaves are seldom the same ones that preserve vertebrate bones and teeth. However, many sites that preserve fossil vertebrates also preserve microscopic plant remains. Such remains include pollen and spores, reviewed by Luke Mander and Surangi Punyasena (2018) in Chap. 11, as well as phytoliths, which are reviewed by Caroline Strömberg and colleagues (2018) in Chap. 12. Pollen and spores have the advantage of being relatively widespread, but this can also be a liability when they record plants living far away from the site in question. Moreover, they are usually only found in relatively fine-grained sedimentary layers. Phytoliths, which are silica bodies that form in plant cell walls, are durable and can often

be found alongside vertebrate fossils, but unlike pollen and spores, a single type of plant can contain many forms of phytoliths. Thus, a primary challenge of phytolith investigations is taxonomically identifying the types of plants these phytoliths represent. Studying phytoliths in deep time is a recent phenomenon, and much work remains to be done in documenting their diversity in modern taxa. Despite the challenges posed by both paleopalynology and phytolith-based paleoecology, these approaches are extremely useful for providing primary evidence about the plants that were living at a particular site in the absence of (or as a complement to) macrofossil evidence. It should come as no surprise that both techniques have effectively developed and tested a diversity of geohistorical and macroecological hypotheses.

In sites that preserve plant macrofossils, these specimens can be a source of detailed information about climate and habitat in addition to species diversity, as summarized by Daniel Peppe and colleagues (2018) in Chap. 13. The close linkages between plants and their environment, combined with the taxonomic information contained in fossil leaves, flowers, and other plant parts, means that associations of plant macrofossils are among the best methods of documenting environments of the past. Paleobotany is a comparatively old field, and much recent progress in this area has focused on quantifying fossil assemblages and creating more accurate algorithms for correlating assemblage characteristics with abiotic variables such as temperature and precipitation. The quest to refine paleoecological interpretations by quantifying form is a second conspicuous cross-cutting theme in this volume and a major focus of Chaps. 14–17.

Thanks to increases in computational power that continue to accelerate, it is now relatively easy to quantify form in ways that were scarcely dreamt about even 10 years ago. Although linear measurements remain more than satisfactory for describing many aspects of a fossil specimen, complex surfaces or morphologies can only be adequately described using more sophisticated methods. Chapter 14 by Sabrina Curran (2018) reviews techniques and applications of what is known as three-dimensional geometric morphometrics: describing morphology in three axes (or sometimes two) using devices such as 3D digitizers, laser surface scanners, and computed tomography (CT) scanners. There is no limit to the types of paleoecological studies that can incorporate such techniques, and the diversity of proven applications continues to expand as the devices used to acquire three-dimensional data become less expensive and more accessible.

The final chapters of this volume focus on broader themes of paleoecological reconstruction that build on the results of the types of studies reviewed in Chaps. 2–7. In Chap. 15, Andrew Barr (2018) describes how one aspect of form – such as a particular aspect of tooth or limb morphology – can be quantified across a broad range of extant species, correlated with an ecological variable such as diet or locomotor style, and used to interpret a paleoecological attribute. The shorthand name now used for such studies is ecomorphology. In our usage of the term, ecomorphological studies parallel paleobiological studies of diet and locomotion such as those described in Chaps. 3–5 but differ in their goal; rather than inferring the habits of a particular species, ecomorphological studies typically use form-function relationships to characterize an entire fauna or to compare associations within a particular group across broad spans of space or time.

Chapter 16, by Kris Kovarovic and colleagues (2018), describes a process whereby ecomorphological data from modern and fossil mammal communities are compared to one another with the goal of reconstructing past habitats and ecological associations, a process known as community structure analysis or ecological diversity analysis (EDA). A typical ecological diversity analysis examines the three primary determinants (or reflections) of an animal's ecological niche mentioned earlier in this chapter – body mass, diet, and locomotor strategy – and uses the collective ecological niches of all members of a mammal community to infer the habitat in which they were living. Like many of the approaches described in this volume, this strategy for paleoecological interpretation relies on observed relationships between living mammals and their environment. Thus, a key consideration in EDA is selecting an appropriate dataset of modern comparative faunas, a task that is much simpler in principle than in practice. Some recent EDAs have also begun to suggest that certain mammalian communities in the past may have been structured differently from any that exist today, a finding that has important implications for understanding niche partitioning, ecosystem functions, and the diversity of mammalian ecological communities.

The final methods chapter in the volume, Chap. 17, by Wesley Vermillion and colleagues (2018), describes an approach to interpreting paleoclimate and paleovegetation known as ecometrics. Like ecomorphology, ecometrics strives to correlate particular traits with environmental characteristics, but it differs in its broader taxonomic scope (typically entire communities), more extensive geographic and temporal focus, and its use of mathematical modeling to understand long-term evolutionary and ecological processes.

Which of the many methods detailed in this volume can and should be applied to reconstructing ancient terrestrial ecosystems depends in large extent on the data that are available. But assuming the best-case scenario – a paleontological site with abundant and well-preserved fossils, a diversity of willing and able-bodied researchers, and generous financial and institutional support – how can results from an array of analyses be combined to create an integrated understanding of a particular place at a specific time

in the past? What additional considerations should be taken into account, and what should one do in the case of conflicting results? The final chapter in this volume, by Denise Su and Darin Croft (2018), addresses these and other questions and attempts to outline a path forward so that knowledge of past ecosystems may one day begin to approach those of the present.

