with an animal that is cognitively so capable, but has a brain anatomy that is so vastly different from us mammals, you start asking questions about our core concepts on the relationship between brain structure and function. So, I came to realize that very different kinds of brains can generate very similar kinds of mental operations. And when you realize this, you start asking yourself how exactly functions are generated in the brain. To take a comparative approach helps you to avoid the trap into which many neuroscientists step when they study mice and humans: Sometimes they think that since a certain function is generated by the same neural entity in mice and men, this neural structure must be a *conditio sine qua non* for this function. With a comparative approach, you may see that the same function can be generated by quite different structures. Thus, we should look for the commonality between, say, pigeons, mice, and humans, at a much deeper level. The differences between species therefore represent experiments of nature that help us to understand the invariant and divergent properties of the neural foundations of cognition. I do not see pigeons or dolphins as a model for us humans. And I also do not study humans to understand pigeons. I must confess that, scientifically speaking, I'm not interested in humans or pigeons or in all the other animals that I study. I'm interested in the mechanisms of cognition. Different animals provide different opportunities to study these mechanisms.

Do you have a scientific hero (dead or alive)? Many. One of them is Juan Delius, whom I mentioned above. I got imprinted like a duckling by his relaxed attitudes, his fascination for discoveries, and his sheer joy for the conduct of science. Another hero is Ludwig Edinger (1855–1918), the leading comparative neuroanatomist of his time. His lifetime goal was to conceive a theory on the evolution of vertebrate brains and of vertebrate cognition. His conception was that of a stepwise addition of different brain components from fish to amphibians, to reptiles, to birds, and finally to mammals. According to his theory, the cortex was the last component that was added with the occurrence of mammals. His thinking dominated neuroscience for a century and had many spin-offs like, for example, the idea of the 'triune brain' in which our central nervous system was thought to consist of a sequentially added reptilian, a paleomammalian and a neomammalian complex. This idea was clearly inspired by Edinger but came out long after his death. The triune brain idea was wrong already when first formulated but still persists in all sorts of courses of managerial psychology. To summarize, the tragedy of Ludwig Edinger is that he was absolutely right in all of his observations, but nearly completely wrong in all aspects of his overall interpretation — and I'm among those who helped to end the dominance of his theory. But still Edinger has to be cherished as an outstanding scientist. He contributed tremendously to our knowledge and, based on what he could know in his time, his theory was just brilliant. I wish our current theories would stand a century.

Do you have a deep scientific conviction? Yes, paraphrasing the famous quote of Dobzhansky, I'm convinced that nothing in neuroscience makes sense except in the light of behavior. Nervous systems evolved to produce behavior. It is futile to try to understand brains without keeping this in mind.

If you would not have made it as a scientist, what would you have become? I cannot imagine myself as a clinical or as an industrial psychologist. Even the sheer thought feels like a nightmare. Possibly, being a taxi driver in a Mediterranean city would be a much more interesting alternative. Excellent weather conditions, long pauses full of daydreaming, and from time to time interesting customers that talk about their lives — that could have been a nice alternative.

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Quick guide

Freshwater sharks and rays

Luis O. Lucifora[1,*], Marcelo R. de Carvalho[2], Peter M. Kyne[3], and William T. White[4]

Hang on, I thought sharks and rays only live in the ocean? That's true for about 95%. However, there are species of elasmobranchs (sharks and rays) that occur regularly at low salinities, often beyond the tidal reaches of the sea. These make up around 5% of living elasmobranchs (roughly 56 out of 1154 described species). Species that are confined to freshwaters are termed obligate freshwater species, and comprise all the freshwater stingrays (family Potamotrygonidae) and several stingrays (Dasyatidae). Species that can tolerate a wide range of salinities, from freshwater to brackish and/or marine waters, are termed 'euryhaline species'. Euryhaline species include sawfishes (Pristidae), several whaler sharks (Carcharhinidae), one skate (Rajidae), and a number of stingrays (Dasyatidae). They range in maximum size from only 20–30 cm disc width in several freshwater stingrays, to at least 6.5 m total length in the Largetooth Sawfish (*Pristis pristis*).

Was the colonization of freshwater a unique event? The invasion of and adaptation to freshwater environments has occurred independently many times in elasmobranch evolution. The mostly late Paleozoic, eel-like xenacanth sharks, for instance, occurred in freshwaters and were perhaps euryhaline, whereas the Eocene Green River stingrays (in present-day Wyoming) were true freshwater species. The modern obligate freshwater stingrays of Africa and Southeast Asia (dasyatids) and South America (potamotrygonids) result from multiple independent colonization events. The potamotrygonids, known from four genera and 28 species (with about 10 known undescribed species), are the only group to have significantly diversified in freshwaters

