Rediscovery of an "extinct" Galápagos tortoise

James F. Parham*

Biodiversity Synthesis Center, The Field Museum, 1400 South Lake Shore Drive, Chicago, IL 60605; and Department of Herpetology, California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118

Over the past three centuries, humans have demonstrated increasing scientific curiosity about biodiversity. During this time, we developed a classification scheme that accelerated the description and codification of species (1), profound new theories to explain diversity (2), explicit frameworks of taxonomic study (3), and DNA-based methods for characterizing lineages (4). Despite these academic advancements, the progress of biological discovery has struggled to keep pace with an increasingly modified natural environment, because the past 300 years have also witnessed the exponential growth of human population (from 6×10^8 to 6×10^9) and concomitant anthropogenic impacts on biodiversity. Human-mediated extinctions, translocations, and genetic pollution obscure and erode natural patterns of distribution and variation (which is especially true for economically and calorically valuable species, like turtles). A study by Poulakakis *et al.* (5) in this issue of PNAS wrestles with all three of these complicating factors and provides an excellent example of the resources and methodologies required to tease apart patterns resulting from natural and artificial processes. In doing so, this study reaches an astonishing conclusion: A species that we thought was eaten to extinction still survives. . . in part.

The species in question is a Galápagos giant tortoise, one of 15 species (13 formally described) from the famous archipelago (5). The Galápagos Islands are well known for bearing the fauna that helped inspire Darwin to develop his landmark theory of natural selection (2). The giant tortoises should be given partial credit for this inspiration, because the diagnostic phenotypes on each island provided Darwin with a clear example of regional variation and adaptation (6). But even as Darwin observed these tortoise populations, they were declining precipitously. Humans had already altered the tortoises' habitat by introducing numerous feral mammals, but primarily reduced their numbers through direct harvest for consumption [even Darwin ate tortoises (6)]. Darwin and the tortoises exemplify the aforementioned challenge of biologists to uncover and record biological patterns while humans simultaneously obscure them. In fact, Darwin arrived at one of the islands, Floreana (also known as Santa María or Charles), in 1835, within years of the putative extinction of its endemic form (7). Both Darwin and the captain of the HMS Beagle remarked on the depredated carcasses and scarcity of the Floreana tortoise, seeing no live tortoises themselves (6, 7). In the case of Floreana, the ultimate result of human activities, extirpation, preceded scientific observation and collection. Consequently, much of what we know about the Floreana species is based on subfossil skeletal remains from caves (8, 9) (Fig. 1*A*). Because extinction is a permanent phenomenon, the Floreana tortoise seemed destined to remain another sad footnote in biodiversity registers, lost like the dodo.

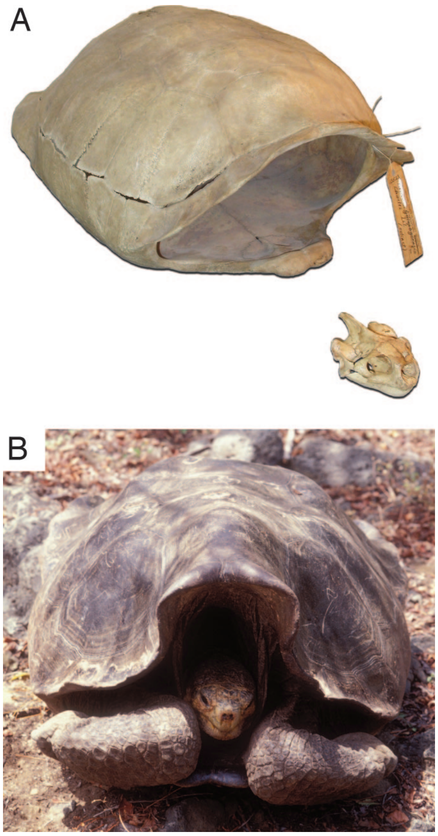

Fig. 1. Galápagos tortoises. (*A*) A subfossil specimen of the species from Floreana Island (Field Museum of Natural History no. 13525). Until the study by Poulakakis *et al.* (5), the Floreana species was only known from museum specimens such as this one. (*B*) A living descendant of the "extinct" Floreana species from Isabela Island (photo by C. Ciofi).

The report by Poulakakis *et al.* (5) provides new data showing that descendants of Floreana tortoises actually still exist (albeit not on Floreana) (Fig. 1*B*). That it is still possible to find such an important result within a well studied group of species is at first surprising. But, in fact, it is the detailed genetic studies of Galápagos tortoises by the Yale University-led team (10–12) that provided the necessary background to achieve this insight. Poulakakis *et al.* augment and use their genetic database to address lineage diversity from a population genetics perspective, applying appropriate markers and methods to elucidate the ancestry of extant individuals. But their work is more than a well executed genetic survey of a celebrated clade. One of the salient aspects of their study is the incorporation of data from long-dead Floreana tortoises into their genetic database. By using historic DNA techniques, Poulakakis *et al.* are able to sequence museum specimens from Floreana. Without the incorporation of these specimens, the true ancestry of the Floreana descendants would still be a mystery. Indeed, their study is another shining example of the irreplaceable role of museum specimens for biodiversity science. No matter how fast and powerful genomics becomes, we always need museums to inform, identify, and compare our findings (13). Older, historic collections are especially valuable, irreplaceable even, because they archive biological data from a time when life on Earth was more abundant and diverse.