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Chapter 2
Estimation of Body Size in Fossil Mammals

Samantha S. B. Hopkins

Abstract Body mass is a fundamental ecological parameter of mammals with implications for a variety of other ecological characteristics. While it cannot be directly measured in fossil taxa, it can be inferred using allometric relationships between skeletal dimensions and mass derived from extant species. Many such relationships have been described, primarily for dental and limb dimensions. Methods of statistical analysis vary widely, however, in ways with substantial implications for the inferred masses of fossil species. The subset of extant species from which the relationship is derived must be representative of the evolutionary and ecological scope of the fossil taxa for which mass is to be estimated. Increasing computing power and an explosion of phylogenetic comparative methods offer the opportunity to gain an understanding of the processes driving these important empirical relationships.

Keywords Body mass • Proxy • Mammalia • Regression • Allometry • Paleoecology

Introduction

Body size is an essential characteristic of animals, with substantial implications for a number of other ecological and evolutionary parameters (Eisenberg 1981; McMahon and Bonner 1983; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; LaBarbera 1989; Blackburn and Gaston 1994). Size is measured in a variety of ways; among animals it is commonly described in terms of either body length or mass, as these parameters offer the greatest predictive value for ecology. Both of these characteristics translate into the constraints on ecology and evolutionary history, from life history to trophic strategy, evolutionary rates to preferred habitats. As a result, reconstructing body size from extinct organisms is an essential step in understanding their ecology.

Among mammals, body size is commonly described in terms of mass; body length is primarily used for mammals too large to be easily weighed, such as whales (Lockyer 1976), although it has been used for other taxa as well (Iskjaer et al. 1989). Body mass does vary significantly through the lifetime of an organism in response to health, lactation, pregnancy, age, food availability, and other factors (Lindstedt and Boyce 1985; Schulte-Hostedde et al. 2005; Toigo et al. 2006), but paleontologists are generally concerned primarily with estimating average adult size for a species. While mass is easy to measure in living mammal species, requiring only a spring scale for the vast majority of mammals, it cannot be directly measured in extinct organisms. There are, however, a variety of skeletal and dental proxies available for the estimation of body mass. All of these proxies depend on isometric or allometric relationships between various skeletal dimensions and body mass.

The most commonly-applied proxies for mass make use of either dental dimensions (e.g., Legendre 1986; Hopkins 2008; Freudenthal and Martín-Suárez 2013) or the diameters of limb bones (e.g., Scott 1983; Gingerich 1990; Rafferty et al. 1995). Ruff (1988, 2003; Ruff et al. 1991) has also had success estimating mass with the articular dimensions of limb bones. Dental proxies, most commonly used for mammals, take advantage of the relationship between food-processing capacity and metabolism (which is driven primarily by body mass; McNab 1988; Whittaker 1999) and benefit from using the most identifiable and preservable elements in the mammalian skeleton, the teeth. Limb proxies, on the other hand, have the advantage of relying on the more direct relationship between body mass and the load borne by the limbs as they support the body on land. In the case of aquatic mammals, for which neither of these proxies may be effective, other proxies such as cranial dimensions

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and estimated body volume are necessary. Multiple proxies are often necessary for a robust estimate of mass, and a variety of approaches have been applied to determining which of the various mass estimates are most reliable.

While the allometric relationships between mass and skeletal dimensions have been studied for more than 40 years, there remain substantial problems still to be solved in body mass estimation. In particular, there is a need to confront the difficulties created by using regressions on log-transformed data for estimation. Another factor that complicates mass estimation is the lack of a consistent physical constraint on morphology that can be generalized across all mammals; it is nearly impossible to use the same proxy when studying a diverse assemblage of mammals, as the relationships between mass and skeletal proxies change across mammalian phylogeny. Reconstruction of the body mass of extinct mammals requires careful consideration of phylogenetic constraints, locomotion, functional morphology, and the statistics of regression analysis, prediction intervals, and error propagation. Nonetheless, despite the challenges in the approaches available to us today, there is reason for hope that new computational approaches will solve or at least control for existing problems, and even the strategies currently available can generate ecologically meaningful information about fossil ecosystems and organisms.

Terms

Accuracy: The degree to which an estimated value approximates the actual value. In the estimation of mass, this is probably the primary basis with which to judge the value of a method for paleoecological reconstruction. This is in contrast with Precision; see below.

Allometric scaling: A description of the relationship of overall size to morphology. As size changes, some aspects of morphology change faster or slower than others, leading to changes in shape with changing size.

Body size: A measure of the total size of an organism. Common measures of size in vertebrates include mass, total length, and snout-vent length.

Body mass: The total mass of a live or recently dead organism, conventionally measured as weight with a spring scale.

Geometric scaling: A scaling relationship in which two characters are related mathematically as predicted by their geometry. That is, a volumetric measurement (such as mass) should be proportional to the cube of length (with or without coefficients arithmetically modifying the slope or intercept of the relationship).

Heteroscedastic: Non-normally distributed and skewed. Commonly used with reference to the shape of a distribution of variables.

Isometric scaling: A scaling relationship in which two characters of interest retain the same proportions with size change, resulting in retention of consistent shape over a range of sizes.

Jackknifing: The statistical practice of establishing the predictive value of a regression by removing the data points one by one, analyzing the relationship between the x and y variables, and then using that regression to predict the y-value of the excluded datum. Iterated over the entire dataset, this approach generates an estimate of the capacity of the regression to predict values for new data.

