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Fossil Focus: Reimagining fossil cats

by Andrew Cuff[*1]

Introduction

One of the biggest challenges palaeontologists face is how to reconstruct whole animals from their fossils. Most fossil remains are just bones, so how do we go from the bones to the soft tissues? For extinct species, we make deductions by looking at their nearest living relatives. This process is called the extant phylogenetic bracket (EPB).

A good example of using the EPB is in reconstructing dinosaurs. Dinosaurs are alive today as their descendants, birds, but the non-avian dinosaurs we all know and love from *Jurassic Park* look very different from modern birds. Dinosaurs also have other living relatives: the crocodilians. Along with the dinosaurs and some other extinct groups, these are part of a group called the archosaurs (which means 'ruling reptiles'). When we reconstruct tissues, such as muscles, we look at both groups of living relatives. If both have the same muscle in the same place, we deduce that the muscle existed in this place in dinosaurs. It gets harder when the muscles are in different places in the two groups, or have been completely rearranged — for example, crocodiles have a big tail muscle called the caudofemoralis, but birds have lost their tails, so in birds this muscle has moved onto the pelvis and is generally much smaller. In these situations, we have to use evidence from the bones (such as scars where the muscles were attached), and sometimes add a warning to our reconstructions!

Cats and their fossil kin

Now that we've covered that background, let's look at felids: cats and their close relatives. There are about 30 living species of modern cat, ranging in size from about 1 kilogram (rusty-spotted cats, *Prionailurus rubiginosus*, and black-footed cats, *Felis nigripes*) to 300 kilograms in the largest lions and tigers. The first cats evolved about 30 million years ago, with the modern groups evolving around 15 million years ago. The exact naming of the groups gets a bit messy, but the living species are split into two: the pantherine lineage (*Panthera* species — lions, tigers, leopards, jaguars, snow leopards — and the sister *Neofelis* species, clouded leopards); and the other lineage, everything from domestic cats to cheetahs (see Fig. 1). Different people use different names for this second lineage, but I will refer to them as felines.

The pantherines are generally the big cats and the only ones capable of a true roar. Most of the felines are relatively small, although cheetahs and pumas are larger. There is also a completely extinct subfamily called the Machairodontinae, or 'dagger-tooth' lineage — the sabre-toothed cats. A good example of the sabre-toothed species is *Smilodon*, which is often known as the sabre-toothed tiger, although it not very closely related to tigers at all. There are a few other lineages of felids that are known from the fossil record, but I won't be focusing on them because few studies have worked on them in much depth.

