Dive First, Run Later? The Role of Endurance Diving in Human Evolution

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submitted: 29 October 2025; revised 12 March 2026; revised 30 May 2026; accepted: 30 May 2026

Handling Editor in Chief: Katerina Harvati

ABSTRACT

Unlike any other primate, humans are characterized by having exceptional physical stamina, as shown by our aptitude for endurance running but also for breath-hold diving underwater. Why are humans so different from other apes? Aerobic endurance and adaptation to a wide range of environments have apparently helped humans to spread globally and thrive from seacoasts to high altitudes, while our closest living relatives are mostly confined to tropical forests. This wide dispersal likely started—or intensified—with early *Homo* populations around 3 to 2 million years ago (Ma). A long-standing hypothesis to explain our stamina is that an ancestral *Homo* population evolved as persistence-hunting endurance runners, like todays San and Rarámuri populations, in response to increasingly dry conditions in Africa after ~3–2 Ma. However, this hypothesis does not address the origin of the remarkable breath-hold diving capacity displayed by many human populations today, such as the Sama-Bajau and the Ama divers, or our ability to adapt to different environments. To fill this gap, we use comparative physiology and anatomy, paleoecology, and paleoanthropology to explore how insights in our breath-hold diving ability may help us understand how humans could have developed endurance running and a remarkable tolerance of life at high altitude. Based on these insights, we propose an alternative hypothesis, 'dive first, run later': a coastal *Homo* population expanded its niche to include foraging for aquatic resources by breath-hold diving, thereby evolving 'heavy bones' (increased bone mass) to provide neutral buoyancy at foraging depth. The enhanced cardiorespiratory functions that also evolved for efficient underwater foraging could later be co-opted for endurance running by more gracile and light-boned *Homo*, as well as for life at high-altitude. Testing hypotheses is outside the scope of this paper, but we do provide examples of possible future research approaches by discussing an array of features that leave traces in the skeleton, and have functional implications for endurance diving as well as running. Our more extensive interpretations of their functionality provide nuclei for further research to ultimately allow balanced evaluation of the hypotheses. We conclude that when studying the origin of human endurance and the evolutionary history of the *Homo sapiens* lineage, it is relevant and imperative to take not only endurance running but also endurance diving into account.

INTRODUCTION: WHY ARE HUMANS SO DIFFERENT FROM OTHER APES?

Humans (*H. sapiens*) last shared a common ancestor with our closest living relatives, chimpanzees and bonobos, at some time between ~8–6 Ma (Shao et al. 2023; Suntsova and Buzdin, 2020). We are genetically very similar to these African apes, yet differ greatly in morphology, physiology, and behavior (Pollen et al. 2023; Vail et al. 2023). Not only do we walk upright and speak, but we are also characterized by having exceptional stamina and aerobic endurance, as shown by our aptitude for endurance running (Bramble and Lieberman 2004; Carrier 1984; Morin and Winterhalder 2024). Moreover, unlike any other primate we have a remarkable ability for long-distance swimming (Knechtle et al. 2020), and notably for breath-hold diving underwater, as practiced by recreational freedivers, by marine hunter-gatherers such as the Sama-Bajau in southeast Asia (Figure 1; Schagatay et al. 2011) and by competitive freedivers (Schagatay 2009, 2010, 2011; McKnight et al. 2021). Humans have a superior ability for aerobic endurance compared to other apes (Shave et al. 2019), as indicated by our efficient breathing and relatively large aorta and cardiac output (Ríos et



Figure 1. Sama-Bajau freedivers spearfishing and collecting seafood in coral reef areas in Indonesia and The Philippines. The Bajau swim down and along the bottom, and may hold the coral to remain still when waiting for fish to harpoon (photos by Erika Schagatay and Erik Abrahamsson).

al. 2023). Aerobic endurance and tolerance to environmental extremes have helped humans to spread globally and thrive from seacoasts to high altitudes and from deserts to the poles—while other apes are mostly confined to tropical forests. This global dispersal and colonization of different environments likely first started sometime around or even before 2 Ma, as suggested by finds of hominin fossils and tools not just in Africa but also across Eurasia (Barash et al. 2022; Curran et al. 2025). The big question is: why is *H. sapiens* so different from other apes? When, where, why, and how did a hominin population in our lineage first evolve our exceptional aerobic endurance, and how would this have influenced human evolution and occupation of such a broad range of environments?

Aerobic endurance can be defined as the ability to exercise at moderate intensity for extended periods of time, with the cardiorespiratory system efficiently supplying oxygen to working muscles for continuous sustainable aerobic work, without accumulating anaerobic byproducts such as lactate[1]. Most body cells, not only working muscle, produce lactate even when oxygen is available. At the same time, other tissues act as a 'sink' and take up lactate from the blood to either oxidate it as fuel—or produce new glucose (liver, kidneys). The level of blood lactate is thus a balance between its production and removal. When lactate production in muscle increases due to increased work, its removal via the 'lactate shuttle' will also increase, to keep up as long as possible, but with elevated work rate lactate will eventually start accumulating (Brooks et al. 2002). If oxygen delivery is not sufficient for the work done, a greater extent of anaerobic metabolism is needed, and when its by-products cannot be removed in the pace produced, their accumulation will lead to fatigue and eventually to an inability to move. During any endurance activity it is therefore crucial to keep work below the 'lactate threshold' to be able to sustain it, without having to stop to rest, an ability which appears to be superior in humans among apes.

A long-standing hypothesis to explain the modern human aerobic endurance is that—in response to increasingly dry and open environments in Africa after 3 to 2 Ma—an early *Homo* population evolved to become persistence hunters using long-distance endurance running to run down prey during the hottest hours of the day; this was seen as an important step in becoming more carnivorous (Bramble and Lieberman 2004; Carrier 1984). The hypothesis of *Homo* and notably *Homo erectus sensu lato*[2] (hereafter: *H. erectus*) evolving between 3–2 Ma as a meat-chasing endurance runner has become popular and is often cited, for instance in association with evolution of increased brain size facilitated by increased meat eating (Glaub and Hall 2017; Okerblom et al. 2018; Pontzer 2017). However, it was recently established that there is no sustained increase in zooarchaeological evidence of terrestrial mammal butchery sites after the appearance of *H. erectus* in the fossil record ~2 Ma (Barr et al. 2022), contrary to expectations based on the persistence hunting hypothesis. While this hypothesis

has also attracted criticism because of the relatively scarce ethnographic evidence for persistence hunting in *H. sapiens* (Halsey and Bryce 2021; Pickering and Bunn 2007), recent reviews of the ethnographic record do support the occurrence of persistence hunting by modern humans e.g., the San in southern Africa and the Rarámuri (or Tarahumara) in Mexico (Brill et al. 2024; Morin and Winterhalder 2024; see also Hora et al. 2025).

Importantly, the fact that *H. sapiens* is capable of endurance running and persistence hunting today does not necessarily imply that our remarkable aerobic endurance evolved because our ancestors started running after prey. As Gould and Vrba (1982) pointed out, current utility carries no automatic implication about historical origin. A recent study demonstrated that not only running but also walking, climbing, and diving (i.e., intentional sub-aquatic locomotion) are important means of locomotion used in modern human foraging (Brill et al. 2024). This systematic analysis of cross-cultural variation in locomotion in 53 hunter–gatherer societies revealed a high level of locomotor versatility among hunter–gatherers, showing that proficiency of running, climbing, swimming, and diving is found in societies across the geographical and ecological breadth of the sample. While running occurred in all 53 groups studied, endurance running for persistence hunting was present in only 17 (32%) of these. Interestingly, swimming was present in 45 (77%) and diving in 23 (39%) of these societies (Brill et al. 2024). In both marine and freshwater systems, purposeful breath-hold diving for foraging was common. This indicates that while modern humans are clearly terrestrial mammals, they can also operate efficiently in and under water. So far, the origin of the remarkable human diving capacity, and its possible role in the evolution of aerobic endurance in our lineage, has not yet been explained.

Breath-hold diving, also called freediving, can be defined as periods of underwater activity during voluntary breath-holding (apnea), relying on body oxygen stores until resurfacing, thus diving without carrying any external air supply. In this paper we explore how insights into modern human freediving ability and the underlying physiology may help us understand how humans developed not only breath-hold diving and endurance running, but also a remarkable tolerance of life at high altitude, where low oxygen availability puts high demands on the cardiorespiratory system. Based on this exploration we formulate new hypotheses for the evolution of human endurance, which address persistence hunting by endurance running as well as underwater foraging by breath-hold diving. We do not aim to test these hypotheses; this would require a major research effort by an interdisciplinary team and is outside the scope of our paper. Our aims are: 1) to provide a wider perspective—as food for thought—on the evolution of human endurance, based on an exploration of the modern human breath-hold diving capacity; 2) to formulate hypotheses on the relevance and potential role of breath-hold diving in human evolution; and, 3) to provide examples of possible future research approaches to test and refine or reject these hypotheses.

THE PHYSIOLOGICAL BACKGROUND TO BREATH-HOLD DIVING

Breath-hold diving species have evolved in nearly every order of air breathers (Butler and Jones 1997), and insights in their adaptations can help understand some human characteristics. A major challenge during diving for all air-breathers, including human breath-hold divers, is the limited access to oxygen when underwater, which makes it necessary to develop means to rely on intermittent breathing. This requires: 1) increasing body oxygen storage before diving, involving large storage capacity and efficient breathing when at the surface (high $\dot{V}O_{2max}$: maximum oxygen uptake), 2) limiting oxygen usage during diving (low $\dot{V}O_{2min}$), and 3) tolerance to hypoxia (Schagatay 2009). Oxygen is stored not only in the lungs, but also in the blood and tissues (Schagatay 2009). Diving mammals are known for their extreme respiratory capacity and enhanced ability to store oxygen, and for having a strong 'mammalian diving response' that conserves oxygen, all of which have co-evolved to enable underwater foraging (Fahlman et al. 2023; Kooyman 1989; Ponganis 2015). Blood oxygen storage can be increased by elevated levels of circulating red blood cells containing the oxygen-binding hemoglobin, and in many divers the blood can be boosted with red cells by having an extra supply of red cells in the spleen that can be recruited during diving (Hurford et al. 1990; 1996). To conserve oxygen during diving, the mammalian diving response minimizes oxygen usage by constricting selected blood vessels and supplying mainly the heart and brain with oxygen, as they are most sensitive to hypoxia (Scholander 1940, 1963). With a more limited circulation to supply, the heart rate drops, which reduces the oxygen consumption of the heart and contributes to saving oxygen (Elsner 1966). This system efficiently conserves oxygen and prolongs dive duration. Working muscle is also to some extent prioritized with blood flow (Butler 1988), however in diving mammals the local oxygen storage is enhanced through increased quantities of oxygen-binding myoglobin (He et al. 2021; Mirceta et al. 2019).

The mammalian diving response is present in humans as well, and it efficiently reduces heart rate and oxygen consumption during diving (Andersson and Schagatay 1998; Schagatay and Andersson 1998; Figure 2). The diving response is present to some extent in all studied mammals but clearly correlates with their involvement in diving; the human response is in the range of otters and beavers, while pigs trained to dive have a less pronounced response (Schagatay 1996). In human freedivers, just as in seals, increasing the amount of circulating red blood cells by spleen contraction enables larger available blood oxygen stores, which prolongs dives (Schagatay et al. 2001). Moreover, local oxygen storage in trained human freedivers' muscles is enhanced through increased quantities of myoglobin (Elia et al. 2019).

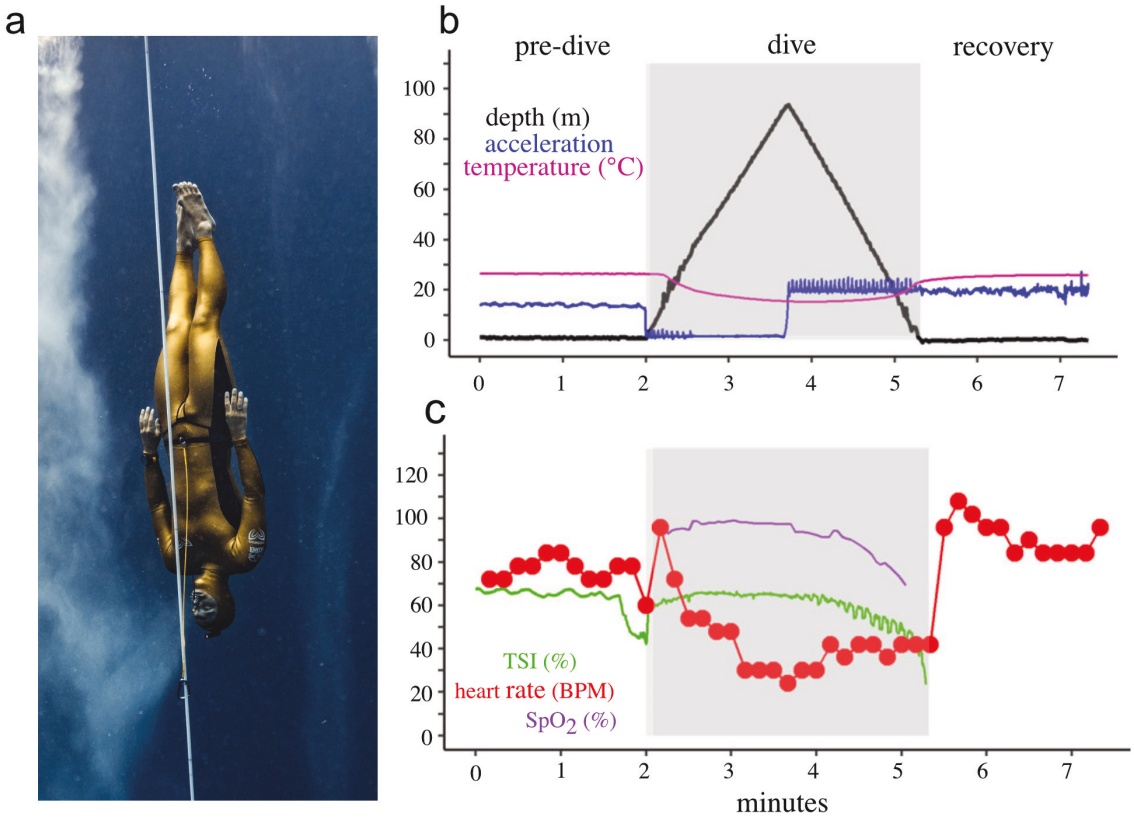
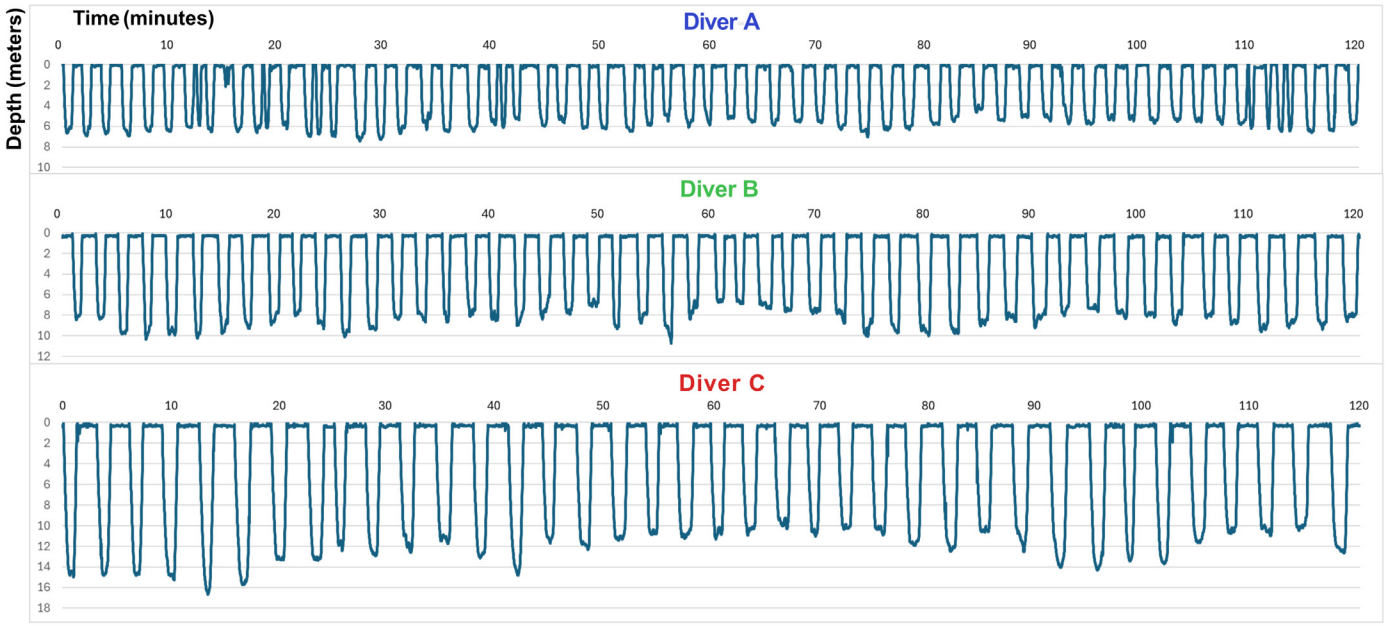


Figure 2. a) Competition freediver Alexey Molchanov freefalling during a deep dive without fins (photo courtesy of Daan Verhoeven); b) Logged data from a trained competition freediver diving to 97m and back in ~3.5 minutes, showing depth profile, swimming movements, and water temperature. Note the free fall phase without swimming on the way down from ~30m to 97m; c) The diving response reduces heart rate to ~ 30BPM during the free fall, and it rises to ~ 40BPM during swimming up against negative buoyancy. Cerebral oxygenation shown via Total Saturation Index (TSI), heart rate (BPM: beats per minute) and arterial oxygen saturation (SpO_2) during the dive. (b and c, reproduced parts of Figure 2 in McKnight et al. 2021).