Metabolic scaling: A scaling relationship predicted by the mathematical relationship between size and metabolic rate. The metabolic theory of ecology (Brown et al. 2004) predicts that metabolism scales with $mass^{3/4}$. Hence, other features, such as tooth area, used in fueling metabolism are expected to scale with $mass^{3/4}$. This is in opposition to volumetric scaling, which would predict area scaling with $mass^{2/3}$.

Multiple regression: Linear regression that simultaneously considers multiple independent variables to account for the correlations among those variables in estimating the strength of their linear relationships with the dependent variable. The regression equation takes the form $y = m_1x_1 + m_2x_2 + m_3x_3 + \cdots + b$, rather than $y = mx + b$ as in an ordinary linear regression.

Overfitting: A statistical error in which a regression attributes more of the variation in the dependent variable to the independent variable(s) than is actually causally driven as a result of violations of the distribution assumptions of the statistical method.

Power law regression: A method of regression analysis that, rather than fitting a linear relationship between the independent and dependent variables, looks for the exponential relationship that best explains the distribution of values; the regression equation takes the form $y = ax^m$ rather than $y = mx + b$ as in an ordinary linear regression.

Precision: The uncertainty in an estimated value; the exactitude to which an estimated value is articulated. In its simplest terms, this could be the number of decimal places to which the value is estimated. Note that precision is not the same as accuracy, defined above. A mass estimate value can be highly precise, in terms of being highly replicable and not particularly variable in magnitude, but also quite inaccurate, in being quite distant from the actual mass of the animal.

Rectangular area: The estimated surface area of a roughly quadrangular feature (for the purposes of this chapter, tooth surface area) estimated by multiplying length by width.

Standard error of the estimate: A measurement of the uncertainty in a dependent variable value estimated using a regression. It is commonly calculated as $\sigma_{est} = \sqrt{\frac{\sum (Y-Y')^2}{N}}$

Training data: The data used to generate a predictive statistical relationship. In the case of body mass estimation, these are commonly derived from skeletal measurements of museum specimens of extant species associated with individual body masses. The allometric equations produced from the training data can then be used to estimate body mass where only skeletal dimensions are known.

Volumetric estimation: An approach to body mass estimation wherein the 3-dimensional outline of an organism is reconstructed from its skeleton, and that volume is used to infer mass given either an assumed density or an allometric relationship between volume and mass.

Theoretical/Historical Background

Current approaches to the estimation of body size in extinct mammals trace their roots to a paper by Gould (1975) in which he pointed out that the area of mammalian postcanine teeth scales against mass with positive allometry, likely as a result of metabolism and/or the changes in dietary strategies with increased habitat grain. This work provided a basis for straightforward reconstruction of body mass in any fossil mammal known from teeth. While Gould's descriptions of these allometric relationships for a few key mammalian clades were foundational, subsequent work discussed the drivers of variation in the relationship between size and dental dimensions (Gingerich et al. 1982; Fortelius 1990; Smith 2002). Certainly, the assumption underlying the use of allometric relationships derived from extant mammals to infer mass in extinct species is that the processes shaping those relationships in living species were the same as those in place when the fossil of interest evolved. Whether or not this assumption is true depends on whether our explanations for this allometric relationship are correct (Fortelius 1990).

Many authors have suggested that the relationship between tooth size and body mass is constrained by the energetic demands of size and their relationship to food processing needs (e.g., Gingerich et al. 1982; Fortelius 1985). If this is true, then the fossil taxa for which we reconstruct mass must be similar in physiology (so that energetic demands scale similarly with size), the types of food consumed, and digestive strategy to the range of extant mammals used to produce the allometric curve from which fossil mass is inferred. Tooth size-body mass allometry was proposed by Gould (1975) to represent ¾ power metabolic scaling and hence presumably be similar across all crown group mammals. For a discussion of the complexities of metabolic scaling in mammal teeth, see Fortelius (1990). It has also been proposed that the relationship between tooth area (which is a function of length squared) and body mass (which is directly related to volume, a function of length cubed) should show ⅔ power geometric scaling (Gingerich et al. 1982). There is enough noise in the relationship between mass and tooth area (as a result of measurement error, individual variation in tooth size and mass, and interspecific variation in the relationship between the two), and enough different ways of measuring tooth dimensions that the nature of the scaling relationship remains controversial (a problem that plagues the geometric/metabolic scaling problem in general; White et al. 2009). As a consequence, most approaches to mass reconstruction are empirically-based rather than having a strong theoretical foundation.

While early efforts used the area of the entire postcanine tooth row to infer allometric relationships with mass (Gould 1975), Gingerich et al. (1982) and several subsequent authors (Legendre 1986; Van Valkenburgh 1990; Gordon 2003) demonstrated a strong relationship between body mass and the areas of individual teeth, in particular the first molar. The first molar is particularly useful because it tends to have relatively low levels of intraspecific variation and lower levels of sexual dimorphism, likely as a result of its eruption early in ontogeny, prior to puberty (Gingerich 1974). Inferring mass from individual teeth adds to the metabolic scaling assumption by assuming a consistent relationship between the size of that tooth and that of the rest of the tooth row. This assumption can often be assumed to hold true where the dental formula and gross dental morphology remain similar but becomes more questionable with changes in the functional role of the individual tooth within the tooth row. Changes in diet that emphasize the function of particular teeth cause increases or decreases in the relative sizes of teeth, changing these allometric relationships. A widely-used set of regression equations of lower first molar (m1) rectangular area (that is, length × width, rather than the actual area measured within the tooth outline) against body mass for a variety of mammalian clades was developed by Legendre (1986), which led to the adoption of m1 area as the most common proxy for mammalian body size. This proxy has the additional advantage that the lower first molar of the vast majority of mammalian species is among the most taxonomically diagnostic of skeletal remains.