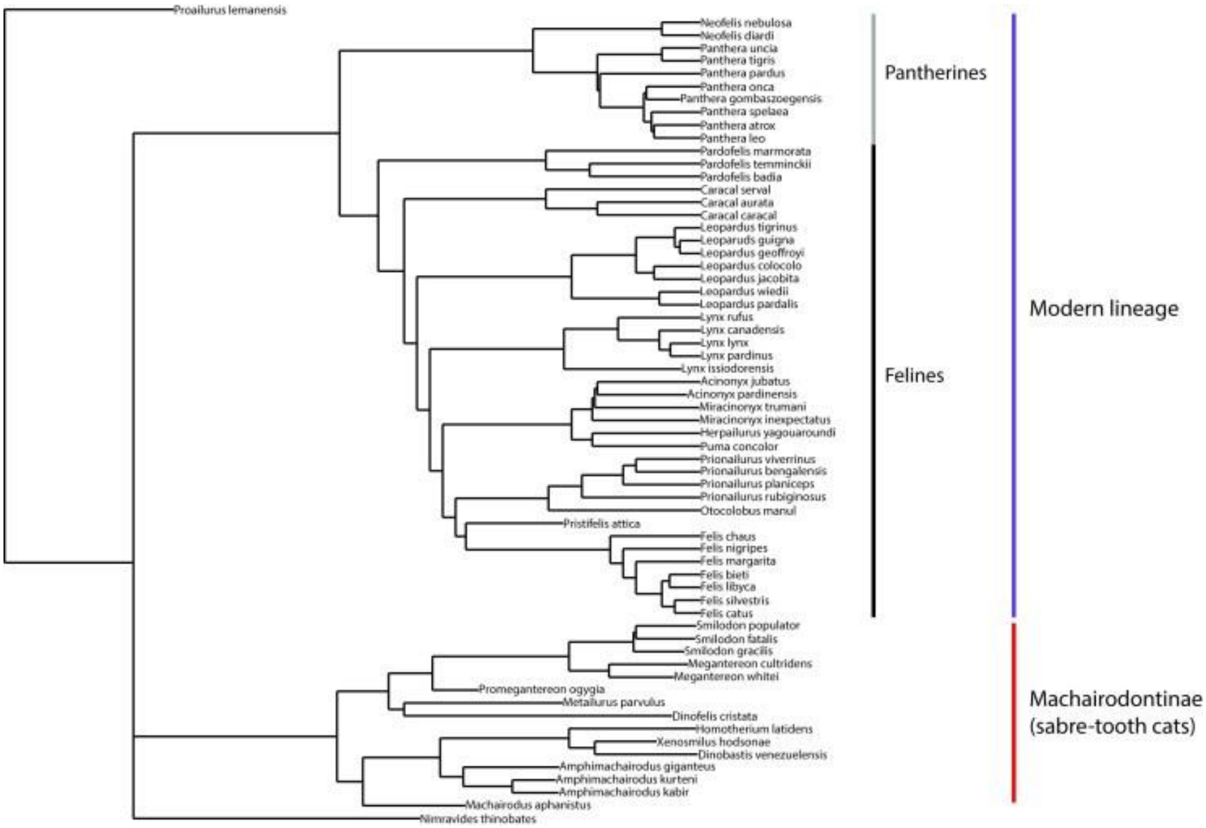

Figure 1 — Felid family tree, modified from Piras et al. (2013). Branch lengths are scaled so that modern is on the right. DOI: [10.1093/sysbio/syst053](https://doi.org/10.1093/sysbio/syst053)

How to reconstruct a fossil cat

So how do we go about reconstructing cats? The first step is understanding living cats. For me and my colleagues, this meant working with and dissecting the bodies of animals that had died in zoos around the United Kingdom. (All exotic cats are protected by a treaty called the Convention on International Trade in Endangered Species of Wild

Fauna and Flora, so they cannot be moved between countries without lots of permits.) Shortly after death, each animal was weighed, then CT scanned. After that, we located every muscle, and worked out where it was attached to bone. We then removed the muscles and weighed and measured them. This is important because the mass of a muscle is proportional to its volume (volume × 1.06 g/cm^3 = mass), and can be helpful for scaling, as well as for other measurements, including working out how much force the muscles can produce. From the results, we can draw a graph plotting the lengths and masses of the muscles against the masses of the cats. By drawing a line through the points, we can get an equation that we can use to estimate the mass of any cat, if we know its size. However, as with the EPB, it is best if we can check the results against closely related species. We are likely to get the most accurate results for extinct species that are closely related to the living species we looked at. The results for other species will probably get less accurate the longer ago their branch of the evolutionary tree split from the living species.

Next, we need some extinct felids to reconstruct — and ideally ones with mostly complete skeletons. For this, we turned to the La Brea Tar Pits in Los Angeles, California, a set of natural tar pools that trapped animals and preserved their bones. The tar pits contain a lot of fossils of predators (and so are often known as 'predator traps') because any prey animals caught in the tar would continually attract predators, who themselves would then get trapped and die. The pits preserve hundreds of felids, particularly *Smilodon fatalis*, but also the North American lion, *Panthera atrox*. The pits are usually jumbles of bones, but some fairly complete individuals exist for both *S. fatalis* and *P. atrox*. These are what we used for our experiments. We got permission to scan the bones from the George C. Page Museum (part of the Natural History Museum of Los Angeles). Once we had scanned the bones, we created digital models of the cats, with all the bones reconnected in the right places. However, even the most complete *P. atrox* had parts missing (or at least they weren't all scanned) and the reconstruction lacked its ribs, tail and paws. We used CT scans of an Asian lion (*P. leo persica*) that we had dissected to reconstruct the bones of the missing bits, scaled to match the expected size. This gave us the skeleton that you can see in Figure 2.