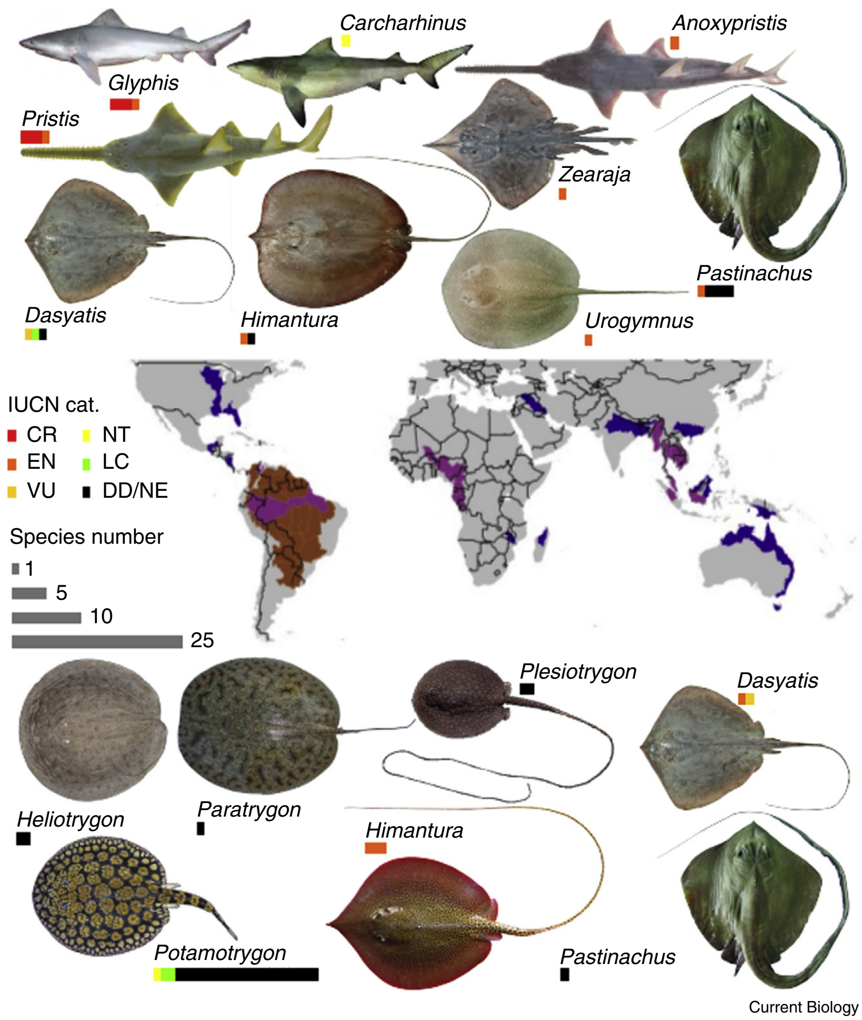

Figure 1. Freshwater elasmobranch diversity.
Freshwater elasmobranchs include euryhaline sharks and rays (above the map), which are essentially marine species that are able to enter freshwaters and stay indefinitely in them, and obligate freshwater rays (below the map), which complete their life cycle exclusively in freshwaters. They inhabit tropical and subtropical freshwater ecoregions (map) that may contain only euryhaline species (blue areas), only obligate freshwater species (brown areas), or both (purple areas). Freshwater elasmobranchs are generally at a high extinction risk or too poorly known to be evaluated, according to the International Union for Conservation of Nature (IUCN). Bars indicate the number of euryhaline or obligate freshwater species in each IUCN category for each genus. CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD/NE: Data Deficient/Not Evaluated. Photo credits: Alec Moore (*Carcharhinus*), Kirsten Jensen and Janine Caira (freshwater *Himantura*), CSIRO (*Glyphis*, *Pristis, Anoxypristis, Dasyatis,* euryhaline *Himantura*, *Pastinachus, Zearaja*), John E. Randall (*Urogymnus*), and Fernando Marques (*Paratrygon*).

from a common marine ancestor. They represent a separate and more ancient freshwater colonization than dasyatids, dating from at least the early Eocene, some 50 million years ago.

How do they cope with freshwater? Elasmobranchs keep their internal environment close to equilibrium with sea water by having a high concentration of urea in their blood and excreting salts through a specialised organ, the rectal gland. When entering freshwater, euryhaline elasmobranchs are able to excrete urea and take salt from the environment through their gills. Obligate freshwater elasmobranchs have lost the capacity to keep high concentrations of urea in their blood, and their rectal gland has atrophied. They cannot concentrate urea in their blood when exposed to increased salinity, as they lose urea through their gills.

