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## Human fist evolution: a critique

We were eager to read the manuscript entitled ‘Protective buttressing of the human fist and the evolution of hominin hands’ (Morgan and Carrier, 2013), for it potentially offered insight into our own evolution. The human hand is a complex and utilitarian anatomic structure and we have little doubt that its form has been influenced by natural selection. Sadly, we feel the authors fall short in demonstrating that the strike power of the fist was a key evolutionary force driving of the shape of the human hand. Mutations provide the raw material for evolutionary forces to act upon, and the resulting evolutionary changes can generally be explained by either selection or genetic drift (Futuyma, 1998). However, the confounding effects that result from the presence of exaptations and the difficulty in selecting traits that are discrete attributes make it risky to attribute each and every human feature to natural selection. The perils of this kind of thinking were well illustrated in the 1970s by evolutionary biologists such as R. C. Lewontin, S. J. Gould and E. O. Wilson. Morgan and Carrier claim that the evolution of the well-buttressed fist was driven by sexual selection, but provide no compelling evidence to reject the null hypothesis that this fortuitous structure was the result of either random genetic drift or exaptation (Gould and Lewontin, 1979). Is ‘protective buttressing’ even a legitimate, isolated trait? Or is it simply a tangential consequence of natural selection on other structural features – one that our species has learned to use to its advantage?

For the last 30 years, the phylogenetic comparative method has been used to ascertain the evolutionary forces on traits (Felsenstein, 1985; Harvey and Pagel, 1991). As an example of how this method is used, consider the anatomy of dolphins and sharks – both of which have a dorsal fin. Because this trait arose independently in each of these lineages, we deduce that this was the result of natural selection and that a similar driving force acted on both lineages (the need for stability, etc.). The evolution of similar traits in more than one lineage is strong evidence for natural selection. Morgan and Carrier did not show that the buttressed fist trait evolved in any other independent lineage. The ‘club trait’ has evolved several times. The dinosaur *Ankylosaurus* had a formidable club at the end of its tail and some artiodactyls have evolved parts of their heads to be used as clubs. A version slightly more similar to a fist can be seen in male kangaroos (*Macropus*), who are said to punch one another with their forelegs, but of course lack any ability to make a fist at all, buttressed or otherwise. These club-

like features may be considered functionally convergent in the very broadest of terms, but are different enough in form and function from the human fist that they cannot be considered truly analogous, much less homologous. So it appears we cannot make a convergent evolutionary argument for the selection for the well-buttressed fist in *Homo sapiens*.

Another means of inferring natural selection is to identify evidence of coevolution, or what is sometimes termed ‘an evolutionary arms race’. The traits of the signal transmission and signal reception are typically paired yet independent, and can usually only be supported by natural selection. For example, male silkmths are more attracted to chemical pheromones than to the visual cues of a female silkmth (Schneider, 1974). For this type of interaction to evolve, one expects the mechanism of pheromone release to develop at the same time as the evolution as the receptors for detecting the pheromone. The coupling of these traits is more likely under natural selection, where the signal and reception of the signal coevolve (Futuyma and Slatkin, 1983).

In the case of a fist evolving for the purpose of dominating other males, and specifically for the purpose of punching, the obvious coevolutionary response one would expect is an increased ability to withstand punches. If the body part receiving the blow was already resistant to such impact, we would expect that trait to be maintained.

According to Morgan and Carrier, it is reasonable to consider that the fist evolved for use in male–male competition, where individuals beat on each other with well-buttressed hands. A reasonable question to ask is what body part received these punches? Was it the head? The stomach? Based upon current human behavior, the head and neck area seem to be the most common areas to hit during fist fights. However, in the hominid lineage the jaw and brow features have become less pronounced in our current facial structure – which is the exact opposite of what we would expect. Specifically, over the past 500,000 years of evolution the modern human face has developed a less robust jaw and upper palate than our extant sister taxa, *Pan*, as well as our extinct cousins with non-buttressing hands. Similarly, our suborbital tori, or eyebrow ridges, have become significantly thinner and more sensitive to breakage during impact. This observation begs the question, why has the fist evolved to do damage to one’s competitors but the site of damage evolved to be less resistant to fist impact (Fig. 1)? If natural