The allometric scaling of limb bones with mass has seen a great deal of work (e.g., Gingerich 1990; Biknevicius 1999; Christiansen 2002), but one key realization is that the load-bearing strength of a columnar limb is proportional to its cross-sectional area (Ruff 1990), so one can use the cross-section of limb bones to infer mass in extinct mammals. This method was shown to predict mass much more reliably

than dental dimensions in an array of studies that arose out of a workshop on body mass held at the University of Florida (Damuth and MacFadden 1990), as well as some subsequent work (e.g., Egi 2001). However, this approach has a different set of assumptions that can be violated by extinct mammals. For example, using humeral cross-sectional area as a predictor of body mass assumes similar posture to the modern dataset from which the fossil species' mass was inferred. This has been problematic in some past studies (Sánchez-Villagra et al. 2003; Millien and Bovy 2010; Basu et al. 2016), which have concluded that weight-bearing posture differed in the extinct species under study. Other studies have shown that this scaling relationship may change over the range of extant mammals (Biewener 1990; Christiansen 2002) as the physical constraints change in importance allometrically, so inferences should be made with reference to species within the size range of extant comparators. Ruff (2003) showed that the distribution of bone within the shaft (measured as the section modulus) is more effective at predicting mass than the breadth of the bone shaft, so where precision is important and fossil material is well-preserved, this more labor-intensive approach may yield greater accuracy.

Breadths and areas of limb bone articular surfaces provide another functionally constrained parameter; while they may be affected by locomotor behavior (Ruff 1990, 2002), there is some evidence (Ruff 1988, 1990, 2003) to suggest that they may be more reliable than many other proxies for mammalian body mass. The articular surface area is assumed to be constrained by mass in that excessively large forces exerted on articular surfaces in the joints increase the chances of damage to cartilage and soft tissue. These methods require preservation of identifiable limb elements with complete articular surfaces, but have proven to predict mass well in primates (Ruff 1990, 2003). They have not yet been widely applied among other mammalian groups.

Recently, there has been a dramatic increase in the application of phylogenetic comparative methods to paleoecology. Given the limitations mentioned above to body mass estimation, it is worth asking whether evolutionary history has a substantial influence on the outcome of body mass reconstructions, given that these methods are often applied to fossil taxa with no close living relatives. Campione and Evans (2012) determined that limb bone circumferences do show some component of phylogenetic signal in the fit between limb dimensions and mass but concluded that it was not significant for reconstructions of ecology. No study has made a comprehensive effort to examine the influence of phylogeny in dental reconstructions of body mass, but studies at the ordinal level within mammals (Legendre 1986), between families of primates (Kay and Ungar 1997; Scott 2011), and within families and superfamilies of rodents (Lindsay 1988; Morgan et al. 1995; Hopkins 2008) have shown that regression equations can differ substantially between clades, suggesting the importance of phylogeny in constraining these relationships.

Approaches

Given the variety of proxies available, any study of fossil mammal body mass has a number of methodological options. Choice of an appropriate proxy for body mass reconstruction should be dictated by the biology of the group under study. Where possible, multiple proxies should be used and compared to determine which estimate is most likely to be correct and the range of possible values for body mass. While one can obtain a very precise (but not necessarily very accurate) estimate of mass from previously-published allometric regressions, even a very good mass proxy generally has notable (though often poorly reported) uncertainty, and an honest reconstruction of mass for a fossil mammal includes an assessment of this uncertainty.

The methodology is similar for almost all proxies commonly used. Data are collected on the proxy measurements and body mass from a training dataset of extant species, commonly from mammalogy collections, which often have live mass data for many of their museum specimens. There is disagreement about whether or not it is necessary to collect data from a sample of individuals for each species or not; the argument has been made (Legendre 1986; Hopkins 2008) that the goal is a species average, so individual variation isn't essential to the outcome. However, if the single individual measured is unusual, it can be misleading, especially if the training dataset is small. Even a small sample of 3–5 individuals can increase the robustness of estimates. Values for the sample are often averaged to generate a data point for the species. Many studies use individual masses from the specimens measured (e.g., Reynolds 2002; Hopkins 2008), but others simply use published average masses for the species (e.g., Gingerich et al. 1982; Janis 1990; Mendoza et al. 2006) or a mix of published and individual masses (e.g., Ruff 1990; Freudenthal and Martín-Suárez 2013). Published values are adequate when necessary, but the correspondence is likely to be less accurate; the individuals sampled may or may not be representative of the species average for dental measurements, and a mismatch could lead to an inaccurate placement in the allometric equation. The species data, both mass and proxy, are generally log transformed (either natural log or base 10), and then a linear regression is applied to establish the allometric relationship between the proxy and mass in log-linear space (Fig. 2.1). For some fossil taxon of interest, the proxy is then measured, and the regression equation can be used to infer mass.

