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Review of *MAMMALIAN TEETH: ORIGIN, EVOLUTION, AND DIVERSITY* by Peter S. Ungar

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Ungar, Peter S. 2010. Mammalian Teeth: Origin, Evolution, and Diversity. The Johns Hopkins University Press-Baltimore, Maryland, 304 pp. ISBN-13: 978-0-8018-9668-2, price (hardbound), $95.00.

Peter Ungar has written a book on mammalian teeth, a topic close to the heart of mammalogy itself and most mammalogists. His distillation of the massive literature on teeth into a succinct whole will appeal to scientists and professionals across disciplines. With paleontological and extant dental research in one place I no longer have to search these areas separately to find what I want. Ungar's broad background includes physical anthropology, anatomy, and paleontology. Further, he has been one of the pioneers using dental microwear to analyze diets in primates and geographic information systems (GISs) on a microscale to study cusps and valleys of teeth instead of mountains and valleys of landscapes.

Illustrations are abundant, in the same orientations, and with the same simple but effective drawings. Visually, dental material often is presented in a variety and mixture of media: photos, drawings, partial teeth, partial toothrows, right and left sides, and so on. Here, entire toothrows can be compared easily in occlusal and lateral views because cusps are outlined clearly against a gray background of the outlined shapes of teeth. Cusp names and comparisons make for difficult reading for everyone, and spatial consistency here is not just appreciated, it is essential. Now in a single volume we have a reference with representative illustrations for teeth of every mammalian family. The breadth of Ungar's overview of mammalian teeth is described in the *Introduction*, where he reminds us (p. 4) that "Teeth and food are in a perpetual death match." The rest of the book tells us why and how. In Chapters 1 through 4 the author describes many aspects of teeth with the clarity of a sole writer, and this portion of the book should be required reading for all mammalogists. Topics covered here are gross morphology, histology, microstriae, chemical makeup and isotopes, development, diet and nature of foods, mechanics and processing, and others. These chapters are followed with a comprehensive summary in Chapter 5 of extant mammal phylogeny, which includes the latest thinking of how biogeography has affected classification of mammals. It is good material for a lecture on the topic. Chapters 6 through 9 describe evolution of teeth and mastication by drawing upon recent discoveries from ancestors of modern mammals. Here is a complex integration of material that draws upon an extensive knowledge of paleontology, comparative anatomy, and the development of mastication. Chapters 10 through 13 review the diversity of teeth representing families of mammals in Monotremata and Marsupialia (Chapter 10), Xenarthra and Afrotheria (Chapter 11), Laurasiatheria (Chapter 12), and Euachontoglires (Chapter 13). These are followed by a succinct summary chapter. The book's 14 chapters are short and dense and would fit easily into a semester schedule for upper-level undergraduate or graduate students.

Ungar has completed the gargantuan task of illustrating 2 views of toothrows of representatives of each mammal family. The author states that we may not see teeth of our favorite taxon configured, and that he had to leave something out. This is understandable, but using the highly modified sanguinivore, *Desmodus* (figure 12.10A), to represent Phyllostomidae (about 160 species) obscures that family's amazing diversity of insectivores, carnivores, nectarivores, and frugivores. Some of these are described in the text, but I might have expected *Artibeus* to be included as a figure, because it is a speciose and abundant genus. The widely arced, frugivorous teeth of *Artibeus* and other stenodermines are unlike those of either other frugivorous bats, Pteropidae, or other mammals such as phalangers, tupaiids, primates, or kinkajous. One stenodermine, *Sphaeronycteris*, has a skull that is strangely human in miniature, complete with chin.