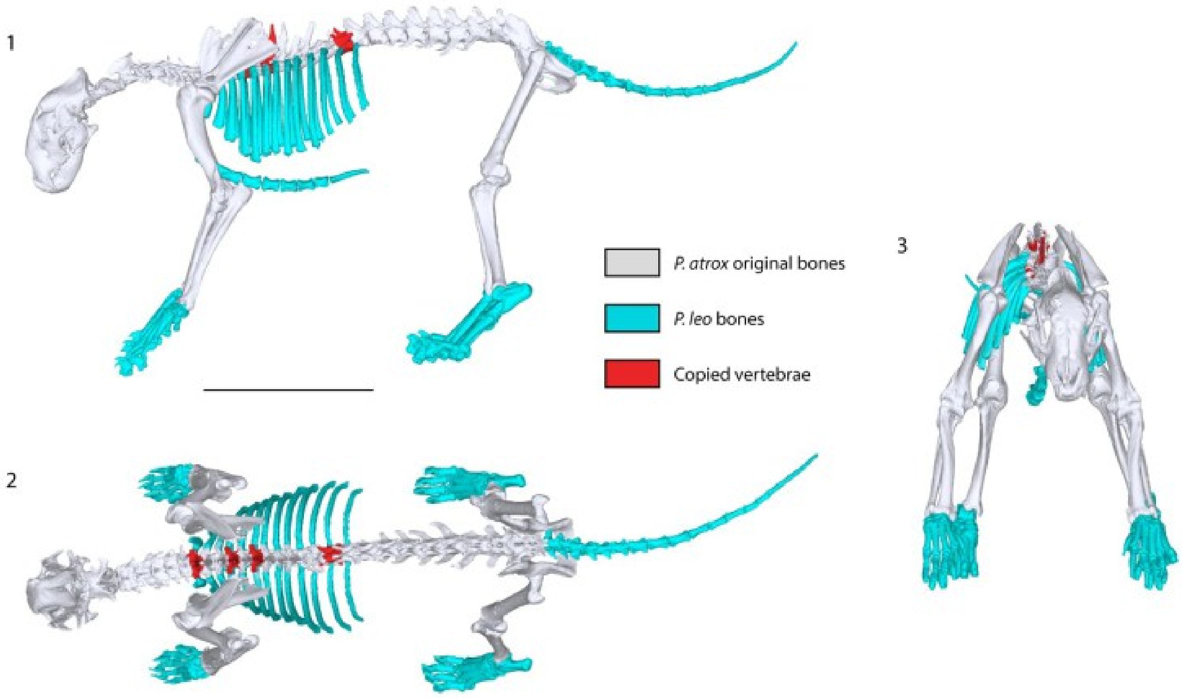

Figure 2 — From Cuff et al. (2017). Skeletal reconstruction showing the original bones from *Panthera atrox* and those that have been copied from other vertebrae (red), or from *P. leo persica* (blue). 1, side view; 2, view from above; 3, view from the back. Scale bar is 50 centimetres. DOI: [10.26879/688](10.26879/688)

Adding flesh to the bone

The scans of the Asian lion also had another use: unusually, they showed some of the muscles. We isolated these from the CT scans, as we did with the bones (see Fig. 3). Using the predicted mass of the skeleton for *P. atrox* (an average of 207 kilograms) and our scaling equations, we estimated the masses of the muscles for *P. atrox* from the Asian lion muscles:

$$\text{Mass}_{P.atrox} = \text{Mass}_{P.leo} \times \text{length scale factor} \times \text{width scale factor}^2$$

Not all of the muscles could be isolated from the CT scans (particularly the ones attached to the vertebrae) and neither could most of the tendons of the paws. We reconstructed the tendons by creating a tube of material coming off the muscle and extending it to the attachment point on the bone, while matching the volume to the predicted mass as closely as possible (see Fig. 4).