MAXIMAL HUMAN DIVING CAPACITY VERSUS ENDURANCE DIVING FOR FOOD

Human record freediving achievements are striking, and competitions are regularly held in a number of disciplines aiming for maximal duration, distance, or depth reached on one breath (for review see Schagatay 2009, 2010, 2011). The current record in underwater breath-hold duration ('static apnea') is 11 min., 35 sec.; records in swimming dives achieved without the use of fins are 250m for horizontal diving ('dynamic apnea no fins') and 103m of depth ('constant weight no fins') reached on one breath of air (www.aidainternational.org). These diving feats are far beyond the capacities of any studied terrestrial mammal (Fahlman and Schagatay 2014). In trained human freedivers, increased oxygen storage by having large lungs (Rahn and Yokoyama 1965; Schagatay et al. 2012) and a large and contractile spleen (Hurford et al. 1990; Schagatay et al. 2012), together with an enhanced diving response (Schagatay and Andersson 1998), extends their 'aerobic dive limit' (ADL). The ADL refers to the maximum time an air-breathing diver can stay submerged based on mainly aerobic metabolism—thus prior to elevation of anaerobic metabolism to the level leading to lactate accumulation (Butler 2006; also referred to as 'diving lactate threshold'). Should the ADL be surpassed by the diver, lactate will accumulate, requiring a long period of recovery breathing at the surface before diving can be resumed (Schagatay 2009). While the ADL is prolonged in competition divers, they may fully explore also the anaerobic capacity to produce a single maximal dive, leading to high levels of lactate accumulating in the blood (Schagatay 2011a). This is fine for competition divers, as afterwards they may take extended periods to recover (Schagatay 2010; Rodriguez-Zamora et al. 2018). However, to make maximal dives would be disadvantageous for foragers who need to minimize recovery time at the surface (Schagatay 2014), as will be explained below. For them, the maximal dive duration will only provide some reserve capacity in an emergency.

Fortunately, a capacity to make long-duration dives is not necessary for humans to successfully forage underwater (Schagatay et al. 2011). Instead, for foraging to be efficient, subsistence freediving relies on what we call 'endurance diving;' short-duration dives that continuously alternate with surface breathing intervals at a constant



Diver A	Dive (s)	Interval (s)	% submersed	Depth (m)
Mean	51.8	59.3	46.6	6.2
SD	10.5	20.0		0.6

Diver B	Dive (s)	Interval (s)	% submersed	Depth (m)
	64.7	80.8	44.5	8.8
	10.1	10.2		0.9

Diver C	Dive (s)	Interval (s)	% submersed	Depth (m)
	83.0	108.6	43.3	12.6
	8.0	12.1		1.7

Figure 3. Recordings of depth-time profiles across two working hours by three female Ama divers (aged 40–45 years) during 'endurance diving;' repeated dives with short breathing pauses at a very regular pace. Deeper diving requires longer dives, as part of the dive duration involves swimming down and up, which in turn prolongs recovery intervals even more, resulting in a lower percentage of the working time spent submersed. ***Diver A*** *makes 65 shallow dives spending 47% of the working time submersed.* ***Diver B*** *makes 50 dives to a medium depth spending 45% of the working time submersed.* ***Diver C*** *makes 38 deeper dives spending 43% of the working time submersed (see detailed metrics in figure). Original data from Schagatay et al. (2011).*

pace over a long period of time. Such dives must remain within the ADL and thus must be mainly metabolically aerobic, keeping the arterial oxygen saturation high, generally above 90% (ES observations). During normal constant breathing, arterial oxygen saturation is kept at around 98%, and the lowest tolerable level to stay conscious is just above 50%—under which the human oxygen-craving brains are normally triggered to shut down and fainting occurs. In trained competitive freedivers who do single maximal effort dives, the arterial oxygen saturation can drop to values lower than 50% in the conscious diver (McKnight et al. 2021; Mulder et al. 2021), and safety divers are ready to assist should a diver surpass individual limits and faint from lack of oxygen (hypoxia).

While the current freediving world records reveal human maximal capacity, such single, long, partly anaerobic dives are thus not useful for a forager as they require recovery periods much longer than the dive (Schagatay 2009). Instead, during foraging it is essential to recover quickly to spend maximal total time foraging underwater where the resources are located. This can be achieved by conducting a series of short aerobic dives requiring only short recovery intervals breathing at the surface (Schagatay 2014). By keeping dives short, the risk of fainting from hypoxia is also minimized. Endurance diving for food is still practiced by several extant human populations such as the Ama in Japan who can dive for hours daily at a dive-to-breathing interval duration of 1:1 in shallow dives (Schagatay et al. 2011; Figure 3). Similar methods are used by Haenyo in Korea (Lee et al. 2016; Rahn and Yokoyama 1965), Polynesian divers in Tonga and Tuamotu (Malm 1999), Moken in Thailand and Myanmar, Orang (Suku) Laut in Singapore, Malaysia, and Indonesian Riau Islands, and Sama-Bajau in Indonesia, Malaysia, the Philippines, and Brunei (Abrahamsson and Schagatay 2014; Bellina et al. 2021; Chou et al. 2016; Kusuma et al 2017; Rodriguez et al. 2022; Schagatay et al. 2011). The three latter groups are often referred to as Sea Nomads and while most are no longer nomadic, many still live as marine hunter-gatherers (Bellina et al. 2021).

UNDERWATER FORAGING BY ENDURANCE DIVING – HOW DOES IT WORK?

A good example of efficient marine hunter-gathering endurance divers are the Sama-Bajau (hereafter, Bajau; see Figure 1). When endurance diving, they make extended series of short dives with short breathing intervals, to a maximum depth of about 20m. The dives are essentially aerobic, and the foraging work can be done steady-state across extended periods as their efficient diving response limits oxygen usage to a minimum (Schagatay 1996). In ad-

dition, their large spleens (Ilardo et al. 2018) and efficient breathing capacity will increase their oxygen stores between dives, and thereby extend their aerobic diving limit (ADL). During shallow diving to 5–7m, their dives lasting ~30s are interspersed with surface intervals of just ~20s, i.e. they can spend 60% of the time underwater (Schagatay et al. 2011). The working time spent immersed is typically between 2 and 6 hours per day, which usually yields sufficient catch (ES observations). However, the Bajau can do up to 9 hours of immersed work daily, and with a submerged diving time of 60% of the total working time, the maximal amount of usable time for underwater foraging is up to 5 hours per day (Schagatay et al. 2011). To allow rapid recovery, endurance divers must keep repeated dives short, but with deeper diving, longer dives are required as more time will be used to swim to and from the bottom, and sufficient time must remain for foraging at depth. In dives to 10m of depth the Bajau dives lasted ~42s with the same duration of recovery intervals, thus 50% of the immersed working time was spent underwater (Abrahamsson and Schagatay 2014). The consequence of depth on dive and interval duration can be seen in the Ama divers as well, where the percentage of time spent underwater is reduced with increased depth (see Figure 3). Among the Bajau, most dives are within 1 minute duration, and maximal single dive durations, for example to tie the boat to the reef, did not exceed 3 minutes (ES observations). Often reproduced accounts of much longer duration dives—of up to 13 minutes—are likely based on misconceptions and not on direct observations. Other anecdotal reports that they walk on the seafloor when fishing have never been confirmed when diving with them during our many visits (ES observations); they clearly swim efficiently or stay on the bottom to ambush fish, as described below.

The traditional Bajau diving is done without using any modern freediving equipment, thus without nose clip, weights, fins, or wetsuit. Only a few generations ago did they start using goggles. Children still often dive without goggles, contributing to the catch from age 4–5 years. While in general human underwater vision is poor, the Bajau appeared to see quite well underwater without goggles, enough to catch food (Schagatay 1996). It was later shown in the Moken, who use similar diving methods, that they have improved underwater vision via heavy accommodation and concurrent pupil constriction (Gislén et al. 2003). To efficiently dive down without weights, the Bajau typically descend feet first after a powerful swim stroke that elevates the upper chest above the surface; the weight of the upper body will then submerge the entire body (ES observations). In this way the downward pointing nostrils will not flood with water. When the Bajau then turn to swim downwards, they close off the nose efficiently by using the back of the tongue to elevate the soft palate to keep nasal airways closed from inside (Figure 4). While descending, they equalize pressure in their middle ears hands-free, by using muscles of tongue, soft palate and throat to tense the soft palate and open the Eustachian tube between nasal cavity and middle ear (see Figure 4). Equalization of all body air spaces is a critical element of breath-hold diving, as the air is compressed by the increased hydrostatic pressure. The effect is described by Boyle's law, where Pressure x Volume is Constant (PxV=C). As 10m of water exerts the same pressure as 1 atmosphere (atm) of air, the effect is most notable in the upper 10m of the water column where the pressure doubles from 1atm to 2atm, and air volumes must shrink to half (see Figure 6 below). At greater depths the rate of pressure change is slower, but if equalization fails, the diver must stop the descent.

Once underwater, the Bajau swim using alternating circular leg strokes in a propeller-like manner, while keeping the hands free for foraging (ES observations). This 'propeller stroke' is very energy efficient and can move them in every direction with precision, unlike the strokes used in competitive swimming and diving. The Bajau have unusually big feet that make their swimming efficient without fins (ES observations). Even without weights they can remain submerged at foraging depth without any downswimming effort, due to compression of the lungs by the hydrostatic pressure (see Figure 1 and Figure 6 below). These divers have large lungs but do not usually inhale fully for shallow diving. If necessary to remain submerged at very shallow depths, they may exhale to reduce buoyancy (ES observations). Common foraging methods among the Bajau are spearfishing using a wooden rubber-sling speargun for coral reef fish (e.g., parrotfish, grouper, triggerfish) and nearshore pelagic fish (e.g., jackfish, barracuda), when they often swim along or remain at the bottom to ambush fish. They also routinely collect seafood from the seabed including molluscs (e.g., sea snails, clams, octopi), echinoderms (e.g., sea cucumbers, sea urchins), crustaceans (e.g., crabs, langoustes, lobsters), and various taxa of sea worms and algae. Turtles, birds, and marine mammals are sometimes hunted, and large marine mammals may occasionally be scavenged. Both men and women dive, including young children and the elderly, with the men mostly focusing on spearfishing and women and children often on collecting, but with no strict division of labor (see Figure 1). There are no observed physiological sex differences in their diving performance, and the roles seem to be mainly traditional in nature—just as among the Ama, where women do most of the diving for socio-economic reasons (Abrahamsson and Schagatay 2014; Holm et al. 1998; Schagatay et al. 2011). Many Bajau divers in their 7th–8th decades are still contributing actively to the family economy, just as the Ama divers do (Rahn and Yokoyama 1965). Underwater foraging in this way yields enough high-quality seafood for daily sustenance, while working only part of the day; in good conditions 2–3 h per day (Abrahamsson and Schagatay 2014). The diversity of easily accessible marine resources on shallow coral reefs is striking; Malm (1999) documented the gathering of more than 230 folk taxa of marine invertebrates and seaweeds for some 50 different purposes in Tonga.

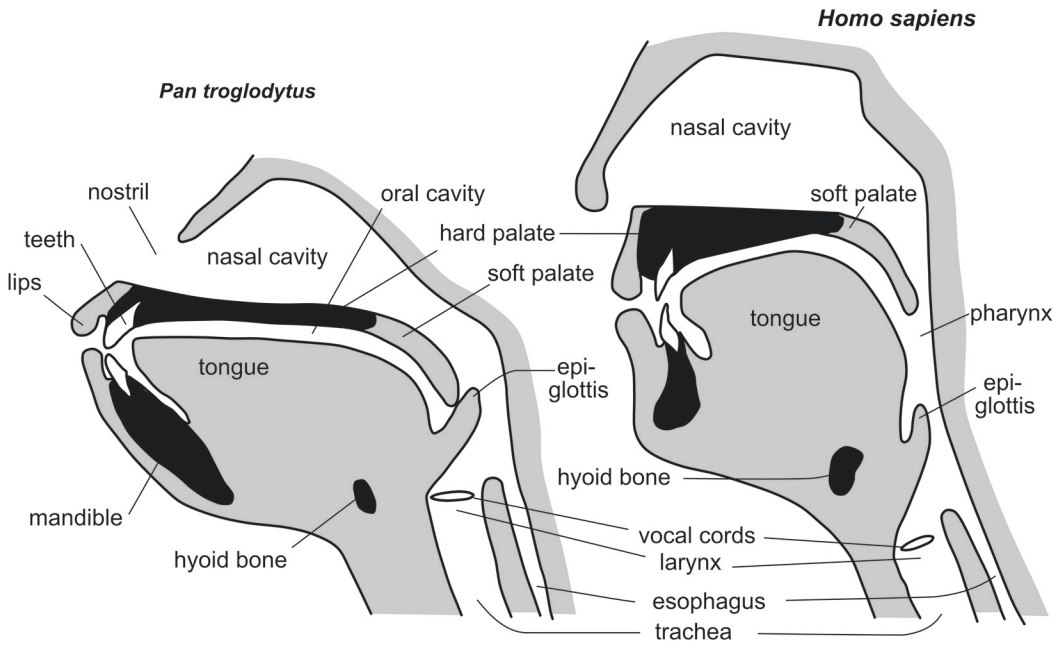


Figure 4. Mid-sagittal section of chimpanzee and adult human head (adapted from Vaneechoute et al. 2011). Note the protruding human nose with downward pointing nostrils creating an airlock, a short, arched palate, a large mobile tongue in contact with the pharynx, and a descended larynx creating a distance between the soft palate and epiglottis. In contrast, in chimpanzees and in human infants the larynx is situated higher up and the soft palate and epiglottis overlap. Equalization of the middle ears is a critical element of breath-hold diving, as all air spaces in the body (middle ear, sinuses, airways, and lungs) are compressed with increasing depth and eardrums may rupture without active equalization. Freedivers may use different equalization techniques depending on the diving depth, e.g., hands free equalization, Valsalva, Frenzel, mouthfill. These techniques involve voluntary closure of the nose and/or mouth airway and require fine control of the tongue muscles, epiglottis, and muscles of the soft palate and throat. The diver learns to voluntarily lower or raise the soft palate from its neutral position to efficiently equalize pressure of the middle ear. During swallowing, the epiglottis automatically closes the trachea to prevent food and liquids from entering the lungs, but a freediver can also voluntarily control the epiglottis to open and actively overfill the lungs by pumping down air and thereby allow equalization at greater depths (Örnhagen et al. 1998). When reaching an individual depth limit, set by the starting lung volume and lung flexibility, the diver has to stop the descent, or damage (barotrauma) of ears, lungs or airways will occur due to the pressure.

COMPARATIVE ASPECTS OF HUMAN DIVING

Adaptation to underwater foraging in mammals is most extreme in deep diving seals and whales, but evident also in many less-studied semi-aquatic groups. How well does the human diving ability compare with that of other diving mammals? Mammalian breath-hold divers can be specialized in deep diving, regularly diving to 200m and having the ability of reaching >1000m of depth (e.g., sperm whales; Irvine et al. 2017). While these extreme divers have been the focus of many physiologists' studies, they are not typical of diving mammals (e.g., Kooyman 1989); most other diving mammals do not have these abilities. A much larger number of species of mammalian divers are found in the category 'moderate divers,' defined by regularly diving to 100m but with the ability to reach 200m occasionally; or in the category 'shallow divers', with a typical range within the first 50m of depth and occasionally reaching maximum depths of ~100m (Fahlman and Schagatay 2014). This shallow diver group contains semi-aquatic taxa including e.g., beaver (Castoridae), river and sea otters (Lutrinae), hippos (Hippopotamidae), many seal species (Pinnipedia), as well as the fully aquatic sea cows (Sirenia; Wall 1983). Humans fit well among other shallow diving mammals—they have a regular depth range of 20m for foraging, can spend 50–60% of the foraging time underwater, and have the ability to make maximum single dives of around 100m depth (Fahlman and Schagatay 2014). The diving pattern of endurance divers such as the Bajau, together with the extreme feats of competitive freedivers, reveals a striking similarity with the bimodal diving range of the sea otter (*Enhydra lutris;* Schagatay 2011b). This semi-aquatic mammal typically makes short dives to <20m spending 60% of the time underwater, and only in very rare cases dives to ~100m (Bodkin et al. 2004). So how did this human ability to dive like a semi-aquatic mammal, apparently unique for a terrestrial mammal, evolve?

ENDURANCE DIVING REQUIRES ENHANCED AEROBIC CAPACITY

In endurance diving it is crucial to sense exactly for how long the stored oxygen will last; overreaching by just a few

seconds involves accumulation of byproducts of anaerobic metabolism including lactate, and results in having to spend a longer time recovering at the surface to get rid of it. Once at the surface between dives, an efficient ventilation and oxygen transport to oxygen-craving organs is key (high $\dot{V}O_{2max}$). An absolute ability to regulate breathing across conditions from voluntary apnea to maximal oxygen loading is central in all diving mammals, including human endurance divers. When you breathe only half of the time, you must breathe twice as much when you breathe. Diving requires fine-tuned respiratory regulation that is achieved mainly via sensing of high carbon dioxide levels in the blood (hypercapnia), which results in an urge to breathe before O_2 levels drop to alarmingly low levels (Schagatay 2009). Sensing oxygen levels, which start dropping later, would lead to a later signal to breathe and thus a too late warning. Trained competition divers can sustain elevated carbon dioxide levels and likely better sense low oxygen levels (Hawkes and Kendall-Bar 2025; McKnight et al. 2025; Schagatay 2009). During the dive, competition freedivers can override the urge to breathe to prolong their dives beyond the ADL, thereby exposing themselves to low oxygen levels (30–40%; McKnight et al. 2021; Mulder et al. 2021) that they to some degree learn to tolerate. For an untrained diver such critically low oxygen levels could lead to sudden hypoxic syncope ('blackout'), during which an unassisted diver will likely drown. To avoid such risk, and to remain within the ADL, endurance divers like the Bajau and Ama must obey the urge to breathe—hence the short dives of 30–60s—to be ready for the next dive after only a short surface interval. Enhanced fitness involving both respiratory and cardiovascular systems allowing the diver to remain aerobic, and a capacity for pacing the activity under the lactate threshold, are essential requirements not only for endurance running but also for endurance diving.

Endurance diving also requires a way of keeping work rate at its minimum; it is the economic use of the oxygen stores, and the rapid shifts between attaining $\dot{V}O_{2max}$ and $\dot{V}O_{2min,}$ that enable the diver to work at an even pace for long periods despite intermittent breathing. High $\dot{V}O_{2max}$ is required when filling up oxygen stores, and a low $\dot{V}O_{2min}$ is necessary during the dives. The latter is achieved by good work economy and a strong diving response prioritizing blood flow to the most oxygen-craving organs (heart, brain, working muscles) and thereby minimizing oxygen consumption during diving. By these means endurance divers can conduct repeated breath-hold diving at steady state for hours, spending about half of that time underwater, without ever developing alarming hypoxia or accumulating lactate. This endurance diving capacity thus shares features—like improved cardiorespiratory fitness, efficient mouth breathing, and fine regulation of blood flow and lactate levels—with endurance running.