Where do they live? Euryhaline elasmobranchs can be found in most major tropical and subtropical river basins, even thousands of kilometers upstream (Figure 1). Obligate freshwater elasmobranchs are restricted to the major drainages of South America (e.g. the Amazon, Río de la Plata, Orinoco, Magdalena, Maracaibo, Parnaíba, and the Guianas), Africa (Congo, Niger, Sanaga, and Cross), and southern Asia (Mekong, Irrawaddy, Maekhlong, Chao Phraya, and Bornean, Sumatran and peninsular Malaysian rivers; Figure 1). They inhabit lakes too, but, especially for the larger species, their main habitats are large, floodplain rivers. Euryhaline species move extensively along rivers and between rivers and the sea. There is one known instance of a transcontinental introduction and subsequent invasion by an obligate freshwater elasmobranch, as a by-product of the aquarium trade — the South American *Potamotrygon motoro* in Singapore.

Are they important to humans? People tend to be afraid of freshwater elasmobranchs. Sharks have been involved in some biting incidents in rivers, and stingrays are notorious for accidentally stinging bathers in rivers. In South America, stingrays are killed, maimed or scared away from river beaches where they aggregate. Increasingly in recent years, the larger species have become a popular target of big-game anglers in Asia and South America, representing a source of income for many local guides. Smaller species, given their unusual and colourful appearance, are popular in the international aquarium trade. Artisanal exploitation for human consumption as food occurs in some areas. Freshwater elasmobranchs are important icons in indigenous cultures of Australia, South America and elsewhere, appearing in legends and tales.

Why are many freshwater elasmobranchs at risk of extinction? Sharks and rays are well known for their inherent vulnerability to population decline and collapse. This is a consequence of their 'slow' life history — late age at sexual maturity, long lifespan, low fecundity, and low levels of natural mortality; all of these factors result in a susceptibility to population depletion from overexploitation and a limited ability to recover once depleted. In addition, freshwater elasmobranchs suffer from an elevated exposure to threats in their more restricted habitat. Over a third of all obligate freshwater species are threatened with extinction; amongst the euryhaline species, the sawfishes and river sharks (*Glyphis*) face an extremely high extinction risk (Figure 1). Unregulated fishing, high value products (such as fins), susceptibility to capture (e.g. the sawfish's rostrum is easily tangled in nets) and habitat degradation combine to threaten species. For South America's freshwater stingrays, risk comes from habitat degradation, persecution and the international aquarium trade.

What else do we need to know about freshwater elasmobranchs? Occurrence in remote habitats in often poor and under-developed regions and countries has limited research. Therefore, we know very little about these fascinating creatures. Basic biological information, such as lifespan and fecundity, is lacking for the vast majority of species; movement patterns, migrations and critical habitat requirements are largely unknown. Assigning levels of fishing and trade that a species can sustain relies on this basic information; as does assessing the impacts on species from developments, such as dams or increased water extraction. The International Union for Conservation of Nature ruled that a lack of information prohibits assigning an accurate conservation status to over half of all obligate freshwater elasmobranchs.

What is the future of freshwater elasmobranchs? Only two species of obligate freshwater elasmobranch can be considered to have a secure status. For threatened species, national protection helps but is often limited to developed countries. Even if implemented in Asia, Africa or South America, enforcement and compliance are ongoing issues. There is also a role for international treaties; the listing of sawfishes on the Convention on International Trade in Endangered Species (CITES) prohibits international trade. Consideration is being given to list South America's freshwater stingrays, which would be a positive step. The task ahead is to first of all try and obtain the knowledge to understand their current status and sustainability and, secondly, to secure populations, is considerable.

Where can I find out more?

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Primer

Equids

Ludovic Orlando

Alongside domestic horses and donkeys, the horse family, also known as equids, comprises six extant wild species of asses and zebras (Figure 1). Equids are extremely well represented in the fossil record, comprising a 55 million-year evolutionary history, punctuated by many episodes of innovation, extinction and migration. Limited to the single genus *Equus* today, in the Miocene (23.0–5.3 million years ago) the equid family flourished, comprising more than twenty genera. The group originated in Northern America, where the earliest fossil forms have been found, the so-called Hyracotheres, no larger than small dogs. These animals were soft-leaf browsers and in contrast to modern equids, which roam on a single toe with a solid keratin hoof, their hindlimbs were three-toed and their forelimbs four-toed. Equids thus form, together with rhinos and tapirs, the perissodactyls, an order of mammals characterized by an odd number of toes. Unlike ruminants, they are hindgut fermenters, which digest plant cellulose in their intestines and not in differentiated multiple stomach chambers.

The evolutionary transition from multiple-toed to one-toed animals can be followed in great detail in the fossil record and represents one of the most popular textbook examples of macroevolution (Figure 2). Equids have experienced many other evolutionary transformations, such as a diversification in tooth morphology, accompanying multiple independent shifts to grazing, but also important anatomical changes, which occasionally led to the emergence of gigantic forms, rivaling present-day draft horses in size.

Out of Northern America

Even though hyracothere-related equids reached the Old World as early as 52 million years ago, they left no descendants there and most of the evolutionary equine radiation took place in Northern America until 23 million years ago, when three-toed *Anchitherium* leaf browsers crossed Beringia, later reaching Eurasia as far West as Spain. Further expansions from North America