More Fun Than Fun: David Wake, Salamanders and the Origin and Loss of Species

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L-R: the author, David Wake (1936-2021), Marvalee Wake and the Canadian botanist John McNeill, on the occasion of the centenary of the International Union of Biological Sciences, Oslo, July-August 2019. Photo: Geetha Gadagkar

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This article is part of the 'More Fun Than Fun' column by Prof Raghavendra Gadagkar. He will explore interesting research papers or books and, while placing them in context, make them accessible to a wide readership.

On April 29, 2021, I received the sad news that David Wake was no more. Despite being somewhat numbed by the relentless news of death and destruction caused by the pandemic, Wake's passing on raised my lugubriousness much more above the background noise.

Fond memories rushed into my consciousness. I first met David Wake in October 1994, when I visited the University of Berkeley to give a seminar at the invitation of my friend and colleague Wayne M. Getz, a distinguished multi-disciplinary scientist with his deft fingers in many pies, including honey bee kin-recognition, wildlife in Africa, conservation science and mathematical modelling.

Museum of vertebrate zoology

After my talk, Dave (as David was affectionately called), who was then director of the famed Museum of Vertebrate Zoology (MVZ), gave me a brief tour of the museum. He said that most museums are roughly similar, so he would show me what was unique about the MVZ. He led me to a series of bookshelves that contained immaculately bound, hand-written field notes of the museum's many illustrious zoologists.

No biographies, memoirs or photographs can be as inspirational as the field notes of famous naturalists – they transport the reader and viewer back in space and time, and make them partners in the process of discovery. I was not surprised by this museum director's admiration for knowledge production in the field (as opposed to in the museum). Dave's career is studded with outstanding fieldwork in the Appalachians, the Pacific Northwest US, Costa Rica, Guatemala, Mexico and California.

David Wake in his office in the University of California, Berkeley. Photo: Museum of Vertebrate Zoology, UC Berkeley, obtained through the kindness of his student Nancy Staub

I was pleased many years later that Harvard University Press published the handsome volume *Field Notes on Science and Nature*, edited by Michael R. Canfield, in 2011. The Harvard biologist Edward O. Wilson says in the foreword,

"If there is a heaven, and I am allowed entrance, I will ask for no more than an endless living world to walk through and explore. I will carry with me an inexhaustible supply of notebooks, from which I can send reports back to the more sedentary spirits (mostly molecular and cell biologists). Along the way I would expect to meet kindred spirits, among whom would be the authors of the essays in this book."

I next met Dave in 2007 during my first business meeting of the National Academy of Sciences in Washington, D.C. After the meeting, the ever so kind and unassuming Dave took me aside and said, "You may not remember me, but I remember well your visit and seminar at Berkeley many years ago". How could I not remember David Wake? I had by then become even more familiar with his remarkable work with salamanders.

Dave was the MVZ's director from 1971 to 1998. He did not see "the museum as a place where taxonomists figured out what's species A or Species B. He used the collection to determine how evolution works and how biodiversity develops over time," according to Michael Nachman, the museum's present director, as recounted in a *New York Times* obituary by Richard Sandomir.

The origin of species

Dave described and named 144 new salamanders. Salamanders are amphibians, though they may look like lizards. Dave's motivation for recording, counting and collecting specimens was to understand their dynamic evolution, not just their static morphology and anatomy. And Dave chose the most difficult of all problems in evolution: what is a species and how does it come about?

Dave and his colleagues have studied species formation, technically called *speciation*, in a group of salamanders called the *Ensatina* complex to address these questions. 'Complex' is a telling term because we do not quite know whether it is one species or many species.

There are several ways to define a species, but one that works best for an evolutionary biologist is the 'biological species concept'. Simply put, two individuals belong to the same species if they can interbreed and produce fertile offspring. Conversely, two individuals belong to different species if they can't interbreed to produce viable offspring. Unfortunately, this evolutionarily sound definition is difficult to apply in practice.

Fortunately, interbreeding individuals usually look similar and non-interbreeding individuals look somewhat different. Taxonomists are, therefore, usually forced to abandon the biological species concept – but luckily, they can bin species according to their appearance.