WHAT IS THE ORIGIN OF THE EXCEPTIONAL HUMAN AEROBIC ENDURANCE?

The abilities to endurance run and endurance dive have evolved at some time(s), in response to ecological pressures. But which came first? So far, besides persistence hunting through endurance running (Carrier 1984), no alternative or complementary hypotheses to explain our remarkable aerobic endurance have been brought forward. We believe this has resulted in a long-standing bias in research focus—the field of paleoanthropology can draw on numerous 'endurance running papers' with data and interpretations produced over the past 40 years (e.g., Bramble and Lieberman 2004; Carrier 1984; Hatala et al. 2013; Hora et al. 2020; 2025; Lieberman 2020; Marino et al. 2022; Morin and Winterhalder 2024; Ruby et al. 2015; Ruxton and Wilkinson 2011; Steudel-Numbers and Wall-Scheffler 2009) without much consideration for possible alternative locomotion and subsistence activities. What if endurance diving for food brought about some of the evolutionary changes that have so far been linked only to endurance running and persistence hunting? There would likely have been several steps of evolution, with each new feature beneficial, before endurance running efficient enough to catch big game would emerge. In contrast to hunting terrestrial prey, it is remarkably easy to get access to food by shallow breath-hold diving (Abrahamsson and Schagatay 2014). This aquatic food is of high quality as it contains not only protein, fat, and carbohydrates but is also, unlike food from the terrestrial food chain, rich in long-chain polyunsaturated fatty acids and micronutrients needed for brain development (Colombo et al. 2017; Cunnane and Stewart 2010; Hixson et al. 2015; Joordens et al. 2014; Kyriacou et al. 2016). We therefore contend that it is time to take not only endurance running, but also endurance diving into account when studying the origin of human aerobic endurance.

The question then is, when and why did hominins start to engage in these two activities, and in what order? Did our ancestors start endurance running for persistence hunting around 2 Ma, and was endurance diving a relatively late development that evolved only in later *Homo* species like *H. sapiens*? Or was it the other way around, i.e., was early *Homo* adaptation to endurance diving the origin of aerobic running endurance in *H. sapiens*? In other words, could it be that the endurance running capacity of *H. sapiens* is an 'exaptation' (Gould and Vrba 1982), made possible thanks to an increased aerobic endurance that evolved due to shallow-water endurance diving for food? The concept of exaptation is defined as a character previously shaped by natural selection for a particular function—an adaptation—that is co-opted for a new use (Gould and Vrba 1982). Exaptation is important to consider because it encourages researchers, who study the origin of a certain character or feature in the hominin fossil record, to look beyond its current functionality and explore how it could result from possible earlier adaptations to very different evolutionary pressures. We propose the idea that the enhanced respiratory and cardiovascular capacity that originally evolved for endurance diving could have been instrumental in initiating the development of our remarkable endurance running capacity.

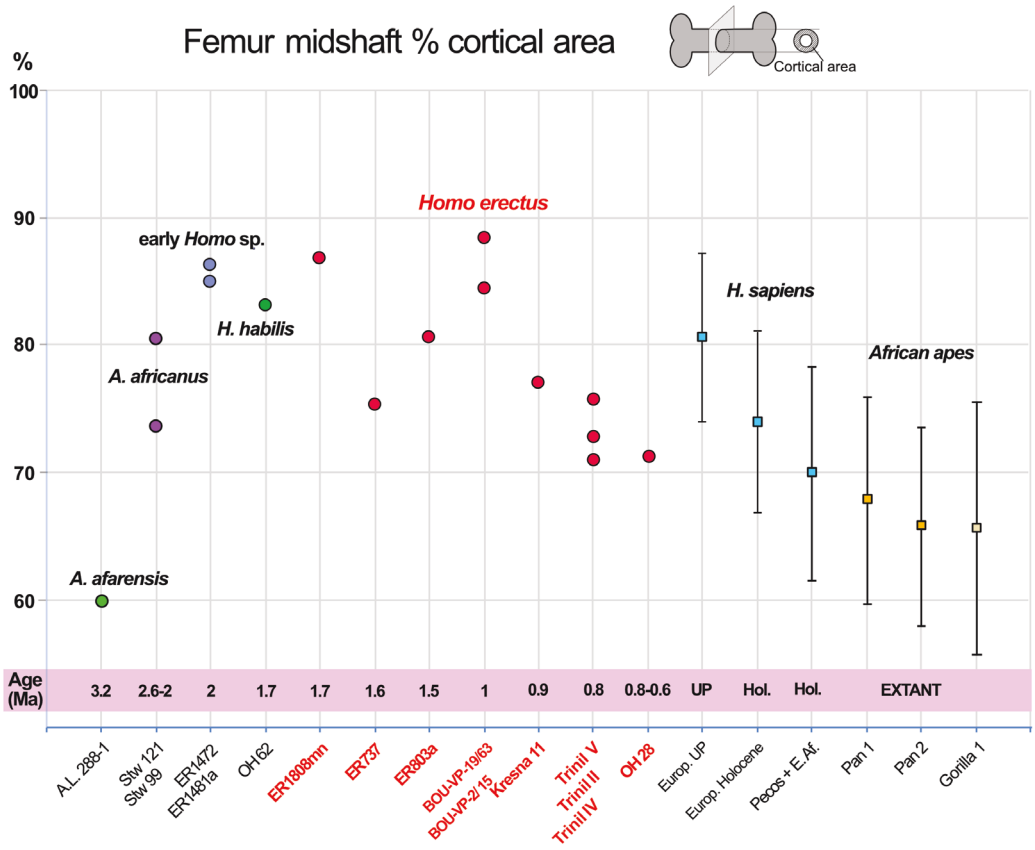


Figure 5. Percentages of cortical area at midshaft of femora from hominin species (individual fossil specimens) as well as from H. sapiens, Pan troglodytes, *and* Gorilla gorilla *(multiple specimens). The full dataset including data sources is presented in SI Table S1 (courtesy of Christopher Ruff).*

'HEAVY BONES' AND THEIR FUNCTIONAL INTERPRETATIONS

To assess the merit of this idea, we first consider skeletal bone mass, which is an important factor in both running and diving. Compared to extant chimpanzees, gorillas, modern humans, and extinct *Australopithecus afarensis*, many early to late Pleistocene *Homo* species appear to have had a heavy skeleton with limb bones with a relatively thick cortex and small medullar cavity (Ruff et al. 1993; 2016; Trinkaus and Ruff 2012; Supplementary Information (SI) Table S1; Figure 5). Moreover, the 'robust' hominins *Paranthropus boisei* and *P. robustus* are also characterized by having high bone mass (Ruff et al. 1999). The ten *H. erectus* fossils featured in Figure 5 show a range of femoral midshaft cortical area values between 71% and 89%, compared to 62–82% in Holocene humans. The data could be interpreted as reflecting the typical range of the widespread long-lasting species *H. erectus*. However, as these data points represent snapshots in time and space over a million-year period, it is possible that we are actually looking at representatives of seven different populations living in certain places at certain times (i.e., paleodemes), that each have a different bone mass range. Similarly, the oldest *H. erectus* cranial fossils from Java —with an estimated age of 1.3–1.0 Ma—reveal remarkably thick skull bones (Westaway et al. 2015) implying a high total bone mass, while cranial bones of some other *H. erectus* populations are not as thick. Moreover, due to the incomplete and biased nature of the fossil record (Barr and Wood 2022), we face the fact that such *H. erectus* populations (from three areas in Africa and one in Asia) are just a fraction of the total number that must have existed between ~2 and 0.11 Ma. Many populations remain completely unknown. Despite these limitations of the hominin fossil record, available evidence suggests that certain early *Homo* populations (e.g., early *Homo* sp. from the Turkana Basin, earliest *H. erectus* from Sangiran, and *H. erectus* from Bouri) did have a remarkably thick bone cortex (Trinkaus and Ruff 2012; Westaway et al. 2015; Ruff personal communication; see Table S1 and Figure 5). This is also the case for Upper Pleistocene *H. sapiens*, but not for Holocene and later humans.

The data presented in Figure 5 indicate that after ~3 Ma, hominin limb bone mass was relatively high compared to earlier (pre-3 Ma) and later (Holocene) hominins. It is not yet clear why this may be the case. Could the observed high bone mass in some hominin species/populations be due to activity-related increased loading or other bone-influencing factors during lifetime such as diet (Goto et al. 2023; Wallace et al. 2023), or was it primarily systemic and heritable, i.e., a result of selection due to environmental de-

mands? It has often been discussed whether a given physical trait is 'genetic' or 'trainable during lifetime,' i.e., if a feature is fixed by our genes or affected by activity or the environment. However, it is becoming increasingly clear that also the individual responses to exposure or training have a genetic background. As individuals, we do not all respond in the same way to various activities; for a given activity there may be high and low responders, and a range in-between (Timmons 2010). For example, the training effects of a given amount of physical activity on muscle mass or oxygen uptake is set by our individual genes (Bouchard et al. 1999; Montgomery et al. 1998; Vellers et al. 2018), and this also holds true for responses of bone to various loads (Hiam et al. 2019; Skerry and Suva 2003). This genetic background to plasticity means that the old 'nature versus nurture' idea is not valid anymore; both heredity and environment shape our phenotypes. A modern human will not develop a Neandertal-like skeleton even when exposed to heavy work. As our genes set the range of the change (accommodation) our bodies can present when exposed, we must seek a functional cause of our features, including bone mass. We therefore ask under what conditions a 'heavy' bone structure could be preferable over a lighter one. Different scenarios of adaptive responses to environmental pressures for different species or populations may include, for example, increased terrestrial locomotion/less tree-climbing, digging for tubers, ambush hunting, endurance running for persistence hunting, and endurance diving for submerged resources. Specifically, how would having such a 'heavy' bone structure play out for early *Homo*, with respect to possible endurance running and endurance diving?

RUNNING WITH HEAVY BONES

While increased bone mass strengthens bones, it also increases body weight and overall body density as bone is our heaviest tissue (Currey and Alexander 1985; Hart et al. 2020; Wall 1983). Carretero et al. (2018) determined how a thick bone cortex (high bone mass) translates to overall skeletal weight. Based on total bone volume of well-preserved virtually complete fossil femora and humeri, they showed that the ~0.4 Ma old Sima de los Huesos *Homo* sp. (with bone microanatomy like that of *H. erectus*, Neanderthals, and mid-late Pleistocene humans) had skeletons that are ~36% heavier than Late Pleistocene-Holocene and extant *H. sapiens* skeletons. What has caused these heavier bones? Was it high mechanical loading or was it systemic bone mass increase resulting from genetic adaptation to factors associated with a certain lifestyle (Amson et al. 2014; 2018; Baab et al. 2018; Carretero et al. 2018)? It is well known that skeletal mineralization and bone mass vary with habitual mechanical loads and activity patterns (Hart et al. 2017). Also, under context-specific conditions genetic factors contribute significantly to the regulation of bone mass (Carretero et al. 2018; Cooke et al. 2024; Hiam et al. 2019; Ruff et al. 2006; Skerry and Suva 2003). Carretero et al (2018) concluded that the high skeletal robusticity of the Sima de los Huesos sample is systemic and part of their adaptive body type selected to support their activity regimes, and that it is formed under tight genetic control. However, what their activities were is not yet known.

Importantly, increased bone mass and thereby body weight would be energetically costly for an endurance runner and would have to be compensated by a higher $\dot{V}O_2$ as shown experimentally by Longman et al. (2022). If a normal human skeleton weighs around 10kg, a 36% heavier skeleton would add 3.6kg of weight, other body measures being unchanged. This would increase energy expenditure and oxygen consumption in a runner, and a heavy skeleton is therefore unlikely to have evolved by running per-se. Running mammals optimize their anatomy to minimize energy consumption rather than, for example, to maximize speed (Christiansen 2002). In comparative mammalian physiology it is well known that medium size mammals that are good runners have a relatively lower body mass than poor runners (Christiansen 2002). Based on the available hominin fossil record, the heavy boned *H. erectus* populations may be a compelling reason to critically reconsider the hypothesized endurance running in early *Homo* species.

DIVING WITH HEAVY BONES

Could having increased bone mass be useful during breath-hold diving? Increased bone mass would not only increase body weight but also body density. If mineralized bone—our heaviest tissue—replaces, e.g., marrow, one of our lightest, the weight would increase without an increased volume (Wall 1983). A heavier skeleton would lead to increased density and help the diver to achieve neutral buoyancy at shallow foraging depths, even with filled lungs (Amson et al. 2014; Houssaye and Botton-Divet 2018; Munro and Verhagen 2011; Wall 1983). With a light skeleton typical of modern humans, this could be achieved only after exhaling, which would shorten the ADL. For the air-breathing shallow diver, it is useful to inhale large amounts of air before diving to increase oxygen stores. Filled lungs will make the diver float as buoyancy increases, which would require more effort for diving down and staying at shallow depths (Figure 6). Modern human breath-hold divers therefore often use 2–4kg of lead weights (more if a wetsuit is used) to be able to dive down without too much effort, and in shallow diving this helps to achieve neutral buoyancy at the target depth. In competitive deep diving, more weights are used to minimize the effort of swimming down—and below the point of neutral buoyancy the divers can passively 'free fall' to reduce oxygen cost (see Figures 2 and 6; McKnight et al. 2021; Mulder et al. 2021; Schagatay 2011a) similar to deep-diving seals (Williams et al. 2000). Correct weighting is essential, because at the maximal depth turning point, where they are most negatively buoyant, deep divers still must be able to safely return to the surface recruiting also their anaerobic capacity (see Figure 6).

For a subsistence diver, it is instead essential to stay within the ADL to be able to dive repeatedly with endurance, without spending oxygen by constantly having to swim down to remain at foraging depth, which would rapidly exhaust oxygen supplies (see Figure 6). For a human

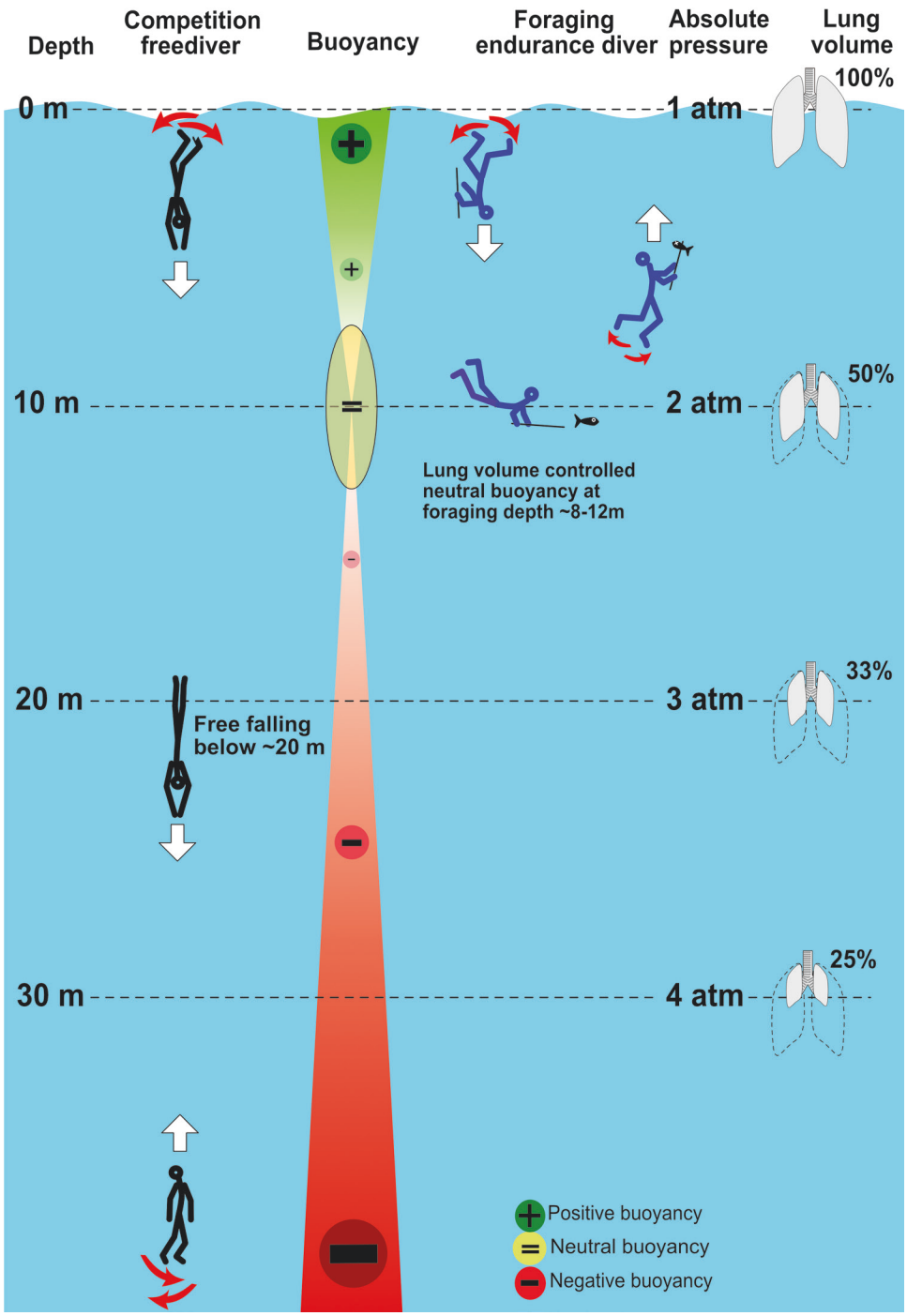


Figure 6. Buoyancy effect at various depths experienced by human competition divers (left) aiming for maximal depth, and shallow endurance divers foraging for food (right). With increasing depth, the lung volume shrinks according to Boyle's law (Pressure x Volume is constant) to half at 10m, where pressure is double that at the surface. Diving with overfilled lungs, the competition deep diver must wear weights to reduce the effort to swim down, and beyond ~20m starts free falling. The shallow endurance diver with filled lungs could reduce the swimming effort by having 'heavy bones' resulting in increased body density and neutral buoyancy while swimming at foraging depth.

diver a heavy skeleton would act as a natural ballast and allow diving without weights at a low oxygen cost, with filled lungs. As the lung air is compressed by water pressure at depth, there will be a depth range where the diver can stay at neutral buoyancy with minimal muscular effort as the diver neither floats nor sinks (see Figure 6). On ascent, first some muscular effort must be applied, but near the surface the lung air will have expanded enough to help the diver reach the surface. Therefore, the energy cost for diving is greatest in the beginning of descent and ascent, while at foraging depth all available energy can be used to move the diver forward. Increased bone mass would be energetically favorable for a shallow water diver.

