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Why do Xenarthrans matter?

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Xenarthrans possess a suite of characteristics that make them among the most unusual of mammals. Understanding the functional significance of these traits is one prominent reason why xenarthrans matter. In addition, Xenarthra is currently considered one of the basal clades of placental mammals, and the only one to originate in South America. Consequently, studies of xenarthrans can provide important insights into the evolution of early placentals. The fossil record contains hundreds of recognized species of xenarthrans but this rich evolutionary history is currently distilled into just 31 extant species. Preserving this heritage through various conservation initiatives is yet another reason why xenarthrans matter. This Special Feature on xenarthrans provides an overview of current work and identifies many areas requiring further study. It is our hope that this Special Feature will raise the profile of xenarthrans among mammalogists and perhaps entice some to consider addressing one or more of the many lingering questions that remain about this enigmatic group.

¿Por qué importan los xenartros? Los xenartros poseen una serie de características que los convierten en algunos de los mamíferos más inusuales. La comprensión del significado funcional de estos rasgos es una de las razones sobresalientes de por qué los xenartros importan. Adicionalmente, los xenartros son actualmente considerados uno de los clados basales de los mamíferos placentarios, y el único que tuvo su origen en América del Sur. Como consecuencia, el estudio de los xenartros puede brindar información importante sobre la evolución de los primeros placentarios. El registro fósil incluye cientos de especies reconocidas de xenartros, pero esta rica historia evolutiva está actualmente concentrada en tan sólo 31 especies existentes. Salvar esta herencia a través de varias iniciativas de conservación es otra razón de por qué los xenartros importan. Esta sección especial sobre xenartros brinda una visión general del trabajo actual e identifica muchas áreas que requieren de estudios adicionales. Esperamos que esta sección especial incremente el perfil de los xenartros entre los mastozoólogos y tal vez atraiga a algunos de ellos para que consideren abordar una o más de las muchas preguntas pendientes sobre este grupo enigmático.

Key words: anteaters, armadillos, ecology, evolution, morphology, research, sloths, Xenarthra

A legitimate case can be made that the title of this article is a bit of a straw man because it is difficult to envision a scenario where any biologist would willingly defend the position that any species does not matter. In broad terms, xenarthrans matter just as much as does every other member of the planet's biota because they represent, among other things, a unique encapsulation of evolutionary history and ecological role. Instead, we posed this question for more practical reasons. Specifically, this article is designed to introduce readers to the contributions that comprise this Special Feature on xenarthrans. As scientists we are all aware that there is a finite amount of time anyone can devote to reading the scientific literature, and the number of papers being published seems currently to be increasing at an exponential pace. Thus, priorities have to be set and decisions made about what is most important and what can wait. So, for mammalogists who study other taxa, why read the papers in this Special Feature? What makes xenarthrans worthy of such treatment? It is our goal to provide convincing answers to these questions here.

Xenarthra

The name Xenarthra stems from the unique articulations of the vertebrae exhibited by all members of the group (Engelmann 1985). Xenarthra is currently considered a superorder (Gardner 2008) that contains 2 monophyletic orders: Cingulata, which consists of modern and fossil armadillos and extinct armored pampatheres and glyptodonts, and Pilosa (Table 1). Pilosa in turn contains 2 clades: Vermilingua, which consists of all living and extinct anteaters, and Folivora (sometimes also referred to as Tardigrada or Phyllophaga—Fariña and Vizcaíno 2003; Shockey 2009), whose living representatives include the 2-toed and 3-toed sloths, as well as a multitude of fossil forms, including the well-known giant ground sloths (Table 1). At one time Xenarthra was embedded within the group Edentata, which also included pangolins and aardvarks (Cuvier 1798), but this arrangement was abandoned in the 1980s as evidence accumulated that similarities among the members of Edentata were due to convergence rather than shared ancestry (reviews in Delsuc and Douzery 2008; Gaudin and McDonald 2008).

Molecular data suggest Xenarthra arose approximately 100 million years ago (mya—Delsuc et al. 2004), although the earliest xenarthrans known from the fossil record date to only about 40–50 mya (Gaudin and Croft 2015). All available evidence indicates Xenarthra represents one of the basal clades of placental mammals (Springer et al. 2005; Murphy et al. 2007; O'Leary et al. 2013), and the only one to originate in South America. Xenarthrans were among the most abundant, as well as some of the largest, mammals found in South America during much of the Tertiary (Vizcaíno et al. 2012) and were also quite diverse. Indeed, McKenna and Bell (1997) list over 200 genera of fossil xenarthrans that have been identified. Nonetheless, for reasons that remain obscure, most of these taxa went extinct by the Pleistocene so that modern xenarthrans consist of just 31 species: 21 species of armadillos, 6 species of sloths, and 4 species of anteaters (Table 1).

