comparison and on whether the remains are associated with archaeological evidence of humans.

Evin *et al.* used three-dimensional (3D) morphometric analysis to compare the physical features of a global sample of 643 canid skulls from the past 50,000 years. This quantitative analytical technique measures fine differences in shape across specimens. A detailed 3D model is created from a specimen using either a laser scanner or photogrammetry, and physical features of interest are identified, measured, and compared across specimens using multivariate statistics. Physical differences between specimens may be markers of domesticated traits, or they may result from other factors, such as changes in diet or environment. Evin *et al.*'s results indicate that a distinctive dog skull morphology emerged around 11,000 years ago, which aligns with the time frame suggested by genetic analyses of ancient dogs (*4*). The results also reveal a high amount of diversity among specimens identified as domesticated, challenging the idea that Victorian-era breeding was the sole driver of the immense diversity of modern dogs.

Evin *et al.*'s analysis has one main limitation. The older a specimen is, the more difficult it is to date it directly and obtain a narrow time frame. The authors used a large, global sample of canids that had been dated by a variety of methods across different laboratories. The uncertainty about the accuracy and comparability of these dates calls into question the apparent alignment of the dog domestication timings obtained from physical and genetic analyses.

Evin *et al.*'s study raises additional questions for further investigation. Their findings indicate that Pleistocene wolves were morphologically more diverse than modern wolves, although the sample size of Pleistocene wolves was small (17 skulls). If ancient wolves displayed great physical variability, this diversity was probably also present in the first domesticated canids, which are their descendants. If early dogs were already diverse, humans might have had less influence on their evolution than previously thought. Could climate, geography, or resource availability have contributed more than people to the diversification of early domesticated canids?

More research is also needed to understand the evolution of morphological and functional features in specific canid groups. For example, how have wolflike morphological features been retained in some modern dog breeds, such as the German shepherd? Are all dogs the product of human interference? Dingoes, for instance, have a narrower range of physical variability than domesticated dogs and, unlike dogs, cannot digest starch. Ethnographic and archaeological evidence reveals diversity in their relationships with people (*6*). Studying the evolution of canids such as dingoes may challenge assumptions that dog domestication was wholly human driven.

The domestication of dogs has captivated attention because of the close bonds that many humans share with dogs. Evin *et al.* prompt a rethink about the timing and development of this relationship. Their research contributes to the wider understanding of domestication as a complex, multifaceted biological and cultural process in which thousands of years of human and animal history are intertwined. □

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EVOLUTION

Sponging away phylogenomic incongruence

Genes with strong and consistent signals favor sponges as humans' most distant animal relatives

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Determining which lineage of animals is most distantly related to humans is among the most important and heated disputes in evolutionary biology. Solving this puzzle is key to revealing the biology of the ancestors of all animals, including how they transitioned from single-celled to multicellular organisms and radiated to the dazzling diversity seen today. Scientists typically decipher the evolutionary relationships between species with phylogenomics, which uses computer models of how sequences evolve to analyze large datasets of genes. On page 751 of this issue, Steenwyk and King (*1*) unexpectedly refresh this phylogenomic inference approach by using only genes with strong and consistent phylogenetic signal for either of two major competing hypotheses. This strategy reveals unprecedented phylogenomic support for sponges (phylum Porifera), filter-feeders lacking organized tissues, as the sister lineage to all other animals and may also have the potential to resolve other difficult phylogenetic problems.

A resolved animal tree of life is necessary as a scaffold upon which to infer the history of genetic and morphological changes and the emergence of key innovations that have contributed to the remarkable evolutionary success of animals. Because they are often considered among the most morphologically simple animals, sponges were for a long time uncontroversially viewed as the most distant animal relatives of humans. If this is true, complex animal-specific traits, such as the nervous system, muscles, and through-gut, are unlikely to have existed in the common ancestor of all living animals and probably first appeared after sponges and other animals diverged. However, since the first phylogenomic efforts to reconstruct the animal tree of life (*2*), a surprising alternative hypothesis that places comb jellies (phylum Ctenophora), free-swimming, gelatinous carnivores harboring complex organized tissues, as humans' most distant animal relatives has garnered substantial support (*2*–*5*). This scenario suggests either that the ancestor of all animals possessed a nervous system, muscles, and through-gut that were later lost in sponges or that the animal ancestor lacked these traits, and they later emerged independently, at least in part, in comb jellies compared with bilaterians (e.g., humans, starfish, butterflies, and snails) and cnidarians (e.g., corals and jellyfish).