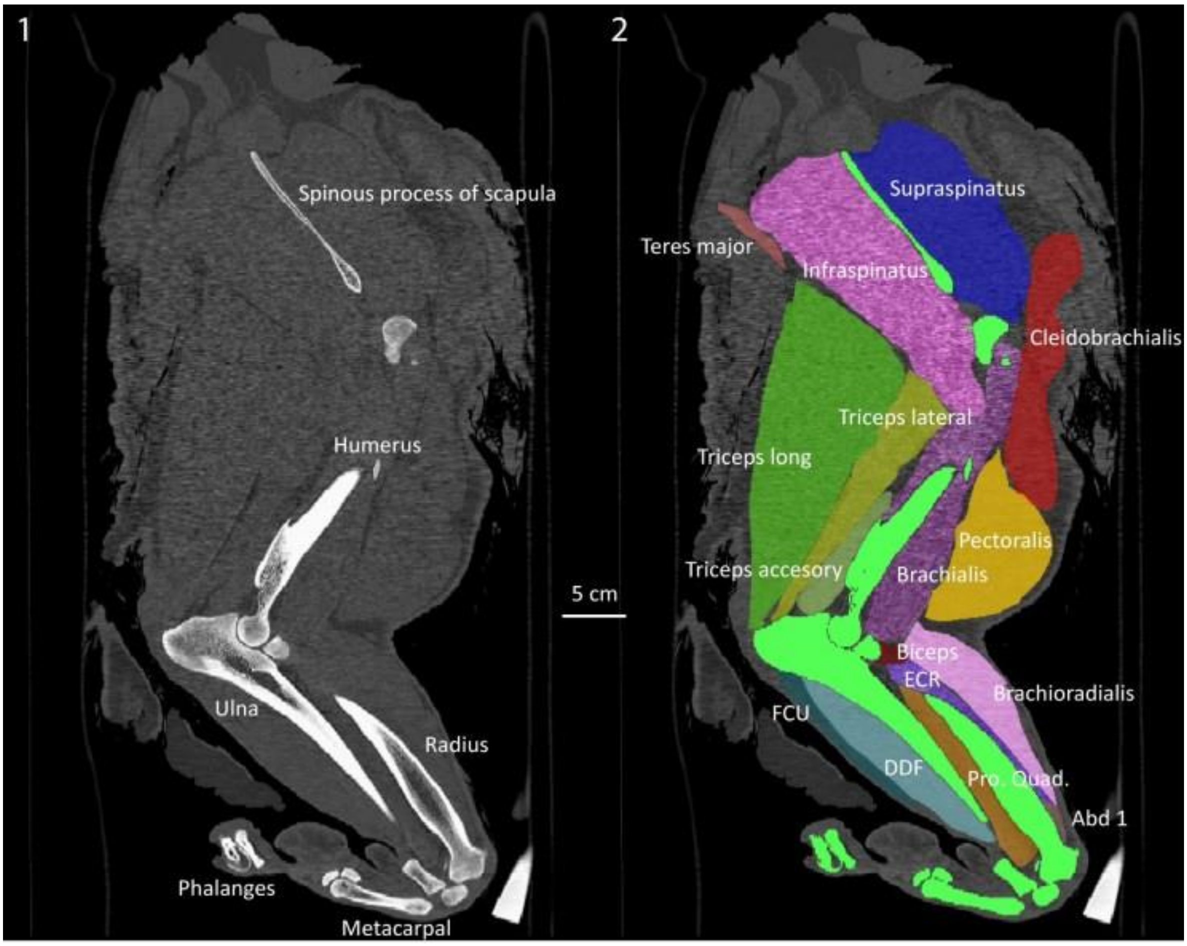

Figure 3 — from Cuff et al. (2017). CT scan slice through the forelimb of an Asian lion. 1) Dark grey is fat and connective tissues; lighter grey is muscle; white is bone. 2) Segment of the lion forelimb with select muscles highlighted. Abbreviations: FCU, flexor carpi ulnaris; DDF, deep digital flexors; ECR, m. extensor carpi radialis; Pro Quad, m. pronator quadratus; Abd1, m. abductor digiti I. DOI: [10.26879/688](https://doi.org/10.26879/688)

The resulting muscle model is missing some tail, neck, skull and abdominal muscles, but otherwise it gives hopefully the most accurate reconstruction yet of the North American lion's muscles and skeletal system. We then used a method called convex hulling to create a fleshy outline over the top of this model (see Fig. 5). Convex hulling is basically geometric shrink-wrapping, in which we draw lines between all the extreme points of the model, creating a 3D shape around it. In the simplest form you could end up with something like a box covering a bone, but generally you get a complex shape. Convex hull reconstructions are often done on skeletons without the flesh, to estimate an animal's mass, but they are not very accurate (convex hulls of the upper arm and leg might be 5–10 times smaller than they would have been in reality). However, if we create a convex hull model over the top of the muscled model, we get biologically accurate limb proportions (based on validation with the same Asian lion).