Table 1.—Taxonomic overview of Xenarthra. Number of species in each extant genus is given parenthetically. Data for cingulates and sloths from Gaudin and McDonald (2008), and for anteaters, from McDonald et al. (2008).

Order, suborder	Family	Extant genera	Common name
Cingulata	Dasypodidae[a]		Armadillos
		Cabassous (4)	Naked-tailed armadillos
		Calyptophractus (1)	Fairy armadillo
		Chaetophractus (3)	Hairy armadillos
		Chlamyphorus (1)	Fairy armadillo
		Dasypus (7)	Long-nosed armadillos
		Euphractus (1)	Yellow armadillo
		Priodontes (1)	Giant armadillo
		Tolypeutes (2)	Three-banded armadillos
		Zaedyus (1)	Pichi
	Pampatheriidae[b]		Pampatheres
	Glyptodontidae[b]		Glyptodonts
Pilosa			
Folivora	Bradypodidae[a]	*Bradypus* (4)	Three-toed sloths
	Megalonychidae[a]	*Choloepus* (2)	Two-toed sloths
	Megatheriidae[b]		Giant ground sloths
	Mylodontidae[b]		
	Nothrotheriidae[b]		
Vermilingua	Cyclopedidae[a]	*Cyclopes* (1)	Silky anteater
	Myrmecophagidae[a]	*Myrmecophaga* (1)	Giant anteater
		Tamandua (2)	Tamandua
	Adiastaltidae[b]		
	Anathitidae[b]		

[a] Mostly extant genera, but families also include some extinct forms.
[b] Extinct.

Overview of This Special Feature

If everyone heeded the advice to focus one's scientific efforts on those species or events that are unique, unusual, or extreme in some way (Bartholomew 1982; Wilson 2013), then the study of xenarthrans would be overrun with devotees. Armadillos, sloths, and anteaters all possess a host of characteristics that have few parallels in other mammals. Unfortunately, the reality is somewhat different. Presumably, most mammalogists have at least a rudimentary knowledge of xenarthrans. However, only relatively few of them could be considered experts. Thus, it appears that, among mammals, xenarthrans have been a relatively understudied and underappreciated group, particularly when compared to other equivalent taxonomic groups such as primates, bats, rodents, and ungulates.

The 1st paper in this Special Feature provides further documentation of the point that research on xenarthrans has not been as extensive as that on other types of mammals (Loughry et al. 2015). They review scientific papers about armadillos published in the last 25 years (1989–2014). The total number of publications they found (n = 1,039) may seem impressive, but pales in comparison to the number of papers devoted to other groups of mammals. For example, using the search term Chiroptera in Google Scholar (accessed 1 August 2014) and limiting hits to only articles where this term was in the title of the publication, we were still able to find 806 papers about bats that had been published in just the last 5 years (2010–2014). Not only that, but as Loughry et al. (2015) show, many publications they found happened to mention armadillos as part of the article, but the animals were not really the main focus of the paper. Thus, the number of publications that were specifically about armadillos was substantially lower (n = 509). Compounding the problem was the fact that many papers were cited very infrequently, if at all. Although no similar sort of detailed analysis has been conducted for sloths or anteaters, a review of the literature on those taxa would probably return many of the same findings. Consequently, it seems reasonable to conclude that xenarthrans have not been tremendously popular study subjects, a fact perhaps underscored by the absence of any papers about anteaters in this Special Feature.

Scientific neglect may be the current fate of most living xenarthrans, but the situation is very different when considering fossil forms. The rich fossil record of xenarthrans (albeit less so for vermilinguans) has led to a long and productive history of study, beginning in the late 1700s (e.g., Cuvier 1798; Owen 1842), and continuing today (e.g., Bergqvist et al. 2004; Vizcaíno et al. 2012; Ciancio et al. 2013). Studies of fossil xenarthrans have been important for a number of reasons, but perhaps most prominent among these are efforts to reconstruct the early evolution of placental mammals. The basal position of Xenarthra means that studies of the ecology, behavior, and phylogeny of fossil xenarthrans will be invaluable in furthering our understanding of the evolution of early placentals.

Recent analyses have allowed reconstruction of the common ancestor of placental mammals (O'Leary et al. 2013), but what were the earliest in the xenarthran branch like? Delineating the key characteristics of early xenarthrans is an important step toward understanding evolutionary relationships within Xenarthra, as well as with other mammals. In this Special Feature, Gaudin and Croft (2015) attempt to identify such characters using data from living and extinct taxa analyzed within a phylogenetic framework. Their results indicate early xenarthrans were myrmecophagous, but with later shifts to omnivory and herbivory in some groups. They were also able to predict certain locomotory habits (e.g., digging and climbing) and habitat preferences. As with any analysis utilizing data from extinct taxa, further progress in understanding the early evolution of Xenarthra will be heavily dependent on the discovery of new fossils. Nonetheless, the information provided by Gaudin and Croft (2015) provides an excellent foundation on which future studies can build.