COMPARING BONES OF TERRESTRIAL AND DIVING MAMMALS

For shallow divers, a heavy skeleton is thus helpful, while it is less important for deep divers as the lung air is compressed more with increasing depth. This explains why, compared to terrestrial mammals, systemic bone mass increase is typical of shallow diving mammals like the capybara, muskrat, North American beaver, polar bear, dugong, manatee, platypus, river and sea otters, and several seal species (Alfsen et al. 2025; Currey and Alexander 1985; Hand et al. 2025; Houssaye and Botton-Divet 2018; Houssaye et al. 2016; Wall 1983). The comparative study by Wall (1983; Figure 7) on forty-eight mammalian genera shows that the limb bone density of semi-aquatic diving mammals is significantly higher than that of terrestrial mammals, and also that shallow divers have a higher bone density than deep diving mammals.

Among the shallow diving mammals, the completely aquatic-adapted sea cows (manatees and dugongs) are a special case: they never have to come on land and are characterized by having vestigial hind limbs and exceptionally heavy dense bones (see Figure 7). In contrast, deep diving adapted mammals like several seal and whale species can exhale before diving and thereby reduce buoyancy, as they can tolerate a complete collapse of their lungs at depth (Kooyman 1989). A benefit of the latter is that they thereby avoid decompression disease (DCS) caused by dissolved nitrogen at depth (Kooyman 1989). These deep diving species manage long aerobic dives without filled lungs thanks to large oxygen storage capacity in blood and tissues (Kooyman 1989). Their bones typically exhibit a lighter construction with a larger portion of spongy inner organization (trabecular bone) to ensure bone strength and homogeneous distribution of mechanical stress (Hayashi et al. 2013; Wall 1983; see Figure 7).

Could the increased bone mass observed in early *Homo* be systemic, as suggested for, e.g., Neanderthals, Sima de los Huesos *Homo* (Carretero et al. 2018), and the Holocene Jomon (Cooke et al. 2024; Mizoshima et al. 2015; Schagatay 2022)? And could such systemic bone mass increase potentially reflect convergent evolution with that of other mammals in response to shallow water foraging by breath-hold diving? As not all fossils attributed to *H. erectus* have high bone mass compared to extant humans (see Figure 5), in combination with other morphological variation in *H. erectus* (Antón et al. 2016; Baab et al. 2025), this suggests that there were populations that differed substantially from each other with respect to foraging behavior. Thus, it is possible that across time and space, depending on climatic and environmental conditions, some *Homo* populations may have been focused on hunting and gathering on land, while other populations became increasingly adapted to underwater foraging by breath-hold diving. This could have promoted evolution of a more – or less – heavy skeleton across different groups. Whether one or more of these different populations have contributed to the gene pool of *H. sapiens* is a question that remains to be explored.

COMBINING A LAND AND WATER PERSPECTIVE

Despite a growing interest of the scientific community in studies on primates (including hominins) foraging in water (e.g., Archer et al. 2014; Braun et al. 2010; de Chevalier et al. 2022; Joordens et al. 2009, 2015; Koops et al. 2019; Muhammad et al. 2024; Nabais et al. 2023; Takenaka et al. 2022; Tye and Jones 2025; Will 2020; Zilhão et al. 2020; Zohar et al. 2023), pre-human hominins are still generally assumed to be purely land-based animals not genetically adapted in any way to foraging in water. This default scope within hominin evolution studies determines—and limits—how anatomical and physiological features of fossils are functionally interpreted. In contrast, in many non-hominin extant and extinct tetrapod lineages the concept of 'secondary adaptation to water' is widely studied (Houssaye and de Buffrénil 2021; Houssaye and Fish 2016). Members of most orders of airbreathing animals were taking to the water to find food, escape predators, and perhaps to thermoregulate (Vermeij and Motani 2018). By definition, fully aquatic tetrapods are adapted for life in water with severely reduced functional capacity on land, while semi-aquatic tetrapods frequent water rather than live there exclusively and exhibit an array of less profound modifications without seriously compromising terrestrial function (Pacini and Harper 2008). Semi-aquatic and aquatic adaptation may cause transformations in behavior, diet, locomotion, body shape, bone anatomy, and physiology reflected in the genome (Houssaye and Fish 2016; Yuan et al. 2021).

Importantly, secondary semi-aquatic adaptations can also be reversed, co-opted for new functions, or developed further into new features if such taxa leave their water-related niche and re-adapt to a fully terrestrial niche. For example, extant echidnas (a.k.a., spiny anteaters, *Tachyglossus aculeatus*) and elephants are now terrestrial mammals, but had semi-aquatic ancestors in the past (Hand et al. 2025; Mirceta et al. 2013). What if this perspective of secondary adaptation to foraging underwater could be applied to the human lineage, too? *H. sapiens* thus shares with semi-aquatic and aquatic mammals several physiological adaptations that facilitate diving, e.g., a strong diving response. The diving response is more prominent in both competition divers and in the Bajau than in non-diving groups (Schagatay 1996; Schagatay and Andersson 1998).

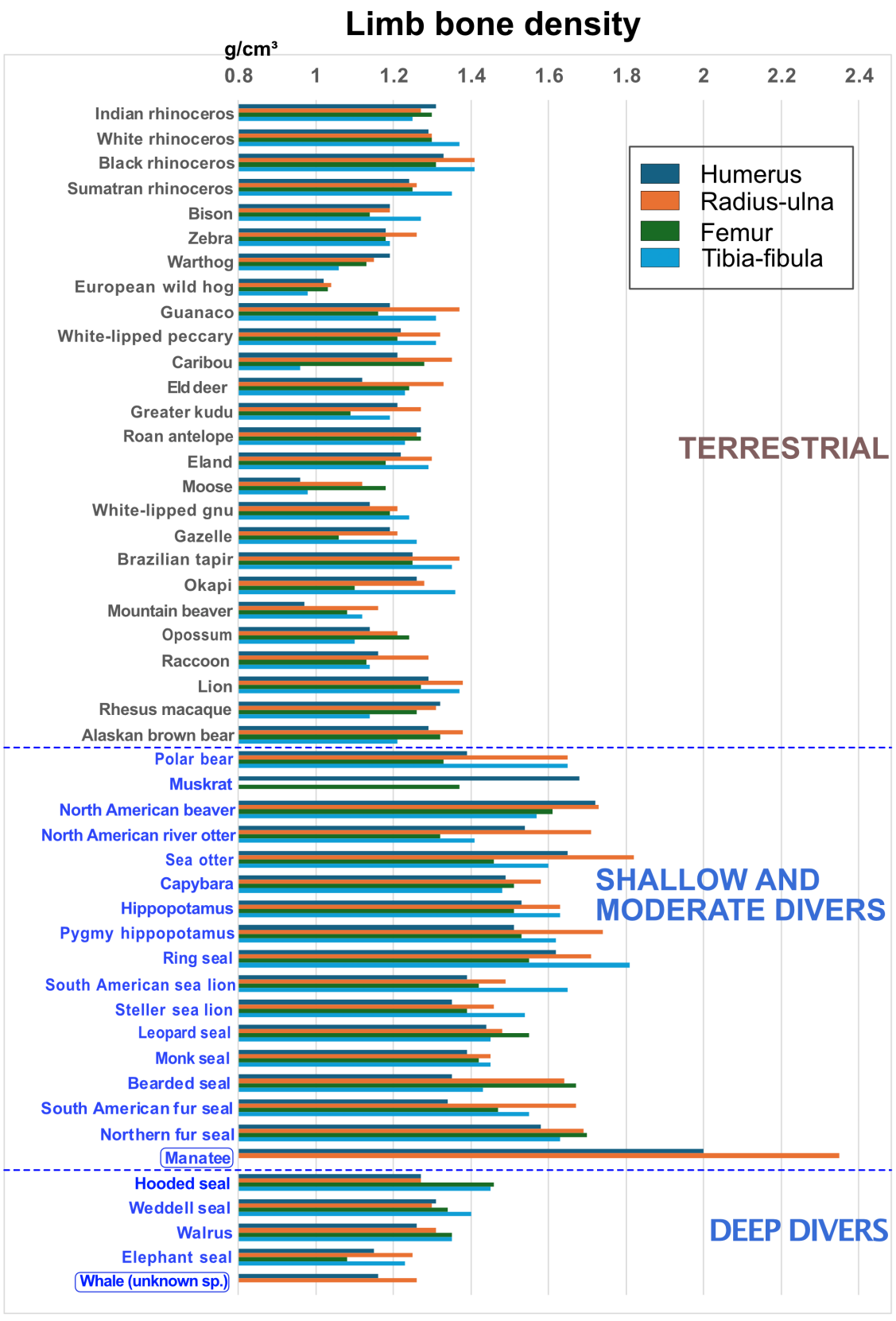


Figure 7. Limb bone density of 26 terrestrial, 17 shallow-moderate diving, and 5 deep diving mammals of different body sizes, showing significant bone density (mass) increase in shallow-moderate diving mammals compared to terrestrial mammals; limb bone density data from Wall (1983), categorizing of divers according to Fahlman and Schagatay (2014). The full dataset is presented in SI Table S2.

Furthermore, having a relatively large spleen is characteristic of both competitive freedivers and the Bajau (Ilardo et al. 2018; Schagatay et al. 2012). This may in part be a result of their frequent diving, as both features have been found to be affected by long-term training or exposure (Bouten et al. 2019; Engan et al. 2013); however, as plasticity is itself heritable (e.g., Williams et al. 2017), these features are a target for selection.

Additional genetic data interpreted as evidence of adaptation to a diving lifestyle have recently been described for the Bajau (Ilardo et al. 2018) as well as the Haenyo (Aguilar-Gomez et al. 2025). A comparative genomic study showed strong selection specific to the Bajau on BDKRB2, a gene likely affecting the human diving response (Ilardo et al. 2018). In addition, selection on variants in the PDE10A gene increased the Bajau thyroid hormone levels, likely causing their increased spleen size (Ilardo et al. 2018; 2022). It is important to note that these genetic adaptations in the Bajau appear to come from selection on standing variation of genes, since the candidate variants in the genes PDE10A and BDKRB2 have a broad geographic distribution among humans (Ilardo et al. 2018). This implies that the genetic variants ('SNPs': Single Nucleotide Polymorphisms) enabling these physiological benefits for diving emerged prior to the emergence and global dispersal of *H. sapiens*, providing standing genetic variation with beneficial variants that turn up in human genomes, and can be selected for if needed, as in the Bajau. This may explain why also non-Bajau can discover a remarkable talent when they happen to take up breath-hold diving, while others find it hard. A striking example of talent is British Sara Campbell, who became a world champion in freediving by diving to 96m of depth after only nine months of training (Johansson and Schagatay 2014). Similarly, such talent is discovered in novice freedivers from all continents (ES observations). This indicates that the capacity for freediving has not uniquely evolved in present-day human diving populations but is a feature that must have a deeper, likely pre-*H. sapiens*, evolutionary origin.

When applying a comparative biology approach in human evolution studies and extending the scope from a strictly terrestrial one, to also consider possible hominin adaptations to underwater foraging, we open a wider vista of research directions and predictions that can be tested. Vrba (2007) pointed out that with respect to environmental change, evidence from a range of organisms has shown that the evolution of taxa does not consist of independent pieces of history but is rule-bound, with qualitative and temporal coherence to evolutionary responses across many lineages. We contend it is now time to treat hominins just like other mammals and follow up on biologically sound ideas, i.e., by examining possible adaptation to a littoral niche including underwater foraging. If not, we risk throwing out the baby with the bath water (Cameron and Groves 2004). Therefore, we urge 'legitimizing' the study of possible semi-aquatic adaptations in hominins, which could lead to a synthesized land-based (terrestrial) and water-based (littoral) perspective on evolution of the human lineage.

It may need to be said that we do not advocate for the 'aquatic ape theory,' as it is often interpreted as suggestive of a fully aquatic human ancestor. This hypothesis has had a long and contentious history (e.g., Foley and Lahr 2014; Groves 1993; Hardy 1960; Kuliakas and Morgan 2011; Langdon 1997; Malm 2007; Roede et al. 1991) and has made many paleoanthropologists wary and dismissive of all water-related human evolution hypotheses (Foley and Lahr 2014; Tuomisto et al. 2018). Multiple lines of morphological, archaeological, and paleoecological evidence make clear that hominins were always living on land; we suggest that a coastal ancestral lineage likely developed means for periodically foraging in shallow water, similar to what many semiaquatic animals and several extant human populations do today. The modern version of the hypothesis, often called the 'waterside hypothesis in human evolution' (Tobias 1998, 2011; Rhys-Evans 2020), does raise many interesting questions that deserve to be studied with an open mind, as this could help explain how modern humans are so well adapted for shallow endurance diving and other endurance activities, and to hypoxic environments.

HOW OLD IS HOMININ ENGAGEMENT IN DIVING?

So, when could the human capacity for endurance diving have evolved? Early *H. sapiens* exploited marine resources on the coast of South Africa at ca. 167 ka (Marean et al. 2007). Recent research has provided evidence for aquatic resource exploitation by Neandertals on the Atlantic coast of Portugal (Nabais et al. 2023; Zilhão et al. 2020) and Neandertals diving for sublittoral living bivalves in the Mediterranean (Villa et al. 2019). This begs the question: could older hominin species have been engaging in shallow diving as well? Is there—in addition to the observed increased bone mass—any paleoanthropological or archeological indication for aquatic foraging and breath-hold diving by earlier hominins?

The earliest evidence for use of aquatic resources by hominins was provided by cutmarks on fossil bones from fish, crocodile, and turtle at ~1.95 Ma in the Turkana Basin (Braun et al. 2010), which seems to coincide with the first appearance of *H. erectus* in that area (Barr et al. 2022). It is now widely accepted that some pre-Neanderthal hominin populations, including *H. erectus,* engaged in foraging for aquatic resources such as freshwater mussels around 0.5 Ma on Java, Indonesia (e.g., Joordens et al. 2015), and in wetlands in the Levant, hominins at ~0.78 Ma caught and cooked fish (Zohar et al. 2023). However, it is not known how these resources were procured—by wading or by diving. Goren-Inbar et al. (2014) concluded that Acheulian hominins were capable of underwater gathering of nuts from a freshwater aquatic plant (e.g., *Euryale ferox*) at depths of 1.5–3m, so indicative of diving.

There may, however, be a more direct indication for sustained water exposure that could be found in the hominin fossil record. So-called 'auditory exostoses' (ear exostoses) frequently occur in adult modern humans engaging in aquatic sports such as surfing, white-water kayaking,

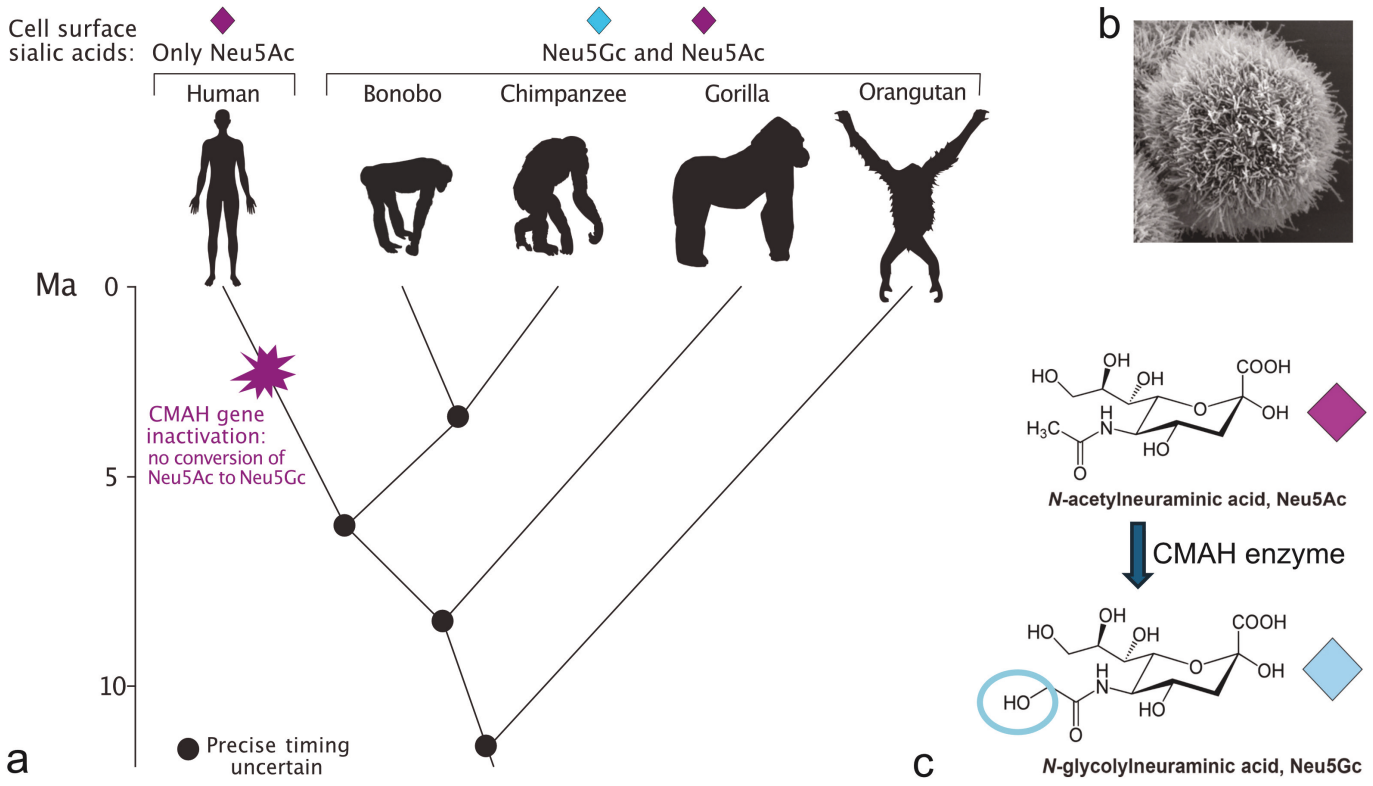


Figure 8. a) Great ape evolutionary tree showing that humans have only the sialic acid Neu5Ac on their cell surfaces, while other great apes have both Neu5Ac and Neu5Gc (adapted from Dhar et al. 2019); b) Scanning electron microscope (SEM) image of a cell with its bushy glycocalyx ('sugar coat') on the surface (photo from Graphical Abstract in Shurer et al. 2019), sialic acids are typically situated at the outer end of these complex branches; c) chemical structure of the sialic acids Neu5Ac and Neu5Gc. The CMAH *gene codes for production of the CMAH enzyme (CMP-Neu5Ac hydroxylase) that converts Neu5Ac to Neu5Gc by adding just one oxygen atom (blue ellipse). Inactivation of the* CMAH *gene, as occurred in the human lineage between ~3 and 2 Ma, means no CMAH enzyme and no Neu5Gc production, and improved oxygen transport into muscles (Okerblom et al. 2018).*

swimming, SCUBA-diving, and breath-hold diving, and are associated with chronic exposure to water and wind chill (Moore et al. 2010; Sheard and Doherty 2018; Wegener et al. 2022). They also frequently occur in human coastal populations engaging in aquatic foraging in rivers and seas, with lower water temperature and higher frequency of exposure being associated with higher prevalence and more severe exostoses (Lorentz and Casa 2021; Okumura et al. 2007; Ponzetta et al. 1997; Rhys-Evans and Cameron 2017; Toyota and Kitagawa 2017; Trinkaus et al. 2019; Ubelaker et al. 2022; Villotte and Knüsel 2016). In the warmer tropics and subtropics, aquatic activites do not always result in the presence of this trait, so here absence of auditory exostoses does not necessarily reflect absence of water-related exposure (Okumura et al. 2007). While auditory exostoses as such do not allow reliable discrimination between different water-related activities, their presence can nonetheless provide relevant information on hominin behavior in wet environments. Auditory exostoses can fossilize, and their presence has been described in modern human divers, e.g., ancient Japanese Jomon period populations (Hudson 2022; Schagatay 2022), and in Middle Pleistocene *Homo*, Neanderthals, Sima de los Huesos hominins, and in *H. erectus* from Zhoukoudian (Dodo 1972; Kennedy 1986; Rhys-Evans and Cameron 2017; Trinkaus et al. 2019; Villotte and Knüsel 2016). As it seems unlikely that these early populations were engaged in sailing or surfing, they likely acquired the exostoses through frequent activities involving immersion in water, such as swimming or diving.