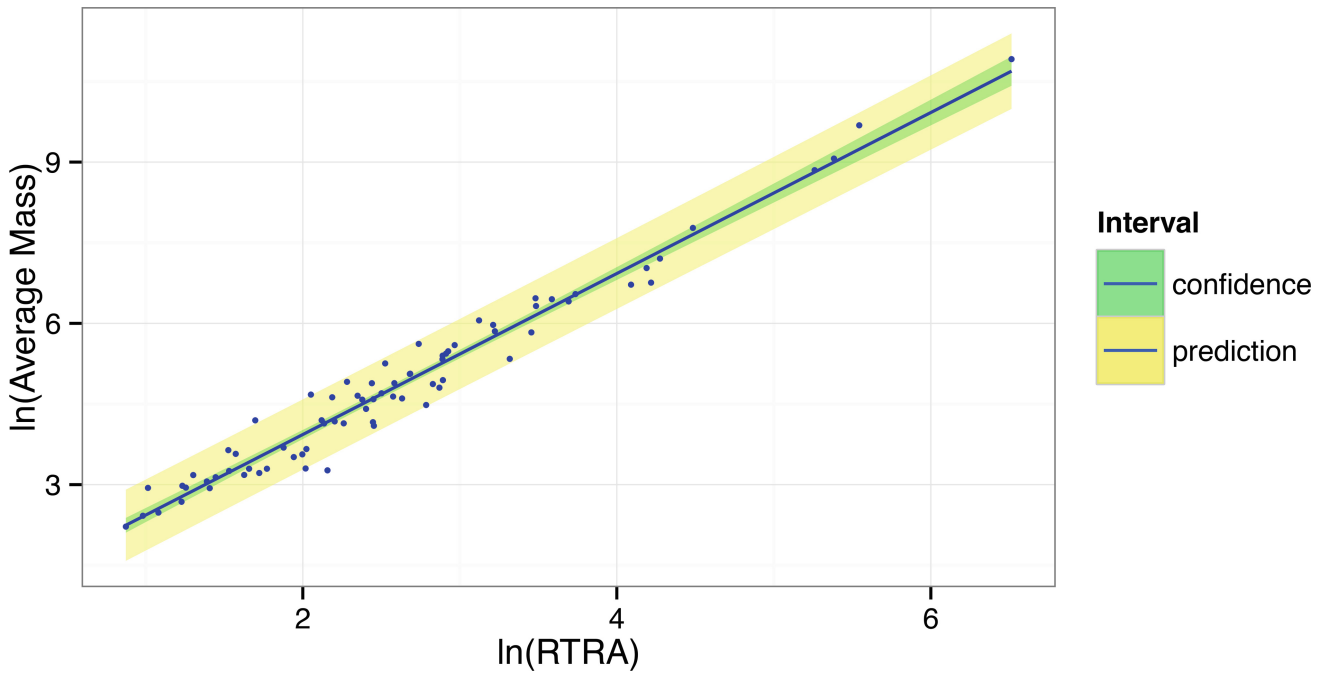

Fig. 2.1 Example regression in ln-ln space of a mass proxy (in this case RTRA, or lower cheek tooth row area) against body mass for a training dataset of 76 extant rodents. Data from Hopkins (2008). Points represent species average values. The green shading shows the 95% confidence interval for the regression line, while the yellow shading represents the 95% prediction interval

Examples of widely-used studies generating mass estimation equations are referenced in Table 2.1 with information about the taxonomic group and morphological proxy or proxies they use as well as the methods applied. The regression equations can be found in the papers, along with information about the training data used to generate them.

Dental Proxies

The most common proxy used to estimate the body mass of fossil mammals is the size of the first lower molar, m1 (Alroy 1998; Gingerich et al. 1982; Legendre 1986; Van Valkenburgh et al. 2004). This proxy is often measured in terms of area, approximated by multiplying the maximum mesio-distal length by maximum bucco-lingual width, assuming a roughly rectangular occlusal shape (Fig. 2.2). Other authors have found length alone to be adequate and, in fact, to be less sensitive to dietary differences when estimating mass of large mammals (e.g., Damuth 1990). Regressions using this proxy are available for a variety of mammalian groups (Legendre 1986) including ungulates (Janis 1990; Mendoza et al. 2006), marsupials (Gordon 2003), carnivorans (Van Valkenburgh 1990), and especially for primates (Gingerich et al. 1982; Conroy 1987; Dagosto and Terranova 1992; Vinyard and Hanna 2005; Copes and Schwartz 2010; Scott 2011). The m1 has the least variation in its fit to body mass of all the cheek teeth (Gingerich et al. 1982; Janis 1990; Gordon 2003) and therefore should be the most precise single tooth dental proxy for reconstructing body mass, though regressions are available for most of the other teeth in the dentition as well (see Table 2.1 for examples).

Because dental formula varies among mammals, another proxy uses the area of the entire postcanine tooth row for body mass reconstruction, taking advantage of the partitioning of function among the mammalian teeth (see also Evans and Pineda-Munoz 2018). As for a single tooth proxy, this value is most commonly estimated by multiplying the maximum anteroposterior length of the postcanine tooth row by the maximum width of the cheek teeth (Gould 1975; Hopkins 2008; Fig. 2.2). Note that this proxy would not be expected to work as well as single-tooth proxies in taxa with substantial curvature to the postcanine dental arcade, as occurs in some primates. Tooth row length can be used similarly (Hopkins 2008) but only in a clade for which the proportions and numbers of teeth are relatively constant. Both of these proxies are useful for taxa such as muroid or mylagaulid rodents with unusual first molars but require a fossil record that preserves undistorted tooth rows. Tooth row area and length can also be approximated from the sum of isolated cheek teeth (Freudenthal and Martín-Suárez 2013), although given mesio-distal overlap of some cheek teeth, this method will necessarily introduce some noise into the estimates of mass.