There are at least two problems with the morphological definition of species. One is that it may not correspond to the biological species concept – i.e. similar-looking individuals may sometimes fail to interbreed, and very different looking individuals might sometimes successfully interbreed.

The more serious problem is that the morphological definition of species suggests that evolution is discontinuous, jumping from one species to the next. In reality, evolution, as Charles Darwin himself knew very well, is a gradual and continuous process. It only appears discontinuous because the intermediate forms are usually extinct, leaving only the two morphologically different endpoints for us to see. The presumed discontinuity and the missing intermediates have been the cause of much misunderstanding and much genuine as well as malicious scepticism about evolution.

The paucity of intermediates in the fossil record, the so-called 'missing links' has been long held as an argument against Darwin's theory of human evolution from ape-like ancestors. Fortunately, that objection has disappeared. Today we see that "the transition from *Australopithecus* to *Homo habilis* to 'archaic *Homo sapiens'* to 'modern *Homo sapiens'* is so smoothly gradual that fossil experts are continually squabbling about where to classify – how to name – particular fossils" (from *Science in the Soul* by Richard Dawkins).

Ring species

A so-called 'ring species' solves the problem of missing intermediates but makes life hard for taxonomists who use morphology to identify species. Ring species were hypothesised in 1905 by the ornithologist Leonard Stejneger, first seen in birds by Ernst Mayr in 1942, and so named by Arthur J. Cain only in 1954. These species have played an important role in our understanding of biological species.

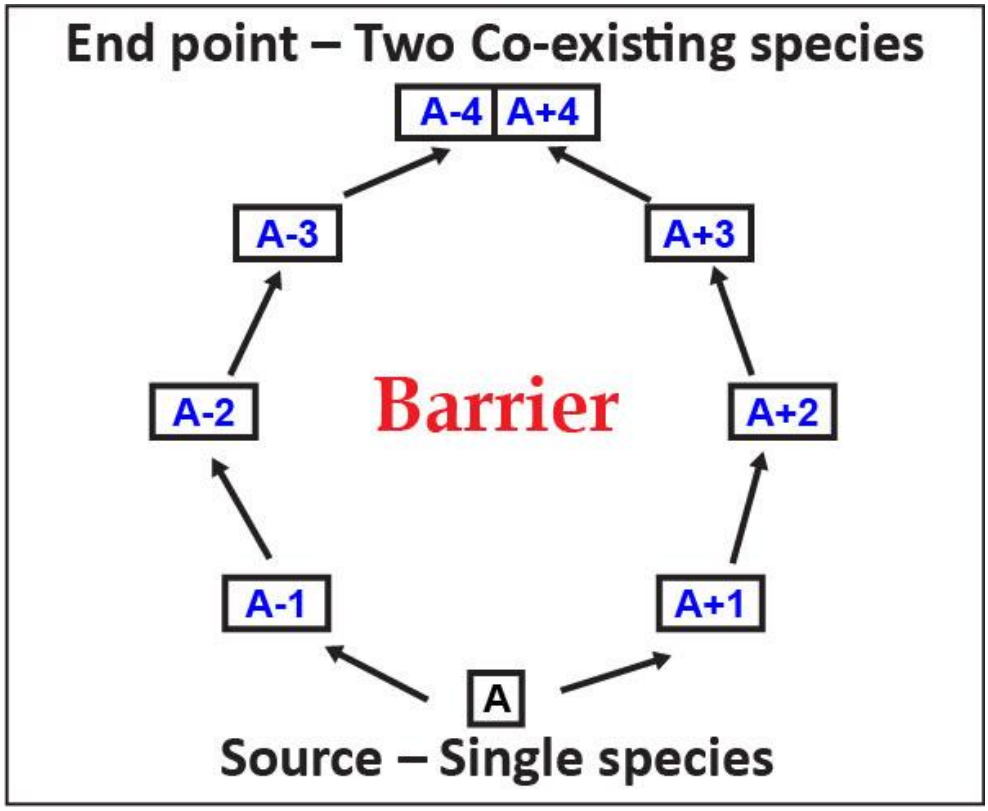
When there is a barrier such as a mountain or a valley, species can only disperse around it but can't cross it directly (see accompanying diagram). As individuals begin to disperse around the barrier, they change gradually but usually not enough to be incapable of interbreeding with their neighbours. However, by the time they meet again at the other end of the barrier, they may have become so different that they can no longer interbreed with each other.