Interestingly, a major genetic change in the human lineage might be a possible indication for underwater foraging by breath-hold diving. In the period between 3 and 2 Ma a key event happened in the human lineage, namely a mutation inactivating the *CMAH* gene (Figure 8; Altman and Gagneux 2019; Chou et al. 2002). This gene influences the efficiency of oxygen transport in the body (Okerblom et al. 2018). The active *CMAH* gene encodes production of the CMAH enzyme that mediates conversion of the sialic acid Neu5Ac to Neu5Gc, by addition of a single oxygen atom (see Figure 8c). However, the 'broken' *CMAH* gene—typical of the human lineage—can no longer code for CMAH enzyme production, so no Neu5Gc can be formed. This has caused a major change in the outer surface ('glycocalyx') of all cells in our body; humans have only the sialic acid

Neu5Ac on their cell surfaces, while other apes and most mammals have both Neu5Ac and Neu5Gc (Altman and Gagneux 2019; Chou et al. 1998; see Figure 8).

Why is the composition of sialic acids on the cell surfaces so important? For many reasons: sialic acids influence interactions between cells, membrane permeability, immunity, susceptibility to pathogens, and also oxygen transfer (Vail et al. 2023). Specifically, it was found that mice with an experimentally induced human-like mutation in the *CMAH* gene are capable of more sustained running and demonstrate improved endurance, at least partly due to increased oxygen transfer to muscles (Okerblom et al. 2018). Because of this it has been suggested that the inactivation of the *CMAH* gene in the human lineage between 3 and 2 Ma may be associated with development of endurance running in *H. erectus* (Okerblom et al. 2018). However, as the increased transfer of oxygen in muscles—and other tissues—would also be highly beneficial for mammalian divers (and mammals in hypoxic conditions such as in torpor or at high altitude), we speculate that inactivation of the *CMAH* gene could instead have first allowed the development of efficient endurance diving in an ancestral population between 3 and 2 Ma. Interestingly, among other extant mammals that have lost functionality of the *CMAH* gene are breath-hold divers such all seals and otters, the walrus and the platypus (Altman and Gagneux, 2019; Lopes-Marques et al. 2020; Peri et al. 2018). A comparative study on the possible relationship between hypoxia and *CMAH* gene loss in a wide range of mammals is underway. Research on ancient DNA has shown that not only humans but also Neanderthals and Denisovans had an inactivated *CMAH* gene (Chou et al. 2002). It is not yet known whether earlier hominin species such as *H. erectus* had an inactivated *CMAH* gene. This question is currently under study, as it is possible to establish this based on fossils even in the absence of preserved ancient DNA (Bergfeld et al. 2017).

Taken together, based on the evidence for: 1) modern human endurance diving capacity, 2) abundance of nutrient-rich food in the littoral area, 3) signs of hominin aquatic foraging as early as 2 Ma, 4) the intriguingly 'heavy' limb and skull bones of some (early) *Homo* populations, and 5) the major genetic change at ~3–2 Ma in the human lineage that increased efficiency of oxygen transfer in tissues, we argue that it is reasonable to hypothesize that also *Homo* species older than Neandertals, such as some early *Homo* or *H. erectus* might have engaged in diving to forage for food.

THE 'DIVE FIRST, RUN LATER' HYPOTHESIS

We propose a 'dive first, run later' hypothesis, that takes the human capacity for both endurance diving and endurance running into account.

Dive first—certain coastal early *Homo* populations after ~3 Ma evolved through littoral adaptation, including breath-hold endurance diving in shallow water to forage for high-quality aquatic food. Like in many shallow diving mammals, this led to increased bone mass and thereby body density, which allowed them to forage at shallow depth with filled lungs. This would extend the ADL and decrease energetic costs of repeated submerged locomotion. In response to the challenges of endurance diving and to prevent hypoxia, they developed a deep and wide thorax and a large lung capacity allowing enhanced oxygen storage during diving and efficient ventilation between dives, and acquired gene variants that conferred physiological benefits for endurance diving. Together, these adaptations would enhance aerobic endurance and allow longer total daily underwater foraging time and thus favor reproductive success.

Run later—the increased aerobic endurance that evolved in response to endurance diving was co-opted for endurance running and persistence hunting by certain younger *Homo* populations or species that developed lighter bones. Examples of such populations could be the relatively light-boned *H. erectus* from Middle Pleistocene Java and Oldupai, and especially the light-boned Holocene to recent *H. sapiens* populations.

These hypothesized niche shifts between aquatic and terrestrial foraging were likely not unique nor absolute and unidirectional. We propose that depending on the prevalent climatic and ecological conditions, such oscillating land-and-water foraging adaptations could have happened multiple times during hominin evolution in marine as well as in freshwater systems. Moreover, we emphasize that the hypothesized endurance diving in the past does not imply that hominins were necessarily diving more efficiently than humans are capable of today. Our hypothesis holds that once diving-induced cardiovascular endurance had evolved, several niches were open to our ancestors; as eurytopic organisms, they were able to tolerate a wide range of habitats and ecological conditions, which may have been key to their success.

Just as not all *H. erectus* fossils display increased bone cortical thickness, *H. sapiens* also varies in this respect. While the skeletons of Holocene and recent modern humans are considerably more gracile compared to those of earlier *Homo* including Late Pleistocene humans (Ruff 1995, 2018), there are notable exceptions (Baab et al. 2018). For example, several Holocene *H. sapiens* populations appear to have retained or redeveloped relatively heavy bones—Alameda (Ohlone) from coastal California, Eva from Tennessee (Baab et al. 2018), and Jomon from Japan (Mizoshima et al. 2015). Interestingly, they are all shell mound builders who may have gathered their staple aquatic molluscs by wading as well as by endurance diving, as indicated by the targeted mollusc species' depth ranges (Schagatay 2022). The Bajau, Ama, Haenyo and other current diving populations are examples of populations that started re-exploiting an underwater foraging niche only a few thousand years ago and likely evolved certain diving features through selection of beneficial standing variation in the human genome (Aguilar-Gómez et al. 2025; Ilardo et al. 2018).

THE ZIG-ZAG BENEFIT

A lifestyle of being comfortable under water (in seas, estuaries, rivers, and lakes) as well as on land poses trade-offs on adaptations such as bone morphology and mass (e.g.,

Nieminen et al. 2024) but also has multiple benefits. Not only could food sources be drawn from a wider range of environments, allowing hominins to shift opportunistically between them as outlined above, but also predator avoidance and thermoregulatory benefits could arise from such adaptations. In both terrestrial and coastal environments, early *Homo* was exposed to predators, likely big cats and hyenas on land, and in water there would have been sharks and crocodiles. Being able to escape into the water when chased by strictly terrestrial predators would have presented survival benefits, if equipped with the means to stay in water until they retreated. In the same way, an animal not having to stay in the water permanently could avoid sharks and possibly crocodiles by fleeing to land. This is how proboscis monkeys avoid their main terrestrial predators (clouded leopards) and their main aquatic predators (false gharials), by rapid shifts between trees and water that cannot be repeated by these predators (Matsuda et al. 2008, 2011). Moreover, aquatic predators like sharks and crocodiles are quite predictable in their behavior and hominins would likely learn when and where these animals would potentially be a threat. In a healthy coastal ecosystem, most reef sharks are regular feeders on fish and very few shark species attack humans. The Bajau do not fear sharks but there are some historical accounts of crocodile attacks on children (ES, discussions with Bajau). Large salt-water crocodiles may be dangerous if hunters enter their territory, but staying out of it will be protective. The inverse may also have been true; in the Turkana Basin, crocodiles and hippos have been on the hominin menu since ~1.95 Ma (Braun et al. 2010) suggesting that these animals may have feared hominins more than hominins feared them.

Thermoregulation in a progressively warmer and dryer eastern Africa may have been challenging for hominins, especially in more open landscapes after ~3 Ma. Thermoneutral air temperature in a naked resting human is around 28°C, after which sweating is needed to dissipate heat. This means spending energy, salt, and body water to defend the healthy inner body (core) temperature of around 37°C. With work, e.g., running, this occurs at even lower ambient temperatures, which requires large amounts of drinking water and causes a dual demand on blood flow for muscles and in the skin to dissipate heat (González-Alonso et al. 2008). To run in a hot environment only works if core temperature is kept below 40°C when fatigue occurs due to high brain temperature (González-Alonso et al. 2008). However, the most efficient means of chilling down is entering water, as the heat-transfer capacity of water is about 25 times that of air. Thermoneutral water temperature is around 35°C, so any water cooler than that can act as an efficient cooling agency where heat will be transferred away from the body. No sweating is needed, and body water can be conserved. When cooled down, it is possible to move again in a hot air environment for some time. Pre-cooling in water has been shown to have clear benefits for endurance sports performances in hot environments (González-Alonso et al. 1990; Kay et al. 2010; Ntoumani et al. 2023). The subcutaneous fat layer of humans, which is more developed than in other apes, would not only allow longer submersion in water before core temperature starts to drop and shivering is induced, but it would also act as an efficient 'blood cooler' when returning to land after submerging; it could have kept our core cold for longer than fur alone would be able to do. Thus, moving between land and water, to cool down and to warm up, respectively, may have provided a great advantage for thermoregulation compared to animals restricted to only one of these environments. A coastal hominin would clearly benefit from being able to use both terrestrial and aquatic environments by moving between them in a zig-zag manner; on short time scales (hours) for, e.g., foraging thermoregulation or predator avoidance, medium (days) due to varying weather conditions, as well as longer (e.g., seasonal and Milankovitch climate cycle) timescales, to safely obtain a range of food sources.

DID DIVING TAKE US HIGHER?

Physiological adaptations to endurance diving could, in addition to potentially facilitating the evolution of endurance running, also be an asset for humans when spreading towards high-altitude regions with limited access to oxygen. Enhanced capacity to take up large amounts of oxygen, to use it carefully and tolerate hypoxia are essential also here, as oxygen partial pressure is low. Humans are known to adapt well to high altitude, for example, lowlanders increase their hemoglobin concentration by increased red blood cell production when going to high altitude—changes that are not evident in the chimpanzee and gorilla (Mortola and Wilfong 2016), but a feature evident also in response to freediving in humans (de Bruijn et al. 2008). Recent research has revealed that several other features and mechanisms important for divers are also protective against chronic hypoxia at high altitude. Just as in divers, typical characteristics of human highland populations are large lungs (Beall 1982; Droma et al. 1991; Fiori et al. 2000) and large spleens (Brutsaert et al. 2024; Holmström et al. 2020), and the same is true for elite high-altitude climbers (Schagatay et al. 2020a). As a response to hypoxia at altitude, the spleen contraction immediately elevates hemoglobin concentration even before red blood cell production has had time to come into effect (Schagatay et al. 2020b). Moreover, it was recently found that the magnitude of the human diving response triggered during apnea at low altitude is predictive of high-altitude tolerance; individuals with a pronounced diving response get fewer symptoms of acute mountain sickness, a major threat at high altitude (Holmström et al. 2018). This suggests that the same cardiovascular priority system is protective against hypoxia in both situations.

We must ask: could it be that high altitude was the driver to begin with, or is it more plausible that diving came first? With an evolutionary origin at high altitude, these mechanisms would likely be even more evident at high altitude. But, in fact, while the same defense mechanisms are active in both these naturally occurring hypoxic environments, the physiological responses are more efficiently triggered during diving. The spleen contraction, which is initiated by

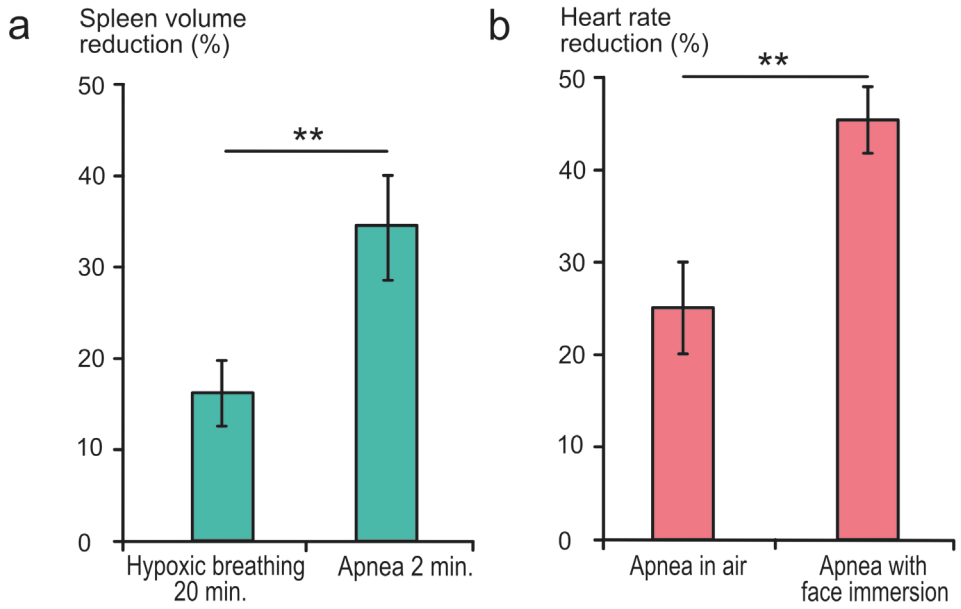


*Figure 9. a) Mean (SE) spleen contraction leading to release of red blood cells during (left bar) simulated altitude of 3300m by 20 minutes of breathing hypoxic air (14.2% oxygen) and (right bar) after 2 minutes of breath-holding (apnea) for the same nine untrained individuals. The hypoxia developed was similar in both conditions, while breath holding also resulted in hypercapnia, which doubled the spleen contraction. Significant difference at p<0.01 is indicated by ** (adapted from Lodin-Sundström and Schagatay 2010 Figure 3); b) Mean (SE) heart rate reduction expressed as % change from resting level, as often used to estimate diving response magnitude, (left bar) during breath holding in air, and (right bar) during breath holding with facial chilling through face immersion, which approximately doubled the response for the same 10 trained divers. Significant difference at p<0.01 is indicated by ** (adapted from Schagatay 1991: Table 15.1).*

hypoxia, is even greater in the presence of hypercapnia as occurs during breath-holding but not at high altitude (Lodin-Sundström and Schagatay 2010; Figure 9a). The more pronounced spleen contraction developed during breath-hold diving would thus be more effective against hypoxia underwater, suggesting that this function came first. In addition, a recent study found that apnea is a stimulus directly involved in triggering the spleen contraction (Persson et al. 2023). The hypercapnia (high carbon dioxide in the blood) developing with breath-holding also acts to increase brain blood flow that increases the delivery of oxygen, while the reverse situation occurs at high altitude where hypocapnia (low carbon dioxide) due to increased ventilation reduces brain blood flow (Willie et al 2015).

Similarly, the diving response will be more efficiently triggered during diving, as it starts already with apnea and is preventive of hypoxia, rather than being an effect of it. Hypoxia developing at the end of a long dive may further enhance the diving response. Moreover, the diving response triggered by apnea is enhanced to the double by chilling of the upper part of the face—which occurs during diving—but not by chilling of any other areas of the body (Figure 9b; Andersson et al. 2000; Schagatay 1991; Schuitema and Holm 1988). The diving response is dependent on a sudden drop in facial temperature as occurs when diving, and not on a constant cold exposure as may occur at high altitude (Schagatay and Holm 1996). This also means the diving response is efficiently triggered in a tropical diver, providing that the ambient air is warmer than the water (Schagatay and Holm 1996). Based on these experimental studies, we infer that from a physiological perspective, the 'dive first' hypothesis provides a logical explanation for the ability of *Homo* populations to expand to high altitude, through exaptation of defense mechanisms to hypoxia that evolved by diving. The richness in biodiversity and biomass in the coastal zone compared to at high altitude may also speak in favor of this scenario.

