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Fossil Focus: Porpoises

by Rachel A. Racicot[*1]

Introduction

Porpoises are among the smallest of modern whales, but they are one of the most amazing groups. They use specialized high-frequency hearing and sound production, and they have one of the best fossil records of any marine mammal. Thanks to modern imaging technology, we have been able to learn about how porpoises are able to sense their environment through echolocation and how they evolved. I will be telling you a bit about a particularly interesting porpoise from the fossil record, *Semirostrum ceruttii* ('Cerutti's half-nose'), and using it as an example of how CT scans help scientists to explore ancient and modern anatomy.

What are porpoises?

People sometimes use 'porpoise' interchangeably with 'dolphin', but scientists use the term to refer to a distinct group of small toothed whales that are closely related to dolphins, belugas and narwhals (their family name is Phocoenidae; Fig. 1). Phocoenids (porpoises), dolphins and narwhals are all part of a larger group called Delphinoidea.

Figure 1 — Relationships of Delphinoidea (highlighted with blue lines), based on genotype (DNA) data. Photographs: Top, bottlenose dolphin; middle, Harbour porpoise (note relatively blunt face); bottom left, beluga; bottom right, narwhal.

Depending on how they are classified, there are six, seven or even more species of porpoise alive today. They inhabit the cooler marine waters of the Southern Ocean, North Pacific Ocean, North

Atlantic Ocean and Black Sea. One population even extends into the Yangtze River in China. Porpoises can be distinguished from dolphins because they 1) do not have a distinct 'beak' or 'bottlenose', but instead have a rounded face, 2) are all rather rotund in body shape (but still streamlined for swimming), and 3) are quite small relative to most dolphins.

Figure 2 — Skull differences between adult bottlenose dolphin (top) and Harbour porpoise (bottom). Three-dimensional reconstructions of skulls based on CT scans of specimens from museum collections (top SDSNH 21212 San Diego Natural History Museum/San Diego Society of Natural History; bottom MVZ 135247 Museum of Vertebrate Zoology, University of California). Copyright Rachel A. Racicot.

Scientists studying porpoises can distinguish them further using some features of the skull. For example, extant species all have spade-shaped teeth rather than dolphin-like conical teeth, and they have distinctive bumps (called premaxillary eminences) on their facial bones, whereas dolphins have flattened facial bones (Fig. 2). Separate analyses of data sets based on physical and anatomical characteristics and DNA find good support for porpoises making up a single related group (a clade), but no single shared derived character has been described for them. Rather, a combination of characters like the list above has been used to distinguish them. This is intriguing because it means that we still don't fully understand what is going on with the fossil history of porpoises and their relationships with other major toothed-whale groups, so there is still a lot more work to do.

The fossil record, and a particularly special extinct species:

The fossil record of porpoises is quite extensive, and there are still species to be discovered in the field and described from museum collections. The oldest described porpoise (and actually the oldest described delphinoid, although it does not seem to be the most primitive in terms of evolution), *Salumiphocaena stocktoni*, is found in rocks from the late Miocene epoch (10 million to 11 million years old) in California. Several species from the later Miocene (9 million to 5 million years old) of Japan have been described. Although mostly found on the Pacific coasts of Japan, Mexico, Peru and the United States, some species have been described from Europe, particularly *Septemtriocetus bosselaersi* from Belgium. This year, a porpoise with a unique jaw shape was described from multiple specimens found along the coast of California, mostly from the San Diego area. It was named *Semirostrum ceruttii* ('Cerutti's half-nose'; Fig. 3). This species had a blade-like lower jaw extending well beyond the upper jaw, unlike anything seen before in a mammal. Some modern analogues such as half-beak fish and skimmer birds exist today.

Figure 3 — Reconstruction of *Semirostrum ceruttii* probing at the sea floor by Robert Boessenecker, modified from Racicot *et al*. 2014 (*Current Biology*).

Looking inside the heads of porpoises:

Unusual species such as *Semirostrum ceruttii* raise many questions. How does such a strange jaw shape develop? What did the species use it for? How many different body and head shapes are possible in porpoises and cetaceans in general? Was there something unique about the environment in which it evolved that drove specialization of jaw shape?

When we first described this species, my colleagues and I thought that it might have used its jaw to probe around and sense for food, like modern skimmer birds and half-beak fish. Looking inside the jaw using a medical [CT scanner](), we were able to see many small canals; these probably housed nerves that increased the sense of touch in the skin of the chin (Fig. 4). This supports the idea that the jaw was used for probing. In the future, a higher-resolution scan of a more completely preserved jaw may help us to test other slightly more exciting hypotheses, such as whether the jaw could withstand bending and thus whether *Semirostrum* might have used its jaw to bat at prey to stun them before feeding. We would also be able to look for more evidence by reconstructing the whole head and body of the animal to test how water would flow around the jaw at different speeds.