So at the starting point, taxonomists can clearly recognise a single species, and at the endpoint, they can clearly recognise two distinct species. But all along the dispersal route, although there is only one discernible species, it is hard to say which one because it's a bit of both. The process of evolution is gradual.

The salamander *Ensatina* is a famous, if somewhat controversial, example of a ring species. Wake's predecessor in the MVZ, Robert Stebbins, first proposed the idea that *Ensatina* should be regarded as a ring species, based on his extensive study of their morphology and distribution. Controversy arises not only in the case of *Ensatina* but in any ring species because, in real life, the observed patterns are never as neat and simple as assumed while defining a ring species.

The species may go locally extinct in some areas along the dispersal route, some individuals may sometimes travel backwards, and occasionally, a few individuals may even cross the barrier. So it requires a great deal of informed and objective judgment to weigh the evidence for or against

declaring or upholding something as a ring species. It is here that we must pay tribute to David Wake, whose salamanders played all the mischief noted above.



A schematic illustration of the formation of a ring species. Starting from a single source species A, individuals disperse around a barrier (a mountain or a valley for example) because they cannot cross over it. They gradually change (shown as A+1, A+2 … on one side and A-1, A-2, … on the other side) as they evolve to adapt to their local habitats but are always capable of interbreeding with their immediate neighbours. By the time they meet up on the other side of the barrier, they are so different from each other (A+4 and A-4) that they can no longer interbreed. Voila! They are two new species.

Salamanders of the genus *Ensatina* are found all around the Central Valley in California. At one place, called the camp Wolahi, two morphologically distinct species, *Ensatina eschscholtzii* and *Ensatina klauberi*, coexist and do not interbreed. But all along the rest of the horseshoe-shaped distribution, various intermediate forms occur and usually interbreed among themselves.

Dave gathered data showing that the *Ensatina* complex "includes a number of geographically and genetically distinct components at or near the species level. The complex is old and apparently has undergone instances of range contraction, isolation, differentiation, and then expansion and secondary contact." Such data has led some to abandon the 'ring species' label and simply conclude that there are several distinct species of *Ensatina*.

His students recall that "When new data yielded results that conflicted with early foundational work, Dave welcomed the discrepancies and sought to learn from them. By his example, he taught his students to never get so attached to their ideas that they forget the value of data. Ideas, Dave always said, "Ideas are cheap. Data are gold."

In an article entitled *Wherefore and Whither the Ring Species*", PhD student Shawn Kuchta and David Wake recently concluded,

> "Like all models of evolutionary change, the ring species concept is an oversimplification, and an ideal ring species has never been found. … The essential features of a ring species are a biogeographic history resulting in a ring-like distribution, and the presence of a single species border characterised by reproductive isolation. … Whether one considers a ring species complex to be one species or many, it does not change the evolutionary message, and the problem (and lessons) presented by the ring species do not go away with taxonomic changes."

The salamader Ensatina complex. Top: The un-blotched Ensatina eschscholtyzii. Bottom: The blotched Ensatina klauberi. Photos by Chris Brown/Public domain

There is a fascinating discussion of the ring species concept in the context of *Ensatina* in the section on *The Salamander's Tale* in Richard Dawkins's *The Ancestor's Tale*: *A Pilgrimage to the Dawn of Life* (an 800-page tome that deserves to be read from cover to cover). First, Dawkins makes the clever argument that ring species show us in space what must always happen, with all species, in time. Then, Dawkins asks us to consider the most profound implication of his argument.

"Suppose we humans, and the chimpanzees, were a ring species. It could have happened: a ring perhaps moving up one side of the Rift Valley, and down the other side, with two completely separate species co-existing at the southern end of the ring, but an unbroken continuum of interbreeding all the way up and back round the other side. If this were true, what would it do to our attitudes to other species?"

Vanishing amphibians

That the amphibians were in a serious existential crisis worldwide entered the public imagination in 1994. Credit for this must go largely to the journalist Kathryn Phillips, who published a slim volume entitled *Tracking the Vanishing Frogs: An Ecological* Mystery, which can only be described as a whodunnit. Her quest was to find out who killed the frogs.