ECOLOGICAL DRIVERS OF NICHE SHIFTS TOWARD AQUATIC RESOURCE USE

What could have been the drivers for the proposed aquatic foraging in hominin populations? Let us examine such evolutionary paths among other mammals, since it can be expected that local environmental conditions may select for similar behaviors in both humans and non-human animals (Barsbai 2021). Studies have shown that seasonal or permanent impoverishment of terrestrial ecosystems is a trigger for aquatic resource use by terrestrial mammals in adjacent productive aquatic ecosystems, notably in carnivores and omnivores (Carlton and Hodder 2003) but also in herbivores (Amson et al. 2014). Littoral foraging is documented for, e.g., brown bears in Alaska (Smith and Partridge 2004), polar bears in the Arctic (Lone et al. 2018), lions in the coastal desert of Namibia (Stander 2019), wolves in coastal

Canada (Darimont et al. 2008), snow monkeys in the Japanese Alps (Takenaka et al. 2022), chacma baboons in South Africa (Lewis and O'Riain 2017), and long-tailed macaques in SE Asia (Gumert et al. 2012; Muhammad et al. 2023). Similar foraging behavior in response to local conditions can be expected from hominins and has been suggested for *H. erectus* at Trinil (Joordens et al. 2009; 2015), Neandertals on the Atlantic and Mediterranean coasts (Cortés-Sánchez et al. 2019; Zilhão et al. 2020) and Pleistocene humans along the coast of southern Africa (Fisher et al. 2020; Marean et al. 2007; 2020). Moreover, once terrestrial species are familiar with foraging in freshwater or marine littoral areas, the easy availability of high-quality aquatic resources may cause them to prefer aquatic foods even when their usual terrestrial food items are also available (Darimont et al. 2008; Gumert and Malaivijitnond 2012). Ultimately, this can lead to substantial niche shifts—including underwater foraging—and consequent speciation, as shown by the emergence of the polar bear (*Ursus maritimus*), sea otter (*Enhydra lutris*), and sea mink (*Neogale macrodon*) as separate species (Work et al. 2025). Taken together, the data show that a niche shift or expansion towards foraging for aquatic resources is often triggered by a combination of push factors such as low terrestrial productivity and resource competition, and pull factors such as high aquatic productivity and easy access to high-quality food. This would promote convergent evolution of features allowing breath-hold diving for aquatic resources, as is evident in a wide range of taxa (Mazin and de Buffrénil 2001).

Hominin evolution during the period 3–2 Ma is key to understanding the origin of our species. What was happening in Africa in the period between ~3 and 2 Ma? Could anything during this period have affected terrestrial productivity and changed niches relevant to hominins? Despite the absence of an abrupt climate change around 3 Ma in global paleoclimate records (Trauth et al. 2021; Van der Lubbe et al. 2021), paleoenvironmental data from eastern Africa indicate a marked transition from relatively humid to arid conditions after ~2.8 Ma (Bibi et al. 2013; Braun et al. 2025; Levin et al. 2015; Robinson et al. 2017; Smail et al. 2025). The latter may be part of a long-term climatic aridification trend but can in addition be attributed to major regional volcanic and tectonic events around 2.8 Ma in eastern Africa. These include the catastrophic eruption and collapse of the formerly 7km high Mt. Kenya, which may have acted as a 'water tower' (Schoorl et al. 2014), and substantial tectonic changes in the Afar Basin (Dupont-Nivet et al. 2008; Rooney 2020). These tectonic-volcanic events at ~2.8 Ma in eastern Africa altered wind and rainfall patterns as well as river drainage patterns, making most of eastern Africa significantly more arid as outlined above, but other areas like the Baringo Basin and possibly southeast Africa temporarily wetter (Mitsunaga et al. 2023; Taylor et al. 2021). The eruptions may also have released large amounts of toxic gases (e.g., SO_2, HF, Hg) temporarily disrupting regional terrestrial ecosystems through acid rain and poisoning of flora and fauna, as did other historic and prehistoric major volcanic events (Lindström et al. 2019; Thordarson and Self 2003; Van de Schootbrugge and Wignall 2016). From ~2.1 Ma onwards, both eastern and southern Africa were affected by the increasing aridification associated with onset of the modern atmospheric Walker Circulation (Van der Lubbe et al. 2021). We propose that the local environmental events at 2.8 Ma and the global climate changes after 2.1 Ma may have been major push/pull factors for hominin niche shifts, both inland and on the coast. In arid coastal areas, this could have led to foraging for submerged aquatic resources.

DISCUSSION

HOW TO TEST HYPOTHESES TO EXPLAIN AEROBIC ENDURANCE?

We have shown that by applying a comparative biology approach and extending the scope to also consider possible hominin adaptations to a coastal niche including underwater foraging for food, we open a wide vista of research directions. If we take on this new perspective, we can formulate two hypotheses to explain modern human aerobic endurance:

H1, the 'dive first, run later' hypothesis: first, adaptation of certain early *Homo* populations to underwater foraging by endurance diving in response to ecosystem disruption and aridification, involving developing heavy bones and aerobic endurance, and in later *Homo* populations exaptation of diving-related endurance features, and developing lighter bones facilitating endurance running for persistence hunting;

H2, the 'run first, dive later' hypothesis: first, adaptation of certain early *Homo* populations to persistence hunting by endurance running in response to ecosystem disruption and aridification, and in later *Homo* populations exaptation of running-related endurance features, and developing a heavy skeleton facilitating endurance diving for underwater foraging.

The next step is to start identifying ways to compare and test these hypotheses, which is a challenge given the sparse hominin fossil record and the spatial, environmental, and effort-related sampling biases (Barr and Wood 2024; Faith et al. 2021; 2025; Maxwell et al. 2018). Specifically, which features make endurance diving possible, or easier? When are these features first observed in the hominin fossil record? How might such features relate to endurance running? Many of the anatomical and physiological features involved in diving are well-studied in other mammals (e.g., Berta et al. 2005; Fahlman 2024; Kooyman 1989, 1997, 2009; Ponganis 2015) and understanding of the human breath-hold diving capacity and underlying physiology has increased substantially during the last decades (e.g., Elia et al. 2021; Schagatay 2009, 2010, 2011a; Schagatay et al. 2011; 2014; McKnight et al. 2021; Mulder et al. 2020; 2025). However, the origin of human breath-hold diving has so far not been systematically evaluated in the hominin fossil record. There are in fact several examples of features leaving fossil traces relating to such physiological functions. We here provide an overview of ten relevant features

reflecting possible adaptations to endurance diving for underwater foraging that can be investigated by studying the hominin fossil record, some of which were not discussed above. We consider these also in the perspective of endurance running and their first known appearance in the hominin fossil record (Table 1). We discuss two of these features in more detail below—thorax morphology and facial and upper airway morphology.

Thorax Morphology

A new reconstruction of the ribcage fossils of the *H. erectus* specimen KNM-WT 15000 showed that it had a wide and dorsoventrally deep thorax with a large respiratory capacity, and was built more like stocky, heavy-bodied Neanderthals than like modern humans who have a relatively narrow and shallow ribcage (Bastir et al. 2020; 2022). This suggests that, contrary to earlier interpretations (Carrier 1984), *H. erectus* did not have the tall, lean, and agile body shape typical of an endurance runner (Bastir et al. 2020). Ribcage measurements indicate greater lung volume and respiratory capacity in KNM-WT 15000 and Neanderthals (Kebara 2) compared to modern humans (Bastir et al. 2022; Garcia-Martinez et al. 2018), except for humans who live in cold areas, who also have a relatively large thorax (Lopez-Rey et al. 2025) in conjunction with shorter limbs to reduce heat loss (Steegmann et al. 2002).

Lopez-Rey et al. (2023) found that while the upper thorax of extinct *Homo* is similar to that of modern humans, the lower thorax is broader and dorsoventrally deeper, more 'bell shaped,' and may have accommodated a larger diaphragm. The diaphragm is the large, dome-shaped muscle located between the thorax and abdomen (see Figure 9a). When the diaphragm contracts, it increases lung volume which initiates inspiration, thus it is essential during breathing and the major breathing muscle during rest. Muscles between the ribs (intercostal muscles) and in the abdomen also contribute to breathing, and their involvement increases with oxygen demand. The bell-shaped ribcage typical of Neanderthals and *H. erectus* would potentially lead to a greater range of diaphragm movement during breathing, and it could have a more important role than in modern humans. In *H. sapiens*, breathing may be more dependent on the upper thorax, thus recruiting a larger involvement of intercostal muscles at a given point (Lopez-Rey et al. 2023). The difference in thorax morphology and diaphragm size has been interpreted as an indication that Neanderthals and *H. erectus* had a higher respiratory capacity than modern humans; the authors suggest that these species needed a higher respiratory capacity because they had a higher metabolic rate, perhaps related to engaging in power locomotion and ambush hunting (Lopez-Rey et al. 2023; 2025).

We suggest that instead, the bell-shaped thorax with a large diaphragm may have been a useful adaptation to breath-hold diving. Efficient diving in humans requires a large maximal total lung volume (TLC) for maximal oxygen storage, and individual diving capacity is clearly related to lung volume (Schagatay et al. 2012). However, for efficient diving, lungs must also be flexible; the smallest attainable volume after exhalation (residual volume, RV) is just as important, as the diving depth is set by the ratio TLC/RV due to the compression of the lung air at depth (see Figure 6). The residual lung volume is constrained by the inward flexibility of the rib cage and determined largely by the length and elasticity of the diaphragm. A large and flexible diaphragm allows the abdominal organs to fill the space left by the shrinking lungs at depth (see Figure 6; Figure 10a). Should a diver descend deeper than the point at which RV is reached, the lungs which are tightly attached to the ribcage cannot shrink more but develop a negative pressure inside, which can result in 'lung squeeze' (pulmonary barotrauma) that compromises gas exchange (Patrician et al. 2021). This is why an important part of competitive freedivers training involves stretching of the chest and in particular the diaphragm (Figure 10b; Schagatay 2011). The 'squeeze-free diving depth' with a normal untrained modern human chest and diaphragm is 25–30m (assuming a RV at approximately 25–30% of TLC), which is deeper than the typical depth regularly reached by Bajau and Ama divers; a longer diaphragm in the Neandertals and early *Homo* could indicate that their 'squeeze-free depth' might have been more than 30m. Both a large total lung volume and a small residual volume—thanks to a large diaphragm allowing safe lung shrinkage with depth—are clearly performance-enhancing features in breath-hold diving (Schagatay 2011; Schagatay et al. 2012).

Facial and Upper Airway Morphology

The modern human face is characterized by an external nose with downward pointing nostrils, very different from the noses of the great apes who have forward-pointing nostrils (see Figure 4; Figure 11). Based on findings of cranial fossils with protruding nasal bones, this feature likely first appeared in early *Homo* and notably in *H. erectus* around 2 Ma (Bastir et al. 2022; Franciscus and Trinkaus 1988; Figure 11c). Many hypotheses have been put forward to explain the function of an external nose—e.g., conditioning of the air may be advantageous during terrestrial endurance activities in cold or dry areas—but they remain debated (Bastir et al. 2022; Jacobs 2019; Lieberman 2011; Noback et al. 2011; Zaidi et al. 2017). However, it can be argued that lengthening the airways would increase resistance for breathing, and in a cold climate a short nose is preferrable as cold injury would be more likely in protruding noses.

We propose that instead the external nose could be an efficient and perhaps essential adaptation to endurance diving. The downward nostril orientation prevents the nasal cavity from flooding during swimming and diving, especially upon vertical submergence as done by the Bajau. Semi-aquatic and aquatic mammals have modified respiratory tracts, preventing the incursion of water by closing the nostrils with dilator muscles. After emergence, they open the nostrils actively by dilator muscles (e.g., seals, hippos, whales, dugongs; Maust-Mohl et al. 2018). Modern humans do have similar nasal muscles (consisting of *compressor naris* and *dilator naris*) that can decrease and increase the size

TABLE 1. TRACES OF FUNCTIONALITY IN HOMININ FOSSILS.*

Feature	Possible function in endurance diving	ED	ER	First appearance known so far (species and age)
Bone mass increase	Body density increase, allowing diving with filled lungs	+	-	*Early Homo/H. erectus*, ca. 2 Ma[a] *P. boisei* and *robustus*, ca. 3–2 Ma[b]
External nose with downward pointing nostrils	Allows air lock, preventing nasal cavity from flooding when submerged	++	0	*H. erectus*, ca. 2 Ma[c]
Relatively short, arched hard palate and humanlike hyoid bone	L-shaped tongue fitting against smooth palate and precise tongue movement allow rapid equalizing of middle ear pressure during diving	++	0	Sima de los Huesos, 0.4 Ma[d]
Wide and deep thorax; Large diaphragm muscle	Large lung capacity for efficient breathing and oxygen storage; Small residual lung volume, more flexible lungs allowing compression when diving	+ +	+ 0	*H. erectus* KNM-WT 15000, ca. 1.4 Ma[e]
Wider carotid foramen in relation to brain size	Allows enhanced cerebral blood flow to compensate for arterial hypoxia	+	0	*H. erectus*, ca. 1.4 Ma[f]
CMAH gene inactivation > absence of Gc-CS in fossils	Increased oxygen transfer to muscles (and other tissues)	+	+	Unknown hominin aged 3–2 Ma[g], testable on fossils[h]
Enlarged posterior and anterior semi-circular canals	Head and body stabilization, increased sensitivity for pitch and roll, increased directional sensitivity underwater	+	+	*H. erectus*, ca. 2 Ma[i]
Auditory exostoses	Consequence of exposure to water in the ear, no known function	0	0	Sima de los Huesos, 0.4 Ma[i]
Modern human-like shoulder with laterally facing glenoid	Allows overhead throwing as well as running, swimming and diving	+	+	*H. erectus*, ca. 2 Ma[k]
Large feet in relation to body size	Efficient swimming and diving	+	-	Early *Homo* and/or *P. boisei*[l,m]? *H. floresiensis*[n]

*Ten examples of features with a possible functional role in endurance diving (likely influencing both hominin endurance diving (ED) and endurance running (ER)) and their so far known earliest appearance in the hominin fossil record. + denotes positive influence, ++ denotes essential feature, - denotes negative influence, 0 denotes neutral or negligible effect. References: [a]Ruff et al. 1993; [b]Ruff et al. 1999; [c]Franciscus and Trinkaus 1988; [d]Steele et al. 2013; [e]Bastir et al. 2022; Lopez-Rey et al. 2023; [f]Seymour et al. 2017; [g]Chou et al. 2002; [h]Bergfeld et al. 2017; [i]Spoor et al. 1994; [i]Conde-Valverde et al. 2019; [k]Roach and Richmond 2015; [l]Dingwall et al. 2013; [m]Hatala et al. 2024; [n]Jungers et al. 2009.

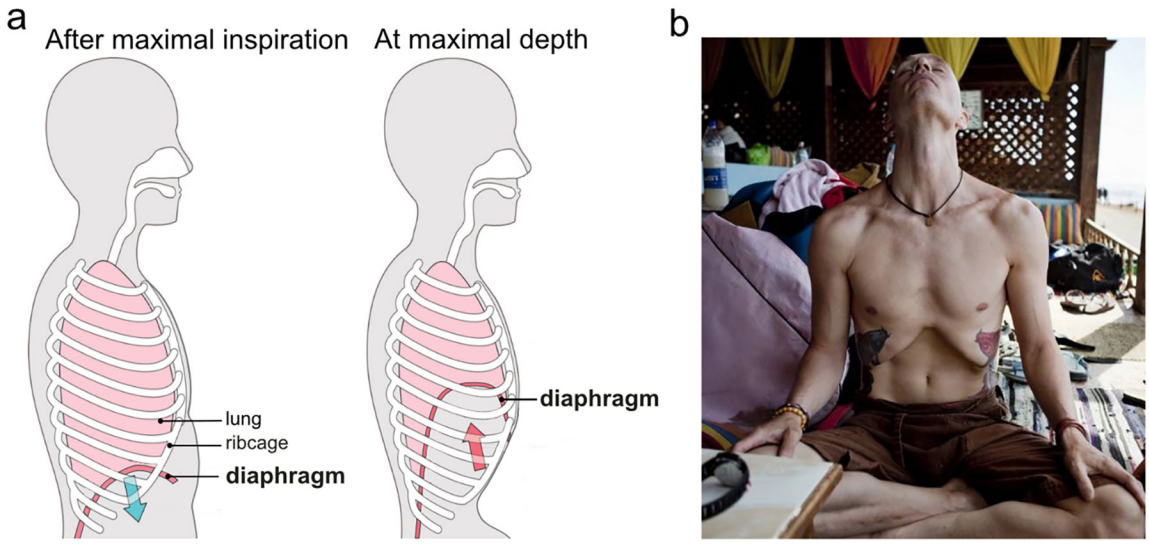


Figure 10. During breathing, the diaphragm contracts and moves down which creates inspiration; upon expiration, the diaphragm relaxes and moves up again. a) The left figure shows the position of the diaphragm when lungs are filled after maximal inspiration; right figure: reaching maximal depth during a breath-hold dive, the relaxed diaphragm is pulled up high in the chest by the shrinking lungs, allowing them to be equalized against the surrounding hydrostatic pressure. When the lungs cannot shrink more, barotrauma with lung damage may occur; b) Freediver performing diaphragm stretching, a central training in freediving, to make the diaphragm longer and let it rise higher into the chest when relaxed, which reduces the smallest lung volume attainable without creating negative pressure in the lungs. This allows deeper diving without the risk of lung injury (photo by Nanna Kreutzmann).