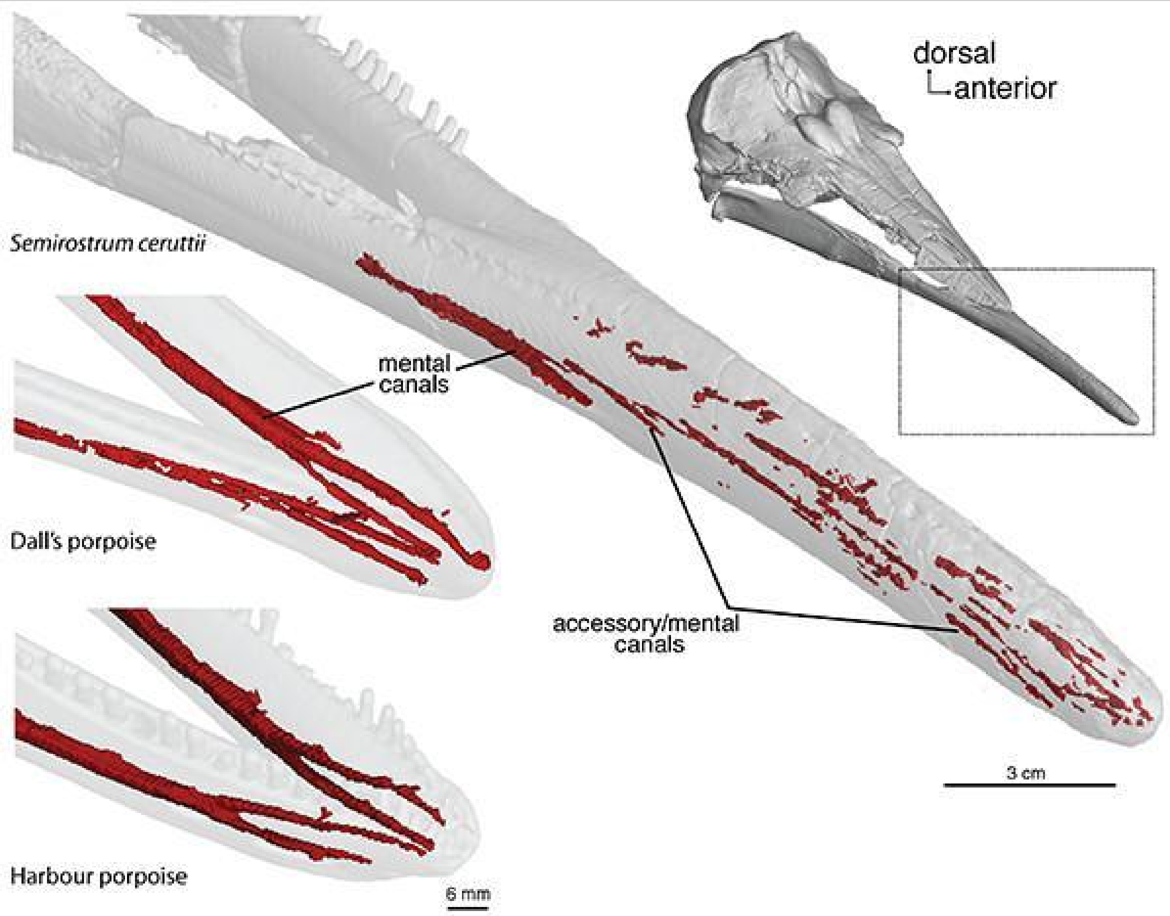

Figure 4 — Long sensory canals in the lower jaw of *Semirostrum ceruttii*, found using CT data, compared with the unspecialized jaws of two extant species. Only the canals in the right side of the jaw are rendered. Modified from Racicot *et al*. 2014 (*Current Biology*).

Additional data gathered from CT scans of skulls can help us to understand more about the importance of different senses, by looking at the shape of the brain and inner ears (Figure 5). The brain is comparatively easy to look at in this way, because more neural tissue grows in regions that are used more or are more important. Cetaceans use hearing for communication, navigation and foraging, so the auditory region of their brains is quite expanded relative to that of terrestrial relatives that rely more on smell or other senses. The brain is directly connected to the ear by nerves, and detailed study of the inner ear can help us predict the frequencies to which fossil and extant porpoises are sensitive. We are slowly coming to an understanding of the complex biosonar system that porpoises and other cetaceans use for echolocation, and how humans can avoid impacting them too heavily.