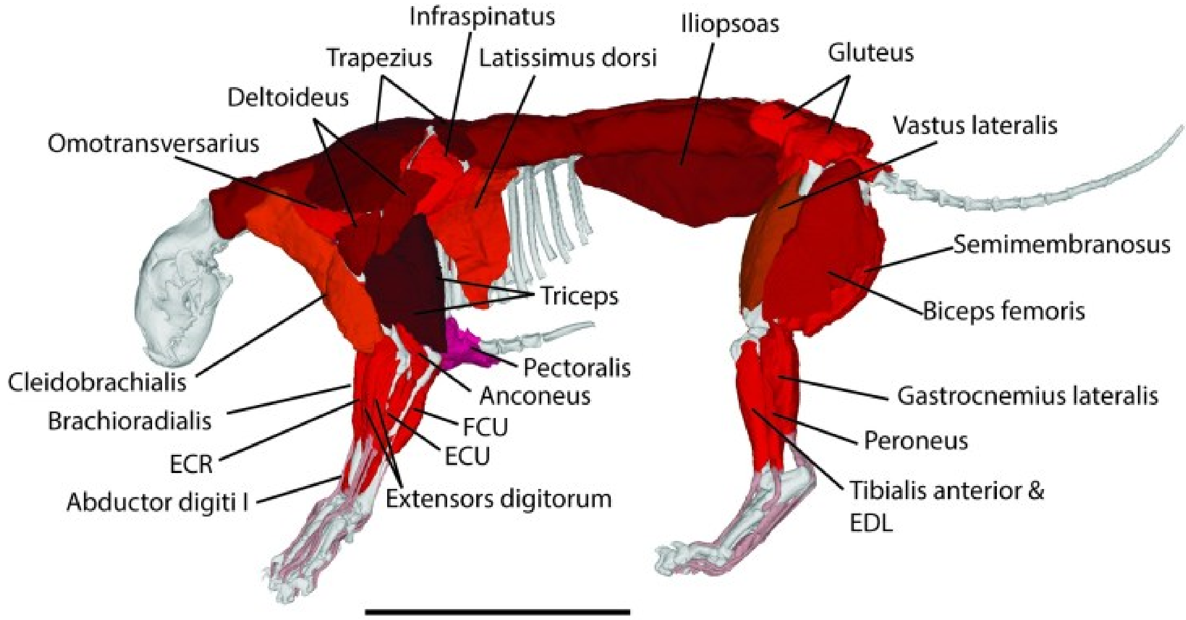

Figure 4 — From Cuff et al. (2017). Reconstruction of *Panthera atrox* showing the major muscle groups from the side. Abbreviations: FCU, m. flexor carpi ulnaris; ECU, m. extensor carpi ulnaris; ECR, m. extensor carpi radialis; EDL, m. extensor digitorum longus. Scale bar is 50 centimetres. DOI: 10.26879/688

We have repeated this process for *Smilodon*, but have not yet published the model. Because *Smilodon* is not as closely related to living cats as *P. atrox* is, it does not scale so nicely! Most of the issues relate to the shape of the shoulder blades, which are longer and narrower in *Smilodon* than in the Asian lion, creating a different shape for the muscles that attach to it. Presumably this has consequences for the amount of muscle and how the muscles move and operate. We are working on testing this.