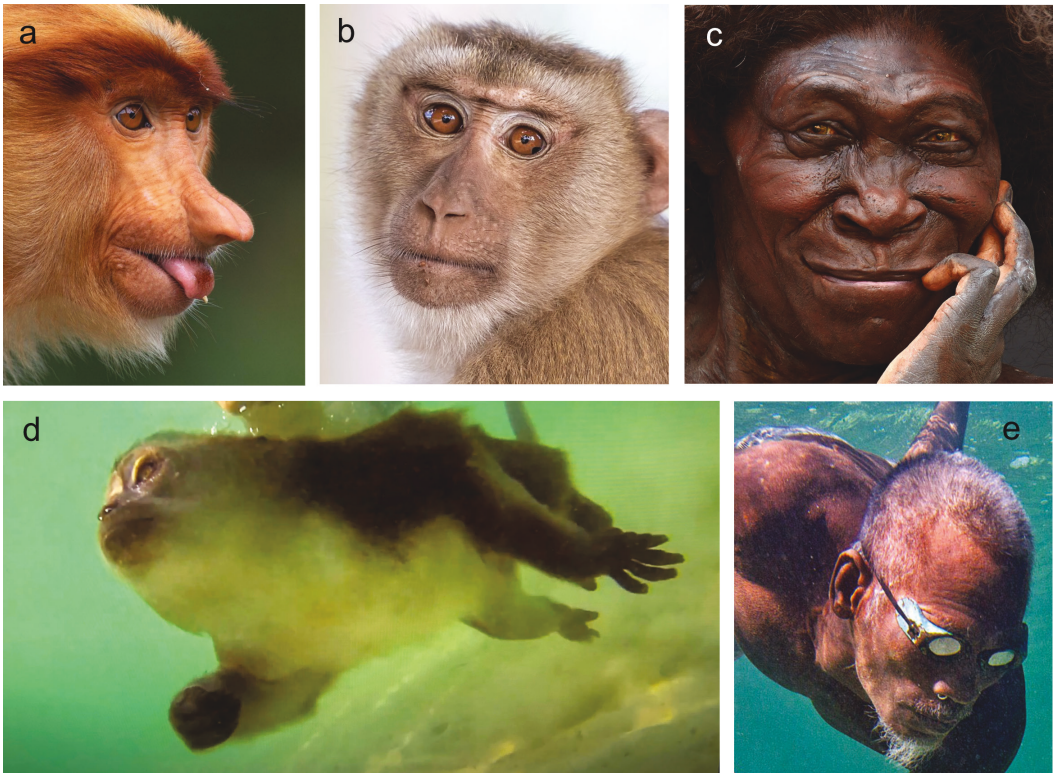


Figure 11. Examples of primate species with external nose and downward pointing nostrils: a) Nasalis larvatus *(proboscis monkey; photo by Mogens Trolle); b)* Macaca fascicularis *(long-tailed macaque; photo by Basile Morin); c)* H. erectus *(reconstruction by paleoartists Kennis and Kennis); d) Underwater swimming long-tailed macaque with air bubbles in nostrils: the air lock that in shallow water prevents water from entering the nasal cavity (screenshot from https://www.youtube.com/watch?v=hr7M4SagHFQ); e) Underwater foraging* H. sapiens *with air bubbles in nostrils (detail from photo by Cory Richards/National Geographic Image Collection).*

of the nasal aperture by narrowing or flaring the nostrils, but the effect is generally limited. It can be speculated that in the past these muscles may have been more developed, possibly allowing full closure of the nostrils. However, in modern humans the modification of the respiratory tract in the form of external nose with downward pointing nostrils is an effective solution, with a flexible tongue allowing equalization and efficient closure of the nasal cavity in the back as seen in the Bajau diving effectively without noseclip. Among extant primates, a few other primates have an ability to swim and dive to some extent. Proboscis monkeys (*Nasalis larvatus*) are avid swimmers and capable of diving and swimming up to 20m horizontal distance underwater (Bennett and Sebastian 1998). Macaques such as the long-tailed macaque (*Macaca fascicularis*, also called crab-eating macaque) can forage for oysters with stone tools (Luncz et al. 2017), swim between islands, dive underwater, and appear to be able to stay submerged for up to 30 seconds (youtube.com/watch?v=6dzZXnBi6jk; Kempf 2009). Proboscis monkeys and macaques are also among the few known other primates who have a nose with more downward oriented nostrils, apparently allowing them to maintain an airlock to close off the nose when underwater at shallow depths (see Figure 11). In water deeper than a few meters this airlock alone would not work to prevent flooding of the nasal cavity, then also the active closure of nasal airways by the soft palate would be necessary; it is not known if proboscis monkeys and macaques are able to do that. While they can dive, none of these species has a breath-hold diving ability comparable to that of humans.

While an external nose and upper airway morphology that allows creating an airlock in the nostrils is beneficial for diving (see Figures 4 and 11), it lengthens and bends the airway (Bastir et al. 2022; Tian et al 2022; Xi et al. 2023), which may be disadvantageous for an endurance runner due to the increased resistance (Bramble and Lieberman 2004). The increased upper airway resistance is why a human diver at the surface always uses mouth breathing for efficient ventilation to rapidly replace oxygen stores, and we speculate that the necessity to close the nose during diving could have been the start of this transition. Once efficient mouth-breathing had evolved, it may have been coopted for improved breathing during endurance running and for life at high altitude.

A NEW PERSPECTIVE

The features discussed above are examples of the potential to re-interpret available data in the hominin fossil record, and to develop new research ideas, when including submerged foraging in the possible hominin repertoire. Looking at available fossil data from a combined land and water perspective may lead to new functional interpretations that were not considered before. We believe that the examples in Table 1 may stimulate further research on the ever-increasing hominin fossil record. Despite its biases and limitations, the fossil record is a key data archive that can contribute to a future balanced evaluation of the 'dive first, run later' hypothesis, and the alternative 'run first, dive later' one. To achieve that, the fossil data should ideally be interpreted in an interdisciplinary context together with data from comparative physiology and genetic research.

If we would speculate what an essentially terrestrial but shallow diving-adapted hominin forager would look like, we predict it would have systemically high bone mass, a wide and deep chest with large total lung capacity and a large and flexible diaphragm to allow efficient breathing as well as safe lung shrinkage at depth, an external nose with nostrils pointing downward, a humanlike hyoid bone reflecting a descended larynx, a short and arched palate accommodating a large and flexible tongue, big feet relative to stature, an inactivated *CMAH* gene enhancing oxygen transfer, and possible presence of auditory exostoses reflecting activities in water.

Furthermore, we expect that fossils of such hominins would be present in or near a paleo-coastal setting, in freshwater as well as marine paleoenvironments, likely together with fossil remains of aquatic prey (e.g., molluscan shells, fish bones). While preservation of fossils in marine coastal settings is rare due to tides and sea-level changes (Bailey and Fleming 2008), and local conditions such as humid coastal forests that do not favor fossilization (Joordens et al. 2019), there are many recent examples showing that with targeted search efforts relevant discoveries can be made (e.g., Bobe et al. 2023; Habermann et al. 2019; Hublin et al. 2026). For example, on the North African Atlantic coast ~0.8 My old fossils of the last common ancestor of Neanderthals, Denisovans, and *H. sapiens* have been found (Hublin et al. 2026), including a relatively 'heavy' femur with ~83% cortical area at ~60–65% of the shaft length (Daujeard et al. 2016). Successful search strategies include deep digging in coastal caves (Martinon-Torres et al. 2021), dredging the seabed of shallow shelf seas (Berghuis et al. 2025a, 2025b; Chang et al. 2015; Tsutaya et al. 2025) and exploring so far understudied early Pleistocene paleocoastal deposits (Widianto and Noerwidi 2020). Fossils of a late Early Pleistocene coastal population have been found already. For example, cranial fossils from Java (Indonesia), such as Sangiran 4, 27, and 31 (Kaifu et al. 2005; 2008; Tyler et al. 1995; Westaway et al. 2015) reflect the presence of a heavy-boned hominin population, attributed to *H. erectus*, living in a coastal forest setting along the Indian Ocean (Berghuis 2026; Bettis et al. 2008; Djubiantono and Semah 1990). We speculate that their so far unexplained 'hyperrobusticity', including extremely thick skulls, could point to a shallow diving adaptation in their lineage.

SUMMARY AND CONCLUSIONS

The 'dive first, run later' hypothesis holds that a coastal hominin population started underwater foraging for aquatic resources and developed an ability for systematic endurance breath-hold diving in a way that is unique among primates, and that this led to adaptations in, e.g., thorax and facial morphology, bone (micro)anatomy, and cardiorespiratory physiology. It is hypothesized that some of these

adaptations, including the aerobic endurance, were later co-opted to use for endurance running on land. We suggest that the environmental drivers for that novel underwater foraging behavior may have consisted of both push and pull factors, which must have been quite strong at some periods. During severe and prolonged environmental crises leading to scarcity of terrestrial resources, niche shifts towards reliance on richly available submerged aquatic resources could have been a life saver, leading to new morphological and physiological adaptations, just as in many other mammals exposed to similar conditions. It may have allowed an isolated coastal hominin population to 'squeeze through' a bottleneck by adding shallow water endurance diving to mainly terrestrial coastal foraging activities.

Recent modelling studies based on genomic data indicate that different groups of early humans periodically interacted with each other within Africa, and that these groups had varying degrees of reproductive connection and isolation across time (Cousins et al. 2025; Ragsdale et al. 2023; Scerri et al. 2018). A recent diagram of modelled human demographic history suggests a deep population structure with two major ancestral branches that were separated around 1.5 Ma and rejoined around 300 ka, the older one derived after a sharp bottleneck and providing 80% of the human genome (Cousins et al. 2025). We tentatively speculate that a bottlenecked lineage could be associated with the origin of shallow diving in an isolated coastal population in response to an environmental crisis, that later converged with a non-diving human lineage. A population structure with several ancestral branches could help explain the wide individual variety in diving talent as well as in running capacity among modern humans. A merge of different branches would have further increased the bandwidth of ecological tolerance through the considerably extended locomotor and foraging repertoire in the human lineage. We propose that a versatile, extended repertoire facilitated the successful hominin dispersal to a wide range of coastal and inland environments at both low and high altitudes.

We conclude that when studying the origin of human endurance, it is vital to take not only endurance running but also endurance diving into account. Based on comparative physiology and our preliminary exploration of the hominin fossil record we tentatively suggest that the 'dive first, run later' hypothesis may have certain advantages over the 'run first, dive later' hypothesis. Nevertheless, we acknowledge that years of further interdisciplinary research will be needed to in-depth test and reject or refine these hypotheses. We hope that our review will inspire researchers from different fields to make functional interpretations of the available and forthcoming hominin fossil record from a wider land-and-water perspective, to deepen our understanding of human evolution.

ENDNOTES

[1]Energy transfer by aerobic and anaerobic pathways are well described, but too complex to include here, please refer to textbooks in physiology for details. Lactate formation and the associated muscle acidosis is not the only cause of muscle fatigue, and the specific role of lactate is controversial. As the details are beyond the scope of this paper, here we let 'lactate' represent the group of factors responsible for muscle fatigue to develop; changes that typically occur together when there is a decline of performance (see Brooks et al. 2002; Cairns and Lindinger 2025; Fitts 2016). Lactate is a metabolic intermediate with many functions in energy substrate utilization, cell signaling, and adaptation (Li et al. 2022).

[2]*H. erectus sensu lato* (s.l.) is an extinct early *Homo* taxon that includes both African and Eurasian fossils (Antón 2013). The so far oldest fossils were found in Africa ~2 Ma (Herries et al. 2020; Mussi et al. 2023) and the youngest fossils in Indonesia ~110 Ka (Berghuis et al. 2025b; Rizal et al. 2020). It is regarded as our possible ancestor, and one of the first versatile hominin taxa that could occupy a range of environments and dispersed beyond Africa (Antón et al. 2020). However, given the long timespan, the wide geographic range, and its large morphological variation (Antón et al. 2016), it is likely that the taxon contains populations that differed substantially from each other with respect to morphology and foraging behavior. Here we use the simple term *H. erectus* while being aware of all these complexities, including the possibility that the taxon *H. erectus s.l.* comprises several species.

ACKNOWLEDGEMENTS

We thank the many expert freedivers, especially Lotta Ericson, for long collaboration with ES during freediving studies, and for introducing JJ to freediving. ES owes thanks to the Ama divers in Japan, and the Sama-Bajau communities in Indonesia and the Philippines for their hospitality and for sharing knowledge concerning their underwater foraging skills during her visits 1988-2025, and to Erik Abrahamsson for interpretation and support during many of these visits. Thanks are also due to the photographers who allowed us to use their photos in this article, to Sven Björkman for critical reading and to Jan Willem Dogger for help with the artwork. We are grateful to Christopher Ruff for providing important data and key references. We greatly appreciate the constructive comments of reviewers Leslea Hlusko, Christopher Ruff, and an anonymous reviewer, and thank Tracy Kivell for providing valuable feedback to an earlier version of the manuscript. Finally, we are grateful to our co-workers and sponsors across the many years of research.

DATA AVAILABILITY STATEMENT

The paleoanthropological and biological data discussed in this study are presented in Supplementary Information Tables S1 and S2 (Excel files are available by request to the corresponding author). The individual human physiology data cannot be shared due to confidentiality agreements with the participants.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

JJ and ES: Conceptualization, Analysis, Writing, Review and Editing.

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REFERENCES

Abrahamsson, E., Schagatay, E., 2014. A living based on breath-hold diving in the Bajau Laut. Hum. Evol. 29 (1–3), 171–183.

Aguilar-Gómez, D., Bejder, J., Graae, J., Ko, Y., Vaughn, A., Clement, K., Tristani-Firouzi, M., Lee, J.-Y., Nordsborg, N., Nielsen, R., Ilardo, M., 2025. Genetic and training adaptations in the Haenyeo divers of Jeju, Korea. Cell Rep. 44, 115577.

Alemseged, Z., 2023. Reappraising the palaeobiology of *Australopithecus*. Nature 617, 45–54.

Alfsen, A., Bianucci, G., Houssaye, A., Hampe, O., Amson, E., de Muizon, C., Lambert, O., Kaffler, A., McCurry, M., Varas-Malca, R., Salas-Gismondi, R., 2025. Broadening the semiaquatic scene: quantification of long bone microanatomy across pinnipeds. Anat. Rec. 1–27.

Altman, M.O., Gagneux, P., 2019. Absence of Neu5Gc and presence of Anti-Neu5Gc antibodies in humans—an evolutionary perspective. Front. Immunol. 10, 789.

Amson, E., de Muizon, C., Laurin, M., Argot, C., de Buffrénil, V., 2014. Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. Proc. R. Soc. B 281, 20140192.

Amson, E., Billet, G., de Muizon, C., 2018. Evolutionary adaptation to aquatic lifestyle in extinct sloths can lead to systemic alteration of bone structure. Proc. R. Soc. B 285, 20180270.

Andersson, J., Schagatay, E., 1998. Arterial oxygen desaturation during apnea in humans. Undersea Hyperb. Med. 25(1), 21–25.

Andersson, J., Schagatay, E., Gislén, A., Holm, B., 2000, Cardiovascular responses to cold water immersions of the forearm and face, and their relationship to apnoea. Eur. J. Appl. Physiol. 83, 566–572.

Antón, S. C., 2003. Natural history of *Homo erectus*. Yearb. Phys. Anthropol. 46, 126–170.

Antón, S., 2013. *Homo erectus* and related taxa. In: Begun, D.R. (Ed.), A Companion to Paleoanthropology, Blackwell Publishing, 497–516.

Antón, S., Taboada, H., Middleton, E., Rainwater, C., Taylor, A., Turner, T., Turnquist, T., Weinstein, K., Williams, S., 2016. Morphological variation in *Homo erectus* and the origins of developmental plasticity. Phil. Trans. Royal Soc. B. 371(1698), 2-150236.

Antón, S. C., 2020. All who wander are not lost. Science 368, 34–35.

Antón, S.A., Middleton, E.R., 2023. Making meaning from fragmentary fossils, early *Homo* in the Early to early Middle Pleistocene. J. Hum. Evol. 179, 103307.

Archer, W., Braun, D. R., Harris, J.W., McCoy, J.T., Richmond, B.G., 2014. Early Pleistocene aquatic resource use in the Turkana Basin. J. Hum. Evol., 77, 74–87.

Arre, A.M., Horschler, D.J., 2021. Swimming and diving as social play in juvenile rhesus macaques (*Macaca mulatta*). Behaviour 158, 529–546.

Baab, K.L., Copes, L.E., Ward, D.L., Wells, N., Grine, F.E., 2018. Using modern human cortical bone distribution to test the systemic robusticity hypothesis. J. Hum. Evol. 119, 64–82.

Barash, A., Belmaker, M., Bastir, M., Soudack, M., O'Brien, H.D., Woodward, H., Prendergast, A., Barzilai, O., Been, E., 2022. The earliest Pleistocene record of a large-bodied hominin from the Levant supports two out-of-Africa dispersal events. Sci. Rep. 12, 1721.

Barr, W.A., Pobiner, B., Rowan, J., Du, A., Faith, J.T., 2022. No sustained increase in zooarchaeological evidence for carnivory after the appearance of *Homo erectus*. Proc. Nat. Acad. Sci., U.S.A. 119 (5), e21115540119.

Barr, A., Wood, B., 2024. Spatial sampling bias influences our understanding of early hominin evolution in eastern Africa. Nat. Ecol. Evol. 8, 2113–2120.

Barsbai, T., Lukas, D., Pondorfer, A., 2021. Local convergence of behaviour across species. Science 371 (6526), 292–295.

Bastir, M., García-Martínez, D., Torres-Tamayo, N., Palancar, C.A., Beyer, B., Barash, A., Villa, C., Sanchis-Gimeno, J.A., Riesco-López, A., Nalla, S., Torres-Sánchez, I., García-Río, F., Been, E., Gómez-Olivencia, A., Haeusler, M., Williams, S.A., Spoor, F., 2020. Rib cage anatomy in *Homo erectus* suggests a recent evolutionary origin of modern human body shape. Nat. Ecol. Evol. 4 (9), 1178–1187.

Beall, C.M., 1982. Comparison of chest morphology in high altitude Asian and Andean populations. Hum. Biol. 54, 145–163.

Beall, C.M., Brittenham, G.M., Strohl, K.P., Decker, M.J., Goldstein, M.C., Blangero, J., Williams-Blangero, S., Almasy, L., Worthman, C.M., 1997. Ventilation and hypoxic ventilatory response of Tibetan and Aymara high altitude natives. Am. J. Phys. Anthropol. 104, 427–447.

Bellina, B., Blench, R., Galipaud, J.-C. (Eds.), 2021. Sea Nomads of Southeast Asia, from the Past to the Present. NUS Press, Singapore.

Bennett, E., Sebastian, A., 1988. Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. Int. J. Primatol. 9 (3), 233–255.

Bergfeld, A.K., Lawrence, R., Diaz, S.L., Pearce, O.M.T., Ghaderi, D., Gagneux, P., Leakey, M.G., 2017. N-glycolyl groups of nonhuman chondroitin sulfates survive in ancient fossils. Proc. Nat. Acad. Sci., U.S.A. 114, e8155–64.

Berghuis, H.W.K., 2026. From the Solo to the Madura Strait: Quaternary Geology, Vertebrate Palaeontology and Hominin Chronology of Eastern Java and Submerged Sundaland. Ph.D. Dissertation. Leiden University.

Berghuis, H.W.K., Kaifu, Y., Prasetyo Wibowo, U, van Kolfschoten, T., Sutisna, I., Noerwidi, S., Adhityatama, S., van den Bergh, G., Pop, E., Adi Suriyanto, R., Veldkamp, A., Joordens, J.C.A., Kurniawan, I., 2025b. The late Middle Pleistocene *Homo erectus* of the Madura Strait, first hominin fossils from submerged Sundaland. Quatern. Environ. Hum. 3 (2), 100068.