Although largely accurate, this work has several things I would correct in a second edition. In defining the cervix or "neck" of a molar tooth on p. 9 the author states that this is the junction between enamel and dentine, or EDJ. Yes, the cervix does mark the boundary of what might show externally of the EDJ as a circumference of the tooth, but the EDJ is an interface that covers the entire above-gum tooth under the enamel in figure 1.1 and is an area of intense interest in odontology. In contrasting the long upper canines of cats with the small incisiform canines of moles and herbivores on p. 10, Ungar is thinking only of American moles, *Scalopus* and *Scapanus.* Family Talpidae originates from the genus *Talpa* in the Old World that has large upper canines as respectable as any small carnivore and are unlike the large chisel incisors of *Scalopus*, *Scapanus*, or even *Desmana,* which is illustrated (figure 12.18D). Tuatara is a reptile, not an amphibian as indicated in figure 6.7B on p. 80. In the 4th line of the last paragraph on p. 132 trigon rather than talon is surrounded by paracone, metacone, and protocone, and trigonids do not appear narrower than talonids as noted in text in that same paragraph for *Dromiciops* in figure 10.3C. The tooth formula of 4 lower premolars for Macroscelidea on p. 148 does not match those lower teeth in figure 11.2C of *Macroscelides* on the previous page. The same is true for 4 upper premolars in Hyracoidea in the text on p. 148 and those upper teeth of *Procavia* in figure 11.3A. Macrochiroptera appears instead of Megachiroptera in the 1st column on p. 166. One of the handiest dental features for distinguishing Old World from New World monkeys is that the root of the 1st lower premolar behind the canine in cercopithecids dips below the gumline. This is not apparent in figure 13.5A on p. 197. The occlusal view of a soricid lower toothrow in figure 12.18C, p. 184, looks upside down and lingual. Buccal views of the murid upper toothrow (figure 13.11C) and echimyid upper toothrow (figure 13.15D) have much of the occlusal pattern showing. These 2 toothrows could be worn obliquely, but a note to that effect would help. Additionally, there are several terms often repeated that I had not encountered or had forgotten. All but 2 of these are defined in the text but not in the index or a glossary. This means searching for where they are 1st mentioned, often within a group of terms. They are: eurytopic—having a broad range of tolerance in variation of environmental factors; hypoflexid—valley between trigonid and talonid that faces buccally; mure—Latin for wall and the base word for murid; opisthodont—rodent incisors that project inward or posteriorly; orthal—simple up and down movement of teeth and may have some shearing; orthodont—rodent incisors that are vertical; palinal—lower teeth move backward; proal—anteriorly directed power strokes of the toothrows; proodont—rodent incisors that project forward (same as procumbent, slanting forward); propalinal—anterior–posterior or front to back movement of upper and lower toothrows; stenotopic—having a narrow range of tolerance in variation of environmental factors; taurodont—roots separate further down toward their apices rather than at the cervix; and teuthophage—a squid specialist.

For the most part vocabularies between physical anthropologists and primatologists on one hand and vertebrate biologists and mammalogists on the other overlap to a large degree. However, there are at least 2 places that are troublesome, where meaning differs subtly but surely. One involves diet and the other anatomical axis. Perhaps the 1st use of the term "faunivory" was by Chivers and Hladik (1980). It was used in a way that many vertebrate biologists use the word "carnivory" to imply consumers of both endo- and exoskeletal prey or vertebrates and invertebrates, respectively (Pough et al. 2009). Mammalogists who study groups or diets in which there are both kinds of prey have been known to use the term animalivory (Castro-Luna et al. 2007; Fleming and Racey 2010; Freeman 1984; Giannini and Kalko 2004; Stevens and Willig 2001; J. S. Findley, University of New Mexico, pers. comm.). This is particularly appropriate in bats because Theodore Gill (1872) distinguished the microchiropterans, Animalivora, from the megachiropterans, Frugivora. Included in Animalivora were bats that eat insects, bats that eat vertebrates, and bats that eat both foods. Admittedly, the syllables get a bit difficult for the term animalivore (an nee MAL ee vore) that does not retain the pronunciation of "animal" in the word (perhaps an extra syllable for smoother pronunciation to animaliavore is needed—an nee mal LEE ah vore). As descriptive and, I think, clear as it is, some may not like this term. I do not know the thinking of Chivers and Hladik (1980), but to many vertebrate biologists "faunivory" implies the eating of the fauna, or the entire assemblage of animals that are in a particular community. Because flora and fauna often are used together, should we be saying floravore instead of herbivore to continue the analogy? Probably the safe path would be to stick with carnivory to mean the broad diet of exoskeletal insects and endoskeletal vertebrates. Differentiating the 2 diets could be insectivory and carnivory (sensu stricto).