The discovery of Foreana tortoise descendants is unexpected, but the circumstances that led to the preservation of this lineage are nothing short of ironic. It was, after all, the massive harvest of Floreana tortoises that ultimately led to the persistence of this lineage. Whereas turtle populations may be vulnerable to decimation, individual animals are durable and capable of surviving great physical hardship (such as desiccation and starvation in the hull of a ship). This preservation potential, combined with a wide appreciation for the taste of tortoise flesh, made Galápagos animals a highly sought after source of protein for

---

Author contributions: J.F.P. wrote the paper.

The author declares no conflict of interest.

See companion article on page 15464.

*E-mail: jparham@fieldmuseum.org.

19th-century whalers, pirates, and other seafarers (7, 14, 15). Historical accounts of hundreds of animals being harvested for a single ship are known (15), as are reports of these tortoises being thrown overboard to lighten loads (16) or otherwise being moved among islands (7). It was this haphazard harvest and translocation that has inadvertently preserved Floreana DNA into modern times. While the endemic population of Floreana tortoises was eaten into oblivion, Poulakakis *et al.* (5) found their genetic signature preserved on a different island. The most likely explanation is that Floreana tortoises were, for some reason, moved there >150 years ago.

The new home of these translocated individuals, Isabela, is the largest Galápagos island and home to five endemic species of giant tortoise (each associated with a volcano). Herein lies one of the more interesting aspects of Poulakakis *et al.*'s results. The Floreana castaways did not maintain reproductive isolation so their living descendants result from the interbreeding with native Isabelan tortoises. Thus, the heartwarming rediscovery of this "extinct" Galápagos tortoise is tempered somewhat by the realization that the lineage is genetically compromised. The conservation and genetic rehabilitation of the Floreana tortoise should prove challenging, but is certainly worthwhile.

Descendants of Floreana tortoises actually still exist (albeit not on Floreana).

The story of the Floreana tortoise is a great example of how complex it can be to establish natural patterns while they are being simultaneously distorted by human actions. The study by Poulakakis *et al.* (5) contends with a range of deleterious impacts (extirpation, translocation, genetic pollution) and demonstrates many of the tools and methods biologists use to see through them to the underlying patterns (long-term study, cutting-edge genetic techniques, biodiversity collections). Some biological patterns may be too modified to recover, but we have the best chance of knowing what was (and was not) lost when we combine modern genetic techniques with traditional museum-based approaches.

ACKNOWLEDGMENTS. My work on how humans impact turtle diversity is supported by the John D. and Catherine T. MacArthur Foundation, the Alfred P. Sloan Foundation, and the Turtle Conservation Fund.

1. Linnaeus C (1758) *Systema Naturae, per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Edito Decima, Reformata.* (Lauentii Salvii, Stockholm), 10th Ed.
2. Darwin C (1859) *On the Origin of Species by Means of Natural Selection* (John Murray, London).
3. Hennig W (1966) *Phylogenetic Systematics* (University of Illinois Press, Urbana).
4. Hillis DM, Moritz C, Mable BK, eds (1996) *Molecular Systematics* (Sinauer, Sunderland, MA), 2nd Ed.
5. Poulakakis N, *et al.* (2008) Historical DNA analysis reveals living descendants of an extinct species of Galápagos tortoise. *Proc Natl Acad Sci USA* 105:15464–15469.
6. Darwin C (1839) *Journal of Researches into the Geology and Natural History of Various Countries Visited by the H.M.S. Beagle, Under the Command of Captain Fitz Roy, R.N., from 1832 to* 1836 (Henry Colburn, London).
7. Pritchard PCH (1996) The Galápagos tortoises, nomenclatural and survival status. *Chel Res Mon* 1:1–85.
8. Broom R (1929) On the extinct Galápagos tortoise that inhabited Charles Island. *Zoologica* 9:313–320.
9. Steadman DW (1986) Holocene vertebrate fossils from Isla Floreana, Galápagos. *Smith Contrib Zool* 413:1–103.
10. Ciofi C, *et al.* (2006) Phylogeographic history and gene flow among giant Galápagos tortoises on southern Isabela Island. *Genetics* 172:1727–1744.
11. Russello MA, *et al.* (2005) A cryptic taxon of Galápagos tortoise in conservation peril. *Biol Lett* 1:287–290.
12. Russello MA, *et al.* (2007) Lineage identification of Galápagos tortoises in captivity worldwide. *Anim Cons* 10:304–311.
13. Thomson KS (2005) Natural history museum collections in the 21st century. *ActionBioscience.org* (American Institute of Biological Sciences, Washington, DC). Available at www.actionbioscience.org/evolution/thomson.html. Accessed on Sept. 7, 2008.
14. Townsend CH (1925) The whaler and the tortoise. *Sci Monthly* 21:166–172.
15. Townsend CH (1925) The Galapagos tortoise in their relation to the whaling industry. *Zoologica* 4:55–135.
16. Baur G (1889) The gigantic land tortoises of the Galapagos Islands. *Am Nat* 23:1039–1057.