Table 2.1 Example body mass proxy studies. This is not intended to be a comprehensive list; rather, it is intended to show some of the diversity of available proxies, particularly those that are widely used or methodologically novel. Abbreviations in methods: MLR = multiple linear regression; OLS = ordinary least squares; PIC = phylogenetically independent contrasts; RMA = reduced major axis

Reference	Type of proxy	Proxy measurement(s)	Regression method	Taxonomic scope
Gingerich et al. (1982)	Dental	Area of each tooth of the tooth row; Cheek tooth row area	Ln transform, OLS	Primates
Anderson et al. (1985)	Postcranial	Total stylopodial circumference	Log_{10} transform, OLS	Ungulates
Legendre (1986)	Dental	m1 area	Ln transform, OLS	Mammals, Chiroptera, Eulipotyphla, Carnivora, Primates, Rodentia, Ungulates
Damuth (1990)	Dental, Whole body	Head-body length, Length, width, and area of individual teeth, molar row, and cheek tooth row	Log_{10} transform, OLS, MLR	Ungulates
Gingerich (1990)	Postcranial, Multivariate	Length and diameter of femur, humerus, tibia, metacarpal, and metatarsal; Ulna length	Log_{10} transform, OLS, MLR	Mammalia
Janis (1990)	Dental, Cranial	Lengths, widths, and areas of each individual postcanine tooth; Premolar row length; Molar row length; Muzzle width; Masseteric fossa length; Occipital height; Posterior skull length; Basicranial length; Anterior jaw length; Posterior jaw length; Depth of mandibular angle; Width of mandibular angle; Jaw length	Ln transform, OLS	Artiodactyla, Perissodactyla, Procaviidae (Hyracoidea), Macropodidae (Diprotodontia)
Martin (1990)	Dental	m1 area	Ln transform, OLS	Cricetinae
Ruff (1990)	Postcranial	Length and breadth of femur and tibia; Cross-sectional shape and area of femur and tibia; Proximal and distal articular surface areas of tibia and femur	Log_{10} transform, OLS	Anthropoidea (Primates)
Van Valkenburgh (1990)	Dental, Cranial, Whole body	Head-body length; Skull length; Occiput-to-orbit length; m1 area	Log_{10} transform, OLS	Carnivora, Dasyuridae (Dasyuromorphia)
Reynolds (2002)	Cranial, Postcranial	Condylobasal length; Skull length; Femur length	Log_{10} transform, OLS and RMA	Beavers and giant beaver analogs
Mendoza et al. (2006)	Cranial, Dental, Multivariate	Lower tooth row length; Premolar tooth row length; Lengths and widths of individual postcanine teeth; Anterior jaw length; Posterior jaw length; Depth of mandibular angle; Width of mandibular angle; Length of coronoid process; Length of masseteric ridge; Occipital height; Posterior length of skull;	Log transform, MLR, phylogenetic weighting	Artiodactyla, Perissodactyla, Procaviidae (Hyracoidea)

(continued)

Table 2.1 (continued)

Reference	Type of proxy	Proxy measurement(s)	Regression method	Taxonomic scope
		Depth of face under orbit; Length of paraoccipital process; Muzzle width; Palatal width; Basicranial width		
Hopkins (2008)	Dental	Tooth row area; Tooth row length	Ln transform, OLS	Rodentia, and several families therein
Millien and Bovy (2010)	Dental, Postcranial, Multivariate	Skull length; Upper cheek tooth row; Upper and lower incisor length and width; m1 length; m1 width; Humerus length; Femur length; Humerus diameter; Femur diameter	Log_{10} transform, OLS and MLR	Caviomorpha (Rodentia)
Campione and Evans (2012)	Postcranial	Total stylopodial circumference	Log_{10} transform, OLS, PIC	Mammalia, Ungulates, Carnivora, Marsupialia, Euarchonta, Glires
Freudenthal and Martín-Suárez (2013)	Dental	Tooth row area	Ln transform, OLS	Rodentia, and several families therein