How can a journalist do that? She read all that she could, accompanied different frog researchers on their field trips, observed science in action and reflected on the personalities of the scientists and uncovered the source of their passion for frogs. Setting a fine example of science writers producing new knowledge, she synthesised the multiple threads of her inquiry better than any of the scientists themselves could do at that time.

A blurb on the back cover of her book says: “In 1990 a group of scientists sounded an alarm heard around the world: from California, Colorado, and Wyoming to Brazil, Switzerland, and Japan, frogs are disappearing at an alarming rate.”

David Wake, it turns out, was one of the first to sound the alarm and raise awareness among other scientists. He noticed the disappearance of frogs and salamanders in the early 1970s. Dave soon became a “spokesman for disappearing frogs”, in Kathryn Phillips’s words, and began to organise and chair meetings of scientists to take stock of amphibian decline and do something about it.

Dave was instrumental in setting up AmphibiaWeb, a database and news archive to help research, educate, and conserve amphibians. It is a beautiful site worth visiting from time to time, even if you are not an amphibian specialist or fan.

David Wake, who mentored at least 47 PhD students and 37 postdocs and inspired innumerable other scientists around the world. Photo: Museum of Vertebrate Zoology, UC Berkeley, obtained through the kindness of his student Nancy Staub

When I visited AmphibiaWeb on June 17, 2021, the first page had the photo of a beautiful frog with the caption “Species of the Week: *Ranitomeya ventrimaculata* | Amazonian Poison Frog”, with a link to more details. The opening page also said, “Current number of amphibian species: 8,350 (16th June 2021)”. Dave, as director of this project, tirelessly oversaw this effort until his death. It is said that Dave considered AmphibiaWeb to be part of his legacy.

It is not hard to measure the impact of these efforts; the number of amphibian species known to science has doubled in the 20 years since the website was set up.

I can’t resist making a digression to survey the situation closer to home. The Western Ghats in India are known to be a hotspot for amphibian diversity. There is evidence that many more species are waiting to be (re)discovered. It is important to create awareness among the public and help educate interested students if we are to meet the challenge of (re)discovering, (re)describing and (re)investigating this rich treasure.

I am pleased to see that we have many young scientists in India who are up to these challenges. They have found and described 223 new species of amphibians between 2001 and 2021, at a rate of about

11 species per year. This accounts for a whopping 48% of the total number of species ever described from India. It is also a matter of great satisfaction that the discovery of new species, and not just of frogs, is greeted with much interest and fanfare in the Indian news media. We have come a long way from dubbing species discovery as mere stamp-collecting. The credit for this welcome change in public attitude must go to the many "sparklingly talented young science writers" to whom I paid homage in my previous article in this column.

I will cite just one of many laudable examples of young Indian scientists smitten by frogs and other amphibians. K.V. Gururaja proudly proclaims his calling as a batrachologist (one who studies amphibians), teaches about frogs, toads and salamanders to postgraduate and doctoral students at the Srishti Institute of Art, Design and Technology in Bengaluru. And, in his spare time, Guru (as he is affectionately called) studies night frogs and dancing frogs in the Western Ghats.

Guru's open access book *Pictorial Guide to Frogs and Toads of the Western Ghats* (2012) is an irresistible invitation into the slimy world of amphibians. (His many public engagements and courses are a perfect antidote to our slow-changing formal education system.)

Gururaja K.V. (left) and his book of 2012 (right). Photos: K.V. Gururaja

Returning from my digression, I note with satisfaction that historians and philosophers of science have begun to scrutinise the life and work of ecologists and evolutionary biologists like David Wake. During the 20th century, we created a rich and fascinating literature on the epistemological and technological underpinnings of molecular biology and, to a lesser extent, of cell biology.

The other half of biology, which deals with the macroscopic biological world and its gaze on whole organisms, population and communities, remains to be similarly explored. Dave and his research methods have themselves now become the objects of study by philosophers such as James Griesemer of the department of philosophy, University of California, Davis. This augurs well for organismal biology and makes David Wake truly immortal.

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