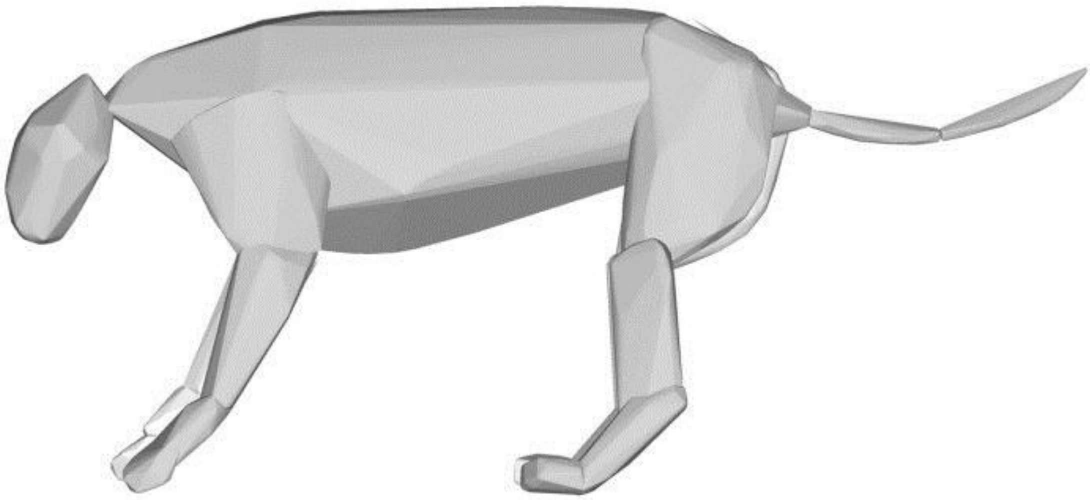

Figure 5 — Reconstruction based on Cuff et al. (2017). Convex hull of *P. atrox* on the muscled reconstruction. DOI: 10.26879/688

Cat-brained

Now we have looked at reconstructing the muscles and bones, there is one other part of the anatomy that we can 'easily' look at, and that is the brain. It says a lot about how important brains are to animal functioning that the other vital organs are only partially protected by the ribcage and sternum, whereas mammals' brains are safely boxed away in our skulls. The result of this is that even when the soft tissues have decayed, the bone that tightly enclosed the brain provides a faithful reconstruction of the organ itself. I should note that technically what we are reconstructing is a cast of the brain (an endocast) rather than the brain itself. Non-avian dinosaurs and reptiles generally have relatively small brains with sinuses packed around them, resulting in endocasts that do not look like the actual brain. Mammals and birds have relatively big brains, so the endocast tends to be a close match to the organ.

Thankfully, cats follow this trend (being mammals) and have endocasts that tell us much about the brains. We can get accurate estimates of how big their brains were relative to body size (called the encephalization quotient — humans have the largest brains relative to their body size, about seven times larger than a cat's brain, proportionally). If we look across felids as a whole, most cats fall very close to the expected scaling line. However, brains get relatively smaller with respect to body size as the body size increases. If intelligence correlates with brain size, you might expect