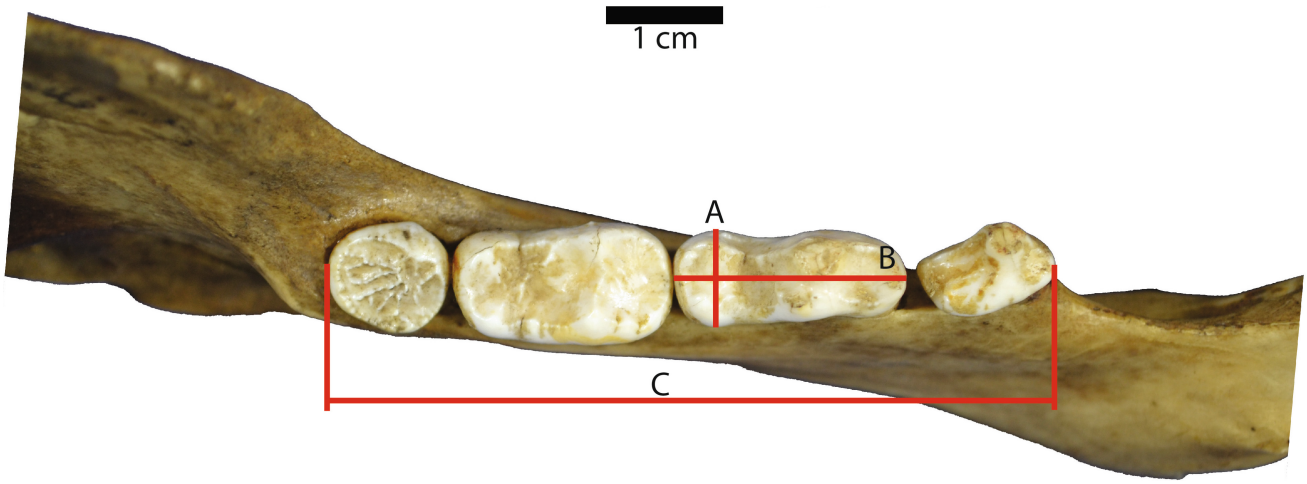

Fig. 2.2 Examples of three dental dimensions commonly used for mass regressions, illustrated on the lower tooth row of a black bear (*Ursus americanus*), University of California Museum of Vertebrate Zoology mammal specimen #8816. **A** = m1 width; **B** = m1 length; **C** = lower tooth row length

Limb Bone Proxies

Limb-based mass estimation of body mass uses a greater diversity of proxies than dental estimation. The most commonly-employed proxies use either lengths of long bones (Gingerich 1990; Reynolds 2002) or the midshaft cross-sectional dimensions of the humerus (Gingerich 1990; Millien and Bovy 2010), femur (Ruff 1990; Reynolds 2002), or both (Anderson 1985). Bone lengths are generally measured with calipers or measuring tapes (Gingerich 1990; Reynolds 2002); this proxy is useful because it is also commonly published in taxonomic descriptions and can be measured from figures in publications with reasonable accuracy. In contrast, cross-sectional dimensions (including area, perimeter, and diameter) usually require direct

measurement of museum specimens; these values are seldom published except in studies of body mass estimation, and only rarely are published images sufficiently accurate to allow measurement of even diameter. In some cases, these proxies are measured digitally from bone scans (Ruff 1990), but they are also commonly measured directly with a measuring tape (Campione and Evans 2012). Limb bone cross-section as a mass proxy depends on the physical relationship between the load-bearing capacity of a cylinder and its cross-sectional area (Campione and Evans 2012), and as long as the work adequately addresses postural differences among species in the training data (Sánchez-Villagra et al. 2003; Basu et al. 2016), these proxies can be among the most universally applicable (Campione and Evans 2012). Long bone lengths require a tight morphological, functional, and phylogenetic match to provide reliable mass estimates; good analogs for locomotor habits of fossil taxa must be used and, as pointed out by Biewener (1990) and Christiansen (2002), large mammals (above 50 kg) have relatively shorter limb bones for their mass than smaller species due to a shift in the primary constraint on limb shape from compressional stresses to bending strain. Because limb-based estimates have been used most often for larger mammals (in part because identifying postcrania of large mammals is often easier), many of which are above this threshold, this change is less problematic than it would be if the proxy were applied more widely. This limitation should be an important consideration in any study reconstructing a wide range of masses.

While limb shaft dimensions are the most widely used proxy for mass estimation, the ends of the limb bones can also be used. Articular surface dimensions, often as linear or approximate area measures, can offer an alternative approach (Ruff 1988, 1990, 2003). However, their reliability as a mass proxy is somewhat contingent on posture (Ruff 1990, 2002), and at least one study (Ruff 2003) found that cortical bone distribution (obtained from CT scans of limb bones) is a better predictor of body mass that external dimensions. In a case where higher precision is required, these more labor-intensive approaches can increase the robustness of the physical relationship on which the inference depends.

Volumetric Estimation

In taxa with no good living analogs, several authors (Bates et al. 2015; Brassey et al. 2015; Basu et al. 2016) have argued that the best method of body mass estimation is to make a complete skeletal reconstruction, overlay soft tissue on that reconstruction, and estimate body mass based on volume and estimated average density. Such an approach enables reconstruction of mass in some taxa for which other proxies fail but requires exceptionally complete fossil preservation and substantial modeling effort. Hence, it is not efficient or even possible for many applications. It has, however, allowed reconstruction of mass in animals such as dinosaurs (Bates et al. 2015; Brassey et al. 2015) and the extinct giraffe relative *Sivatherium* (Basu et al. 2016) for which simpler mass proxies are suspect.

Considerations

Available fossil record: A decision about mass estimation methods begins with the skeletal elements preserved and well-identified for the taxon of interest. If postcrania cannot be confidently identified to species, dental estimates must be preferred in spite of their decreased accuracy. If the study requires reconstructing mass of a large number of distantly-related species, it may be necessary either to use multiple proxies or to choose a proxy that does not necessarily reconstruct mass with the greatest accuracy or precision but that does allow all the species of interest to be included or minimizes the violations of regression assumptions for taxa in the analysis.

Physical constraints: Regression equations only apply where the training data are representative of the species for which mass is being estimated. For example, it is challenging to reconstruct mass for taxa well outside the size range of extant relatives such as the extinct giant rodents *Phoberomys* and *Josephoartigasia* (Hopkins 2008; Rinderknecht and Blanco 2008; Millien and Bovy 2010), as the physical constraints that shape the relationship may change between extant and extinct species (Millien and Bovy 2010; Basu et al. 2016). In these cases, it can be more accurate to use more distantly related but more physically similar species as training data.