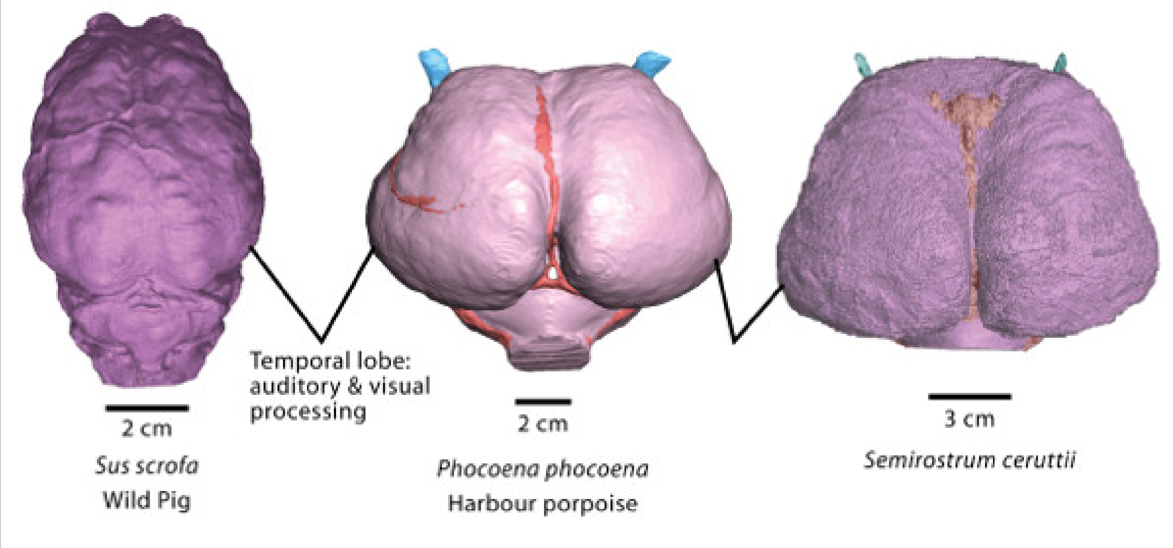

Figure 5 — CT-derived images showing the endocast - the region of the skull in which the brain sits - for terrestrial artiodactyl (the group in which Cetaceans are nested), Wild Pig (data from digimorph.org), Harbour porpoise, and *Semirostrum ceruttii*. Note the large size and lateral expansion of the temporal lobes in both the fossil and extant porpoises relative to that of the land-dwelling pig. The enlarged temporal lobes relate to more processing of sound and sight, as well as long-term retention of visual and auditory memory.

One other unique attribute of porpoises is that they have an extension (called preorbital lobe of the pterygoid sinus) of the air sinus system (a system unique to toothed whales that seems to be involved with echolocation). This extension varies between individuals and different porpoise species; its shape in different species can tell us how they are related. It might have interesting functions relating to species' specialized hearing. The air sinus system probably isolates each ear to let the porpoise hear in two directions separately, which may help them to better 'see' their environment when echolocating. Using CT scans, we have been able to improve descriptions of the shape and volume of these features, and test hypotheses about whether the preorbital lobe could reflect sounds produced in the forehead. We can also tell whether extinct species like *Semirostrum ceruttii* had an extended preorbital lobe. In fact, its pterygoid sinus was very similar to that of the extant species *Phocoena phocoena* (Harbour porpoise) and *Phocoenoides dalli* (Dall's porpoise), as shown in Figure 6 - but there at the moment we haven't found a clear single reason why this has occurred.

Conclusions:

CT scanning can be very expensive, but it allows us to gather information and test hypotheses that are otherwise difficult or impossible to explore. Using these data has helped us to understand more about the sensory abilities of both ancient and modern porpoises. More work still needs to be done to help us to understand how the group evolved and changed through time, especially for fossil species. Exciting fossil porpoises are still being discovered and described by scientists, continuing to enlighten us about their anatomy, biogeography, diversity and differences.

Figure 6 — CT scans of skulls rendered transparent with pterygoid sinuses highlighted in dark blue. Note that the extension of the preorbital lobe in *Semirostrum ceruttii* (bottom images) is similar in shape and length to that of the Harbour porpoise (top images). They both differ greatly in width from the Dall's porpoise, but all three species have longer extensions than those of other extant porpoises. Image modified from Racicot and Rowe (2014, *Journal of Paleontology*), from specimen CAS 15278 (California Academy of Sciences).

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