The other usage that is problematic is more difficult to disentangle and involves anatomical direction. Students of mammals with wide dental arcades (such as primatologists) often use the terms mesial and distal. Mesial means toward the anterior midline of the arcade, and distal means away from the middle and toward the molars. But most mammals have narrow dental arcades with a strong anterior–posterior axis such that middle incisors are the most anterior part of the toothrow. This axis is even stronger for lower teeth. The result is that reading current human or primate dental literature can be difficult because mesial and distal, not anterior and posterior, are commonly used. This confusion occurs in mammals with either wide dental arcades or where the anterior incisors offer a uniform battle front between the 2 canines, as in many bats. Describing corners of these individual dental shapes across the skull's front margin can be confusing, and both anterior–posterior and mesial–distal in combination are necessary (Freeman 1992). Cleverly, Ungar resolves this issue rather simply. For incisors and canines he uses mesial and distal, and for cheek teeth he uses anterior and posterior. I can live with this, and in combination one can describe crannies, cusps, and bulges in every direction.

Who used mesial–distal first? I have not finished that search, but I found interesting leads. Contrary to cusp usage by mammalian paleontologists, mammalogists, and dental morphologists everywhere, Vandebroek (1961) turned dental nomenclature established by the Cope-Osborn theory of mammalian cusp development on its head. Hershkovitz (1971) took the baton and clarified much of what Vandebroek was trying to accomplish, which was to clear up comparative homology of cusps. About Cope-Osborn he states, "Another dire consequence has been the corruption of dental evolutionary thought through use of similar terms for nonhomologous upper and lower dental elements, and dissimilar terms for the homologous element" (Hershkovitz 1971:95). At the time (1970s) changing nomenclature was an unacceptable idea to most neo- and paleo-mammalian scientists working with teeth and who were even said to be hostile to the notion. I will not say here which might be better, and I agree with Ungar that Cope-Osborn cusp names are well established, and changing now would be quite troublesome (but see Van Valen 1994). However, there is irony worth mentioning. A small example of the renaming of cusps by Vandebroek and Hershkovitz can be visualized with a simple triconodont tooth with 3 cusps in an antero-posterior row. The large middle cusp is the eocone, but the 2 little cusps on either side are telling—these are mesostyle (id) and distostyle (id), reflecting the mesial–distal terminology. Perhaps it was the much maligned Vandebroek who started the now common mesial–distal descriptors with teeth.

Hershkovitz's life work was his tome *Living New World Monkeys* (1977), which is an amazing resource for all things dental in spite of some difference in calling paracone or protocone the eocone. In comparing callithricid (now callithricine) species he also contrasted and figured similar features in all other relevant mammals. The title is somewhat misleading because Hershkovitz's 1,132-page book is more an encyclopedia of mammalian dental terminology with well-illustrated examples, comparisons, and extensive index. Although 20 percent of Ungar's book is pages of references, I am sorry the Hershkovitz reference is not among them.

I like Ungar's book and his whole-organism approach. I particularly like thinking about the interface between teeth and food, how teeth fit together and wear away with different diets, and the nature of animalivorous prey. This book deserves to be on your shelf.—PATRICIA W. FREEMAN, *School of Natural Resources, University of Nebraska State Museum, 428 Hardin Hall, University of Nebraska–Lincoln, Lincoln, NE 68583-0974, USA; e-mail: pfreeman1@unl.edu.*

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