Dentition: In using dental proxies for body mass, it is necessary to consider how the dentition compares with that of the taxa from which the regression equation was derived. Taxa with dramatically different diets tend to have somewhat different constraints on the shape and scaling of the cheek teeth (Gingerich et al. 1982; Legendre 1986; Janis 1990; Scott 2011; Evans and Pineda-Munoz 2018). Regressions based on training data including taxa with similar dietary ecology are most likely to reconstruct mass accurately. There are even a few ecologies explored by mammals (for example, colonial insect specialists) that release the constraint on dentition size because teeth are not used in food processing. In such a case, dental proxies are not useful or cannot even be used for mass reconstruction.

Locomotion: In using proxies based on limb bone dimensions, we make the assumption that the limbs are loaded in the same way as those in the training data. If the distribution of weight or the limb loading in locomotion is dramatically different in study species relative to training

data, mass reconstructions will be inaccurate. If the problem is simply distribution of weight (for example, a species that bears more weight on the forelimbs than its extant relatives), combining the limb cross-sectional areas can still yield accurate estimates of mass. However, if there is a difference in locomotor modes, such as a ricochetal (hopping) species whose extant relatives are all terrestrial, reconstructing mass from limbs is much more challenging; the magnitude of forces experienced during locomotion relates to mass quite differently, with the possible result that dental proxies are a better option. Even complex methods that reconstruct 3D body geometry may not be any more accurate in these cases, as reconstructing musculature and body shape requires reference to modern analogs (Carrano and Hutchinson 2002; Hutchinson and Garcia 2002; Basu et al. 2016). Limb posture also dictates which physical constraints are important for limiting limb dimensions, so mammals with unusual limb postures (for example, Mesozoic mammals) should be compared to species with analogous posture where possible.

Evolutionary relatedness: The shape of mammalian teeth, limb posture, locomotor habits, and even body density and muscle mass vary over evolutionary time and show substantial phylogenetic constraints, so it is important to consider evolutionary relatedness in choosing which of the available regression equations to use in reconstructing body mass. Studies of dental regressions, in particular, have demonstrated substantial and significant differences in regression coefficients between different taxa (Legendre 1986; Damuth and MacFadden 1990; Hopkins 2008). There are also some taxa for which these regressions are simply more variable and hence less precise in reconstructing mass. Limb bone dimensions offer a less phylogenetically-constrained proxy that has been argued to be consistent across wide swaths of terrestrial vertebrates (Campione and Evans 2012).

Statistical Methods: For those developing their own mass estimation regressions, a few statistical best practices are worth considering. Choice of regression methods, data transformation, and realistic examination of statistical errors are all very important for generating robust mass estimates for fossil mammals. Existing regressions differ widely in the degree to which these recommendations have been followed; it is worthwhile to consider what effects these methodological differences could have on the resulting mass estimates.

Regression methods: The most commonly used method for linear regression is Ordinary Least Squares (OLS) Regression. While some authors have argued (Ricker 1973, 1984; Reynolds 2002) that a different method, such as Major Axis or Reduced Major Axis Regression, is more appropriate given that they allow for equal levels of uncertainty in the x and y axes, this argument applies primarily to determining the strength and direction of allometric relationships and not to mass prediction. OLS regression assumes that the independent variable (in this case the proxy measurement) is known absolutely, while the dependent variable contains all the error in the system (Zar 2010); this is true for body mass estimation, because the measurement of the proxy is generally accurate to within a very small error, while the mass is generally much less certain, given the issues discussed previously.

Multiple regression methods have sometimes been applied in cases where multiple skeletal elements are available for a given taxon (Gingerich 1990; Mendoza et al. 2006; Millien and Bovy 2010). While it seems intuitive that adding information from multiple proxies would improve the accuracy of mass estimates, this is not always true (Kaufman and Smith 2002); unless the number of species sampled is large, there are problems in overfitting when the ratio of sampled species to predictors (that is proxy measurements) is less than 10 (Smith 2002; Kaufman and Smith 2002). Multiple regression is also not appropriate to selecting the best proxy from among a variety of candidate mass proxies, because the multicollinearity of the proxies makes such a process unreliable (Kaufman and Smith 2002). The practice of generating multiple bivariate regressions and averaging the resulting mass estimates (statistically an unjustifiable approach) does not consistently escape the problems of multiple regression and involves an additional assumption about the independence of measurements that rarely holds true (Smith 2002). In some cases, averaging proxies improves the answer where the errors of the different estimates average out (Scott 1990), but because this relies on the included proxies erring roughly equally in either direction of the true mass, it cannot be relied upon consistently. Instead, it is generally better to choose the most reliable univariate proxy based on the biology of the taxon of interest or to choose a small number of independent proxies for multivariate analysis (Kaufman and Smith 2002).

Data transformation: Size data in living systems often have a heteroscedastic distribution of variance because in larger organisms, the magnitude of variation in size is greater. Hence, the residuals from a regression line suggest that the variance is not evenly distributed, as assumed by the vast majority of linear regression methods. In the past, the solution has commonly been to log-transform the values both for the proxy measurements and the masses (see Table 2.1). This does solve the problem of heteroscedastic variance in many cases, although it is necessary to examine regression residuals to determine whether $\log_{10}$ or natural log adequately account for differences in variance (Zar 2010). In some cases, they do not perform equally well, although both methods have been applied to body mass proxy data. Unfortunately, log-transformation of the mass proxy data creates some analytical problems, a topic discussed below (see "Challenges"); there is currently no clear answer about whether log-transformation leads to values that would be more or less