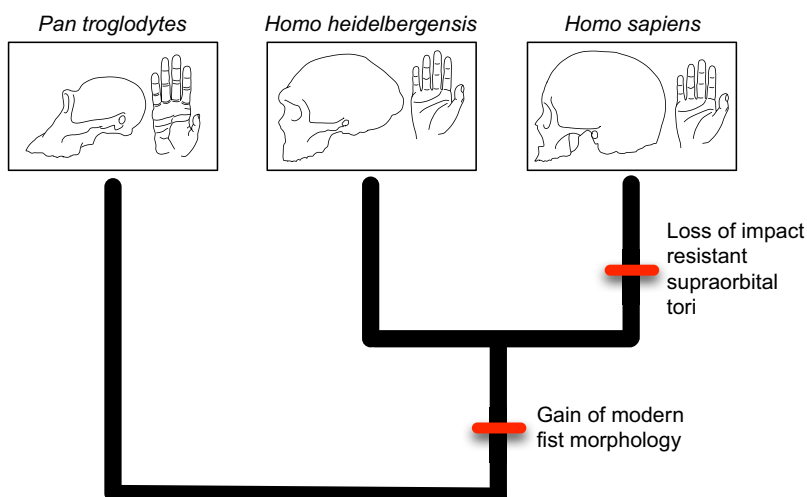


Fig. 1. The evolutionary relationship between *Pan* and two *Homo* species depicting the timing of the evolution of the human fist and the loss of the thick orbital bones around the eye (red bars). The phylogeny demonstrates the decoupling of the traits that would be expected to coevolve if Carrier and Morgan’s (Carrier and Morgan, 2013) assertions were correct.

selection favored an ability to punch, why has the recipient body part of such blows evolved in essentially the opposite direction and become more vulnerable to impact?

We think the most likely answer is that the human fist is essentially a fortuitous trait that would best be categorized as an exaptation (Gould and Lewontin, 1979). That is, a 'tag-along' trait that was not itself the target of natural selection, but came about as the result of natural selection on traits that impart fine motor skills, strong grip, the ability to use tools, etc. It is also worth noting that other extant primates are formidable fighters and have the ability to assert their dominance through use of their superior strength, sharp claws and large teeth. It is our opinion that the authors Morgan and Carrier did not adequately support their argument that the human hands 'reflect, in part, sexual selection to improve fighting performance'. The *Homo sapiens* hand may have some fighting advantages, but there is no reason to believe it is anything more than adventitious happenstance (Sober, 2006). That is, in the words of Gould and Lewontin, the well-buttressed fist is nothing more than a 'spandrel' (a phenotypic characteristic that has been co-opted for a particular use rather than a by-product of natural selection) (Gould and Lewontin, 1979).

## Response to 'Human fist evolution: a critique'

Nickle and Goncharoff (Nickle and Goncharoff, 2013) raise an interesting and, we believe, important challenge to the protective buttressing hypothesis of hominin hand evolution. If the hand of hominins evolved to be a dangerous weapon, it is reasonable to predict that the primary targets of fist strikes would have undergone coevolution resulting in increased robusticity and protective buttressing. However, Nickle and Goncharoff are wrong in their assumption that human-like hand proportions appear for the first time in the genus *Homo*. The proportions of the hand that allow modern humans to form a buttressed fist were present in the earliest hominins, at approximately the same time our lineage became habitually bipedal (reviewed in Morgan and Carrier, 2013). Because human-like hand proportions first appeared in basal hominins, it is in these species, not late archaic or modern humans, that we must look for evidence to test the hypothesis of coevolution. We believe the fossil record of basal hominins is consistent with the evolution of increased robusticity and protective buttressing of the face.

Nickle and Goncharoff are correct in stating that we 'provide no compelling evidence to reject the null hypothesis that this fortuitous structure [i.e. the hominin hand] was the result of either random genetic drift or exaptation'. In truth, hypotheses about ancient genetic drift or exaptation cannot be rejected, and Nickle and Goncharoff join us in Panglossian violation of rigorous comparative methods to test adaptive hypotheses when they propose that the proportions of the human hand are 'the result of natural selection on traits that impart fine motor skills, strong grip, the ability to use tools, etc.'. Functional hypotheses about

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the original selective value of a trait, in contrast, can effectively be rejected if the trait can be shown not to provide a performance advantage for the relevant behavior. In the case of the proportions of the human hand, performance advantages clearly exist for manual dexterity and, as indicated by the results of our study, for fighting by striking with fists. We suspect that selection for improved manual dexterity and fighting were both important. However, the protective buttressing hypothesis may provide a more compelling explanation for the specific proportions of the hand skeleton than does the manual dexterity hypothesis.

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