For more than 15 years, there has been an intense back and forth between studies favoring either sponges or comb jellies as the sister group to other animals, and the attempt to solve this problem has driven an arms race of phylogenetic data and methods (*2–9*). The vast majority of individual phylogenomic analyses, including approaches using "standard" phylogenomic analysis and a number that made efforts to avoid phylogenetic error, have effectively always provided strong support for comb jellies as the sister to other animals. This has led a number of researchers to dismiss the older morphological placement of sponges as sister to all other animals, which was based on far fewer characters (the analyzed units of phylogenetic inference; i.e., homologous morphological traits or nucleotide or amino acid states for each species) that were more subjectively selected and classified, in favor of this new view of animal phylogeny. Contrary to this, others have argued that the recovery of comb jellies in this position is due to systematic error and that in analyses that best account for this (e.g., by sophisticated phylogenetic modeling and/or error-reducing data treatments), sponges are recovered in their traditional position or the data at least shift in this direction (*6–9*). Arguments in turn have been raised against some of the methods used to minimize systematic errors (*4*). This seems to have led to an impasse on which lineage ought to be generally accepted as the most distant animal relatives of humans. At an extreme, the debate has perhaps revealed more about the effects of phylogenetic modeling approaches, data curation, and their intersection on the results of phylogenomic analyses than about animal relationships.

Comb jellies (phylum Ctenophora) have complex organized tissues, including a nervous system, muscles, and a through-gut.

PHOTO: ALEXANDER SEMENOV/SCIENCE SOURCE

Alternative types of data have also been leveraged in the attempt to solve this recalcitrant problem. Perhaps most promising to date is an exciting gene linkage data analysis that strongly supported comb jellies as humans' most distant relatives (*5*). Although compelling and teeming with potential, it must be noted that such approaches are still in their infancy and that the best ways to identify, curate, and analyze these characters are not yet clear (*10, 11*).

The study by Steenwyk and King is thus unexpected in that it both returns to the phylogenomics approach, albeit in a refreshed context, and provides unprecedentedly strong and consistent support for sponges as the sister to all other animals. To resolve the issue of which phylum branched off first, the authors searched for strong, consistent phylogenetic signal in both a large newly constructed dataset as well as in an array of datasets previously applied to this problem. In what they term "integrative phylogenomics," they extracted and tested only genes that show strong phylogenetic signal in both concatenation and coalescence analyses (the two major approaches in phylogenomics) for either sponges or comb jellies as the sister to all other animals. In doing so and while testing a swathe of treatments to avoid common phylogenetic pitfalls, they uncovered unequivocal support across hundreds of datasets for sponges as the most distant animal relatives of humans and little or no support for comb jellies.

Why has this new method recovered such strong and consistent support for sponges as sister to other animals, whereas previous studies were stuck in a phylogenetic stalemate? A concern that sometimes arises with the use of heavily filtered phylogenetic data, such as that used by Steenwyk and King, is whether the resulting smaller datasets can still be representative of the whole genome or species or whether filtering has inadvertently selected for misleading signal. However, although using massive numbers of genes and amino acids is commonplace and even expected, in phylogenomics, large datasets also contribute to the propensity for and impact of systematic errors (*12*). Placing emphasis on dataset size may be particularly misleading for short, ancient branches, such as those deepest in the animal tree, where a much smaller subset of characters (genes and amino acids) actually harbor changes pertinent to the problem at hand. The sizeable datasets that can now be produced might arguably be best used for extracting smaller, signal-enriched, and near–error-free datasets, helping to maximize the signal-to-noise ratio and avoid systematic errors when tackling difficult phylogenetic problems. This version of phylogenomics ironically hues closer to morphological analyses by using fewer and slightly more subjectively curated characters.

Such approaches show signs of success both in the findings of Steenwyk and King and in other studies (*7, 13, 14*) and may also reduce computational requirements, which both bolsters the reproducibility and lowers the carbon footprint of phylogenomic analyses. Nevertheless, further investigation into whether Steenwyk and King's integrative phylogenomics approach might mislead inference of animal relationships may be worthwhile. It seems possible, if unlikely, that selecting for genes with strong signals in the manner applied by the authors could accidentally prioritize genes with strong signals that, whether owing to true complex history or to inference errors, are in conflict with the species tree (*15*).

Although perhaps not the final say on the animal phylogeny, Steenwyk and King's findings imply that the last common ancestor of animals most likely lacked a nervous system, through-gut, muscles, and other organized tissues and was thus morphologically simple. Their integrative phylogenomics approach offers a spark of hope that other long-standing phylogenetic problems may now prove simpler too. □

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