The study by Gaudin and Croft (2015) exemplifies a long-standing tradition of morphological analyses of xenarthrans. Indeed, the unusual anatomy and physiology of xenarthrans has spurred scientific investigations for several centuries (e.g., Owen 1842; Fernandez 1909; Goffart 1971), and functional morphological analyses continue to be one of the more prominent and productive areas in the study of these animals (review in Vizcaíno et al. 2008). Two papers in this Special Feature add further to this tradition. Just as Gaudin and Croft (2015) used morphological data to reconstruct the features of early xenarthrans, Green and Kalthoff (2015) show how detailed analyses of dental microstructure and microwear patterns can allow prediction of the diets of living and extinct xenarthrans. Interestingly, in at least some cases (e.g., some of the extinct sloths), microwear patterns may be more reflective of the habitats in which the animals lived as opposed to what they ate. Data from more taxa, both living and extinct, are necessary to fully realize the potential information available in xenarthran teeth and subsequently incorporate this into various phylogenetic reconstructions.

So far we have described the use of morphological data to predict various aspects of the ecology and behavior of living and extinct species. Additionally, morphological characters can be used to develop hypotheses about the evolutionary relationships among taxa (reviews in Gaudin and McDonald 2008; Pujos et al. 2012). This is the approach taken by Billet et al. (2015). They examine the bony labyrinth of the inner ear and define 17 characters which they then use to build a phylogeny of extant xenarthrans, plus 1 extinct form (the giant ground sloth *Megatherium*). Their results reinforce many of the traditionally recognized nodes within the xenarthran cladogram, as identified in previous morphological and molecular studies (e.g., Möller-Krull et al. 2007; Gaudin and McDonald 2008; Delsuc et al. 2012), but also provide insight into some more problematic relationships, notably among the armadillos.

Further analysis of the evolutionary relationships among armadillos is provided by Abba et al. (2015). They utilize both morphological (various cranial characters) and molecular data to resolve relationships among hairy armadillos in the subfamily Euphractinae. One of their most interesting findings is that the Andean hairy armadillo, *Chaetophractus nationi*, is in fact not a distinct species but rather a high-altitude variant of *C. vellerosus*. This result has important ramifications for the systematics of armadillos but also raises practical concerns regarding conservation because *C. nationi* is currently listed as Vulnerable (VU) in the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species, whereas *C. vellerosus* is considered as Least Concern (LC—IUCN 2014). Abba et al. (2015) argue that protective efforts are still warranted, particularly in countries such as Bolivia where populations have declined severely (Pérez-Zubieta et al. 2009), in order to preserve this unique subset of animals.

Conservation is a major issue for most xenarthrans, partly because the group consists of just 31 (or perhaps now 30) living species. Thus, the entire evolutionary history of one major group of placental mammals is currently contained in just a small handful of extant representatives. Additionally, many of these taxa face an uncertain future because of various negative impacts from human activities (Aguiar and Fonseca 2008; Abba and Superina 2010; Superina et al. 2010a, 2010b). Moraes-Barros and Arteaga (2015) review how molecular genetic data can be used to identify populations that may require conservation efforts. More broadly, they echo a common theme of this Special Feature by showing how population genetic analyses of xenarthrans can be related to past biogeographical events in order to reconstruct the evolutionary history of certain groups. A goal for the future is to expand such studies by sampling additional populations in more areas in order to more fully describe patterns of genetic diversity among xenarthrans and thus provide insight into both evolutionary and conservation-oriented questions.

Conservation issues are at the heart of the final paper in this Special Feature, in which Voirin (2015) provides an update of the critically endangered pygmy sloth, *Bradypus pygmaeus*. This species, first recognized just 14 years ago (Anderson and Handley 2001), is only known from the mangrove forests along the coastline of a single island, Escudo de Veraguas, which is part of the Bocas del Toro archipelago of Panama. Obviously, any species with such a limited range is likely to be at high risk of extinction. Voirin (2015) discusses how human activities may be exacerbating this risk but does provide some cause for optimism because the population of sloths may be larger than currently appreciated. Specifically, data from telemetry tracking of animals suggest that sloths may occupy forests in the interior of the island that have not been as extensively surveyed as the more accessible mangroves along the coast. In order to preserve this species, what ultimately may be needed is a habitat modeling exercise to determine areas where pygmy sloths can survive beyond Escudo, similar to what has been done for other species of sloths (Oliveira Moreira et al. 2014), and other xenarthrans (Anacleto et al. 2006; Abba et al. 2011; Feng and Papeş 2014).

To conclude, each of the papers in this Special Feature provides a partial answer to the question of why do xenarthrans matter? Collectively, we believe they make a compelling case that the study of xenarthrans can be very rewarding. We hope the brief summary of each paper that we have provided here will entice readers to examine these contributions in more detail and thereby discover the many exciting things this talented group of researchers has to report.

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