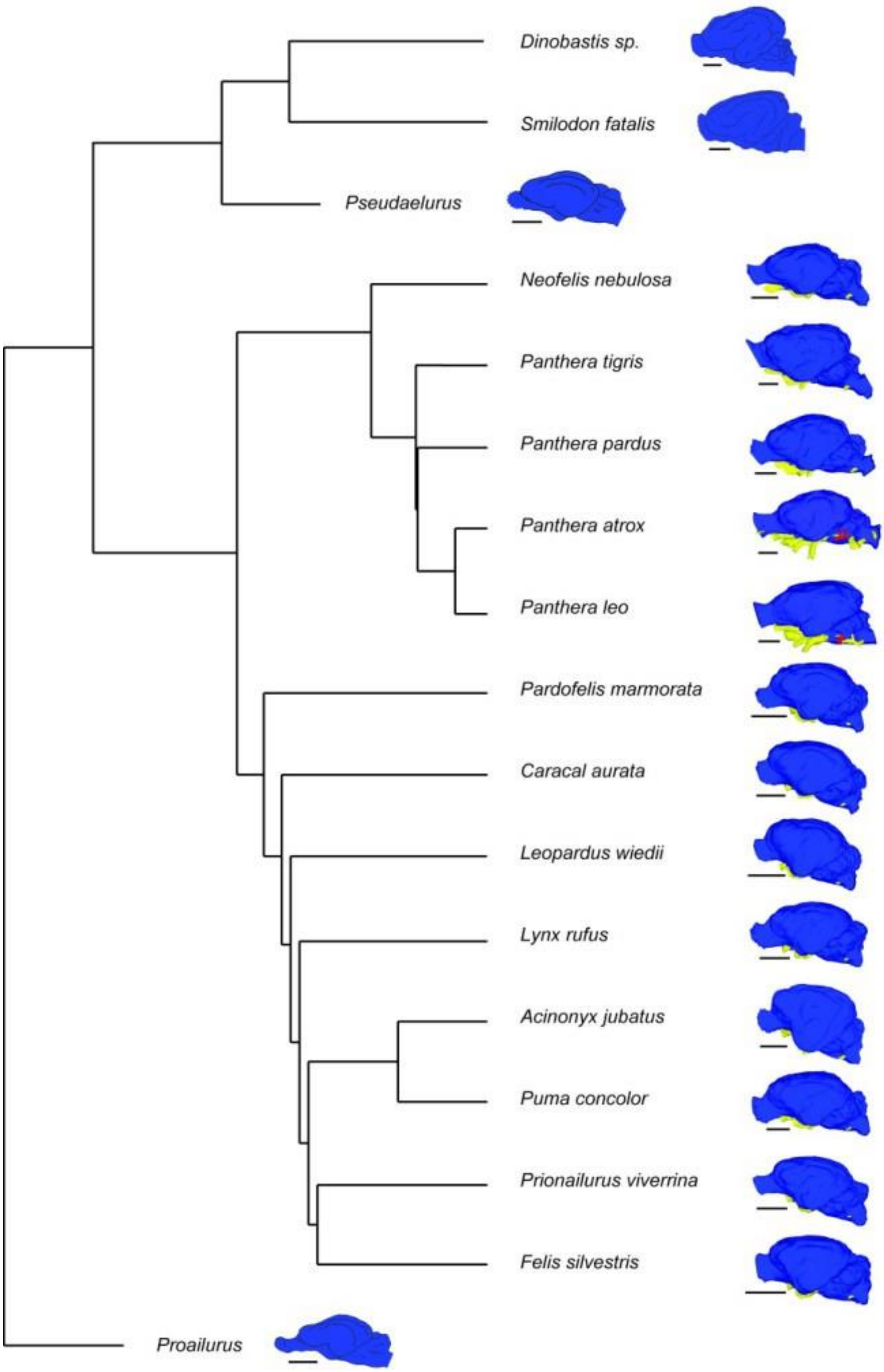

Figure 6 — From Cuff et al. (2016c). Felid brains. Blue is brain, yellow is nerves, and red is endosseous canals (the inner ear bits, reconstructed only for *P. atrox* and *P. leo*). DOI: [10.1159/000454705](https://doi.org/10.1159/000454705)

larger cats to be relatively less intelligent than their smaller cousins. This might well be true, although the 2018 BBC documentary *Big Cats* suggests that even though lions are the biggest of the *Panthera*, they are also the most intelligent, so the relationship probably isn't perfect. A more curious aspect of feline brains is their shape. Surely they all look similar? Well, yes and no. Superficially, they do: the nerves all come from similar locations, and the endosseous canals (where the parts of the inner ear are found in life) are all roughly in the same place. But look closely at Figure 6.

You will see that the brains across the felid family tree all vary quite a lot in their relative 'straightness', with species such as *Neofelis* (clouded leopard) or *Panthera atrox* (American lion) having relatively long, straight brains, and others such as *Acinonyx* (cheetah) having a shortened and rotated brain. In technical terms, the cerebrum (forebrain), is rotated back over the cerebellum (the hindbrain). The folding of brains has been suggested to be a way of increasing surface area without increasing volume. This is particularly focused on the brain's characteristic ridges. However, this does not seem to be the case with cats, and it's a mystery why closely related species such as the Asian lion (shown here as *Panthera leo*) and the American lion should differ so much. Obviously they are constrained by the skull, but is the skull driving brain shape, or is brain shape driving the skull — or a bit of both? And what effect does this have on cat intelligence and ecology?

Reconstructing fossil groups, both their hard and their soft parts, is vital for understanding extinct species and their environments. To check the truth of our reconstructions, we must work on modern animals; this gives us great insight into the living relatives that we might not have appreciated before. And by studying the morphology, or shape, of extinct cats, we are giving them back some of their lost lives. They, in turn, give us new and exciting questions to delve into.

Further reading:

Cuff, A. R., Sparkes, E. L., Randau, M., Pierce, S. E., Kitchener, A. R., Gosawmi, A. & Hutchinson, J. R. (2016a) The scaling of postcranial muscles in cats (Felidae) I: forelimb, cervical and thoracic muscles. *Journal of Anatomy* **229,** 128–141. DOI: 10.1111/joa.12477

Cuff, A. R., Sparkes, E. L., Randau, M., Pierce, S. E., Kitchener, A. R., Gosawmi, A. & Hutchinson, J. R. (2016b) The scaling of postcranial muscles in cats (Felidae) II:

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