Berghuis, H.W.K., Veldkamp, A., Adhityatama, S., Reimann, T., Versendaal, A., Kurniawan, I., Pop, E., van Kolfschoten, T., Joordens, J.C.A., 2025a. A late Middle

Pleistocene lowstand valley of the Solo River on the Madura Strait seabed, geology and age of the first hominin locality of submerged Sundaland. Quatern. Environ. Hum. 3 (2), 100042.

Berta, A., Sumich, J., Kovacs, K., 2005. Marine Mammals, Evolutionary Biology. Elsevier Academic Press, London.

Bibi, F., Souron, A., Bocherens, H., Uno, K., Boisserie, J., 2013. Ecological change in the lower Omo Valley around 2.8 Ma. Biol. Lett. 9 (1), 20120890.

Bobe, R., Wood, B., 2022. Estimating origination times from the early hominin fossil record. Evol. Anthropol. 31, 92–102.

Bodkin, J.L., Esslinger, G.G., Monson, D.H., 2004. Foraging depths of sea otter and implications to coastal marine communities. Mar. Mammal Sci. 20, 305–321.

Bouchard, C., An, P., Rice, T., Skinner, J.S., Wilmore, J.H., Gagnon, J., Pérusse, L., Leon, A.S., Rao, D.C., 1999. Familial aggregation of VO(2max) response to exercise training: results from the HERITAGE Family Study. J. Appl. Physiol. 87, 1003–1008.

Bouten, J., Caen, K., Stautemas, J., Lefevre, F., Derave, W., Lootens, L., van Eenoo, P., Bourgois, J., Boone, J., 2019. Eight weeks of static apnea training increases spleen volume but not acute spleen contraction. Respir. Physiol. Neurobiol. 266, 144–149.

Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. Nature 432 (7015), 345–352.

Braun, D.R., Harris, J.W.K., Levin, N.E., McCoy, J.T., Herries, A.I.R., Bamford, M.K., Bishop, L.C., Richmond, B.G., Kibunjia, M., 2010. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. Proc. Nat. Acad. Sci., U.S.A. 107,10002–10007.

Braun, D., Palcu Rolier, D., Advokaat, E., Archer, W., Baraki, N., Biernat, M., Beaudoin, E., Behrensmeyer, A.K., Bobe, R., Elmes, K., Forrest, F., Hammond, A., Jovane, L., Kinyanjui, R., de Martini, A., Mason, P., McGrosky, A., Munga, J., Ndiema, E.K., Patterson, D., Reeves, J., Roman, D., Sier, M., Srivasta, P., Tuosto, K., Uno, K., Villaseñor, A., Wynn, J., Harris, J., Carvalho, S., 2025. Early Oldowan technology thrived during Pliocene environmental change in the Turkana Basin, Kenya. Nat. Comm. 16, 9401.

Brill, G., Mirazon-Lahr, M., Dyble, M., 2024. Extensive locomotor versatility across a global sample of hunter–gatherer societies. Proc. R. Soc. B 291, 20242553.

Brooks, G.A., 2002. Lactate shuttles in nature. Biochem. Soc. Trans. 30, 258–264.

Brutsaert, T., Harman, T., Bigham, A., Kalker, A., Jorgensen, K., Zhu, K., Steiner, B., Hawkins, E., Day, T., Kunwar, A., Thakur, N., Dhungel, S., Sherpa, N., Holmström, P., 2024. Larger spleens and greater splenic contraction during exercise may be an adaptive characteristic of Nepali Sherpa at high-altitude. Am. J. Hum. Biol. 36 (9), 1–17.

Butler, P.J., Turner, D.L, Al-Wassia, A., Bevan, R.M., 1988. Regional distribution of blood flow during swimming in the tufted duck (*Aythya fuligula*). J. Exp. Biol. 135(1), 461–472.

Butler, P.J., 2006. Aerobic dive limit. What is it and is it always used appropriately? Comp. Biochem. Physiol. A, Molec. Integr. Physiol. 145 (1), 1–6.

Butler, P.J., Jones, D.R., 1997. Physiology of diving of birds and mammals. Physiol. Rev. 77 (3), 837–899.

Cairns, S., Lindinger, M., 2025. Lactic acidosis: implications for human exercise performance. Eur. J. Appl. Physiol. 125, 1761–1795.

Caley, T., Collins, J., Schefuß, E., Dupont, L., Malaizé, B., Rossignol, L., Souron, A., McClymont, E., Jimenez-Espejo, J., García-Comas, C., Eynaud, F., Martinez F., Roche, D., Jorry, S., Charlier, K., Wary, M., Gourves, P.-Y., Billy, I., Giraudeau, J., 2018. A two-million-year-long hydroclimatic context for hominin evolution in southeastern Africa. Nature 560, 76–79.

Cameron, D., Groves, C., 2004. Bones, Stones and Molecules, "Out of Africa" and Human Origins. Elsevier Academic Press, Amsterdam.

Carlton, J.T, Hodder, J., 2003. Maritime mammals, terrestrial mammals as consumers in marine intertidal communities. Mar. Ecol. Progr. Ser. 256, 271–286.

Carretero, J.M., Rodríguez, L., Garcia-Gonzalez, R., Quam, R.M., Arsuaga, J.-L., 2018. Exploring bone volume and skeletal weight in the Middle Pleistocene humans from the Sima de los Huesos site (Sierra de Atapuerca, Spain). J. Anat. 233, 740–754.

Carrier, D.R., 1984. The energetic paradox of human running and hominid evolution. Curr. Anthropol., 25, 483–495.

Chou, C., 2016. The water world of the Orang Suku Laut in Southeast Asia. TRaNS 4 (2), 265–282.

Chou, H., Hayakawa, T., Diaz, S., Krings, M., Indriati, E., Leakey, M., Pääbo, S., Satta, Y., Takahata, N., Varki, A., 2002. Inactivation of CMP-N-acetylneuraminic acid hydroxylase occurred prior to brain expansion during human evolution. Proc. Nat. Acad. Sci., U.S.A. 99 (18), 11736–11741.

Christiansen, P., 2002. Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed. Zool. J. Linn. Soc. 136, 685–714.

Cohen, A.S., Campisano, C.J., Arrowsmith, J.R., Asrat, A., Beck, C.C., Behrensmeyer, A.K., Deino, A.L., Feibel, C.S., Foerster, V., Kingston, J.D., Lamb, H.F., Lowenstein, T.K., Lupien, R.L., Muiruri, V., Olago, D.O., Owen, R.B., Potts, R., Russell, J.M., Schaebitz, F., Stone, J.R., Trauth, M.H., Yost, C.L., 2022. Reconstructing the environmental context of human origins in eastern Africa through scientific drilling. Ann. Rev. Earth Planet. Sci. 50, 451–76.

Colombo, S., Wacker, A., Parrish, C., Kainz, M., Arts, M., 2017. A fundamental dichotomy in long-chain polyunsaturated fatty acid abundance between and within marine and terrestrial ecosystems. Environ. Rev. 25, 163–174

Cooke, N.P., Murray, M., Cassidy, L., Mattiangeli, V., Okazaki, K., Kasai, K., Gakuhari, T., Bradley, D., Nak-

agome, S., 2024. Genomic imputation of ancient Asian populations contrasts local adaptation in pre- and post-agricultural Japan. iScience 27, 110050.

Cortes-Sanchez, M., Simon-Vallejo, M., Jimenez-Espejo, F., Lozano Francisco, M., Vera-Pelaez, J., Maestro Gonzalez, A., Morales-Muñiz, A., 2019. Shellfish collection on the westernmost Mediterranean, Bajondillo cave (~160-35 cal kyr BP), a case of behavioral convergence? Quatern. Sci. Rev. 217, 284–296.

Cunnane, S., Stewart, K., 2010. Human Brain Evolution, The Influence of Freshwater and Marine Food Resources. John Wiley and Sons, Hoboken, NJ.

Cureton, K.J., Sparling, P.B., Evans, B.W., Johnson, S.M., Kong, U.D., Purvis, J.W., 1978. Effect of experimental alterations in excess weight on aerobic capacity and distance running performance. Med. Sci. Sports 10 (3), 194–199.

Curran, S., Drăgușin, V., Pobiner, B., Pante, M., Hellstrom, J., Woodhead, J., Croitor, R., Dobos, A., Gogol, S., Ersek, V., Keevil, T., Petculescu, A., Popescu, A., Robinson, C., Werdelin, L., Terhune, C., 2025. Hominin presence in Eurasia by at least 1.95 million years ago. Nat. Comm. 16, 836.

Currey, J., Alexander, R., 1985. The thickness of the walls of tubular bones. J. Zool. Lon. (A) 206, 453–468.

Darimont, C.T., Paquet, P.C., Reimchen, T.E, 2008. Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. BMC Ecol. 8 (14), 1–12.

Daujeard, C., Geraads, D., Gallotti, R., Lefèvre, D., Mohib, A., Raynal, J.-P., Hublin, J.-J., 2016. Pleistocene hominins as a resource for carnivores: a c. 500,000-year-old human femur bearing tooth-marks in North Africa (Thomas Quarry I, Morocco). PLoS One 11, e0152284.

De Bruijn, R., Richardson, M., Schagatay, E., 2008. Increased erythropoietin concentration after repeated apneas in humans. Eur. J. Appl. Physiol. 102, 609–613.

De Chevalier, G., Bouret, S., Bardo, A., Simmen, B., Garcia, C., Prat, S., 2022. Cost-benefit trade-offs of aquatic resource exploitation in the context of hominin evolution. Front. Ecol. Evol. 10, 812804.

De Vynck, J.C., Difford, M., Anderson, R., Marean, C.W., Cowling, R.M., Hill, K., 2020. The resilience to human foraging of intertidal resources on the south Cape coast of South Africa and the implications for prehistoric foragers. Quatern. Sci. Rev. 235, 106041.

DiMaggio, E.N., Campisano, C.J., Rowan, J., Dupont-Nivet, G., Deino, A.L., Bibi, F., Lewis, M.E., Souron, A., Garello, D., Werdelin, L., Reed, K.E., Arrowsmith, J.R., 2015. Late Pliocene fossiliferous sedimentary record and the environmental context of early *Homo* from Afar, Ethiopia. Science 347 (6228), 1355–1359.

Dingwall, H., Hatala, K., Wunderlich, R., Richmond, B., 2013. Hominin stature, body mass, and walking speed estimates based on 1.5 million-year-old footprints at Ileret, Kenya. J. Hum. Evol. 64(6), 556–568.

Dodo, Y., 1972. Aural exostoses in the human skeletal remains excavated in Hokkaido. J. Anthrop. Soc. Nippon 80, 11–22.

Droma, T., McCullough, R.G., McCullough, R.E., Zhuang, J., Cymerman, A., Sun, S., Sutton, J.R., Moore, L.G., 1991. Increased vital and total lung capacities in Tibetan compared to Han residents of Lhasa (3,658 m). Am. J. Biol. Anthropol. 86(3), 341–351.

Dupont-Nivet, G., Sier, M., Campisano, C.J., Arrowsmith, J.R., DiMaggio, E., Reed, K., Lockwood, C., Franke, C., Hüsing, S., 2008. Magnetostratigraphy of the eastern Hadar Basin (Ledi-Geraru research area, Ethiopia) and implications for hominin paleoenvironments. In: Quade, J., Wynn, J.G. (Eds.), The Geology of Early Humans in the Horn of Africa. Geol. Soc. Am. Special Paper 446, Boulder, CO, pp. 67–85.

Elia, A., Wilson, O., Lees, m., Parker, P., Barlow, M., Cocks, M., O'Hara, J.P., 2019 Skeletal muscle, haematological and splenic volume characteristics of elite breath-hold divers. Europ. J. Appl. Physiol. 119, 2499–2511.

Elia, A., Gennser, M., Harlow, P.S., Lees, M., 2021. Physiology, pathophysiology and (mal)adaptations to chronic apnoeic training, a state-of-the-art review. Eur. J. Appl. Physiol. 121, 1543–1566.

Elsner, R., Franklin, D.L., van Citters, R.L., Kenney, D.W., 1966. Cardiovascular defense against asphyxia, studies of circulatory responses to diving in aquatic and land animals clarify some reactions to asphyxia. Science 153 (3739), 941–949

Engan, H., Richardson, M.X., Lodin-Sundström, van Beekvelt, M., Schagatay, E., 2013. Effects of two weeks of daily apnea training on diving response, spleen contraction, and erythropoiesis in novel subjects. Scan. J. Med. Sci. Sports 23 (3), 340–348.

Faith, J.T., Du, A., Behrensmeyer, A.K., Davies, B., Patterson, D.B., Rowan, J., Wood, B., 2021. Rethinking the ecological drivers of hominin evolution. Trends Ecol. Evol. 36 (9), 797–807.

Fahlman, A., Burggren, W., Milsom, W., 2024. The role of cognition as a factor regulating the diving responses of animals, including humans. J. Exp. Biol. 227 (20), jeb246472.

Fahlman, A., Schagatay, E., 2014. Man's place among the diving mammals. Hum. Evol. 29(1–3), 47–66.

Fahlman, A., Tyson Moore, R., Stone, R., Sweeney, J., Faulkner Trainor, R., Barleycorn, A., McHigh, K., Allen, J., Wells, R., 2023. Deep diving by offshore bottlenose dolphins (*Tursiops* spp). Mar. Mammal Sci. 39, 1251–1266.

Fiori, G., Facchini, F., Ismagulov, O., Ismagulova, A., Tarazona-Santos, E., Pettener, D., 2000. Lung volume, chest size, and hematological variation in low-, medium-, and high-altitude Central Asian populations. Am. J. Biol. Anthropol. 113(1), 47–59.

Fisher, E.C., Cawthra, H.C., Esteban, I., Jerardino, A., Neumann, F.H., Oertle, A., Pargeter, J., Saktura, R.B., Szabó, K., Winkler, S., Zohar, I., 2020. Coastal occupation and foraging during the last glacial maximum and early Holocene at Waterfall Bluff, eastern Pondoland, South Africa. Quatern. Res. 97, 1–41.

Fitts, R.H., 2016. The role of acidosis in fatigue: pro perspective. Med. Sci. Sports Exerc. 48, 2335–2338.

Foley, R., Lahr, M.M., 2014. The role of "the aquatic" in human evolution, constraining the Aquatic Ape Hypothesis. Evol. Anthropol. 23, 56–59.

Franciscus, R., Trinkaus, E., 1988. Nasal morphology and the emergence of *Homo erectus*. Am. J. Phys. Anthropol. 75, 517–528.

Gaddie, J.W., Kennedy, E.P., Green, M., Killen, L.G., Linder, B.A., Heinkel, A.A., O'Neal, E.K., 2021. Effects of three modest levels of proximal loading on marathon pace running economy. Int. J. Exerc. Sci. 13 (7), 1120–1131.

Gislèn, A., Dacke, M., Kröger, R.H.H., Abrahamsson, M., Nilsson, D.-E., Warrant, E.J., 2003. Superior underwater vision in a human population of Sea Gypsies. Curr. Biol. 13, 833–836.

Glaub, M., Hall, C., 2017. Evolutionary implications of persistence hunting, an examination of energy return on investment for !Kung hunting. Hum. Ecol. 45, 393–401.

González-Alonso, J., Teller, C., Andersen, S., Jensen, F., Hyldig, T., Nielsen, B., 1990. Influence of body temperature on the development of fatigue during prolonged exercise in the heat. J. Appl. Physiol. 86(3), 1032–1039.

González-Alonso, J., Crandall, C., Johnson, J., 2008. The cardiovascular challenge of exercising in the heat. J. Physiol. 586(1), 45–53.

Goren-Inbar, N., Melamed, Y., Zohar, I., Akhilesh, K., Pappu, S., 2014. Beneath still waters - multistage aquatic exploitation of *Euryale ferox* (Salisb.) during the Acheulian. In: Fernandes, R., Meadows, J., (Eds.), Human Exploitation of Aquatic Landscapes, special issue Internet Archaeol. https://doi.org/10.11141/ia.37.1

Goto, S., Kataoka, K., Isa, M., Nakamori, K., Yoshida, M., Murayama, S., Arasaki, A., Ishida, H., Kimura R., 2023. Factors associated with bone thickness: comparison of the cranium and humerus. PLoS One 18(3), e0283636.

Gould, S.J., Vrba, E., 1982. Exaptation-a missing term in the science of form. Paleobiol. 8(1), 4–15.

Groves, C., 1993. Book review "The Aquatic Ape, Fact or Fiction? The first scientific evaluation of a controversial theory of human evolution". Hum. Biol. 65 (6), 1038–1040.

Gumert, M., Malaivijitnond, S., 2012. Marine prey processed with stone tools by Birmese Long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. Am. J. Phys. Anthropol. 149, 447–457.

Habermann, J.M., Alberti, M., Aldeias, V., Alemseged, Z., Archer, W., Bamford, M., Biro, D., Braun, D.R., Capelli, C., Cunha, E., Ferreira da Silva, M., Lüdecke, T., Madiquida, H., Martine, F.I., Mathe, J., Negash, E., Paulo, L.M., Pinto, M., Stalman, M., Táta Regala, F., Wynn, J.G., Bobe, R., Carvalho, S., 2019. Gorongosa by the sea, first Miocene fossil sites from the Urema Rift, central Mozambique, and their coastal paleoenvironmental and paleoecological contexts. Palaeogeogr. Palaeoclim. Palaeoecol. 514, 723–738.

Habib, M., Ruff, C.B., 2008. The effects of locomotion on the structural characteristics of avian limb bones. Zool. J. Linn. Soc. 153, 601–624.

Halsey, L.G., Bryce, C.M., 2021. Are humans evolved specialists for running in the heat? Man vs. horse races provide empirical insights. Exp. Physiol. 106, 258–268.

Hand, S., Wilson, L., López-Aguirre, C., Houssaye, A., Archer, M., Bevitt, J., Evans, A., Halim, A., Hung, T., Rich, T., Vickers-Rich, P., Beck, R., 2025. Bone microstructure supports a Mesozoic origin for a semiaquatic burrowing lifestyle in monotremes (Mammalia). Proc. Nat. Acad. Sci., U.S.A. 122 (19), e2413569122.

Hardy, A., 1960. Was man more aquatic in the past? New Sci. 7, 642–645.

Hart, N., Newton, R., Tan, J., Rantalainen, T., Chivers, P., Siafarika, A., Nimphius, S., 2020. Biological basis of bone strength, anatomy, physiology and measurement. J. Musculoskelet. Neuronal Interact. 20(3), 347–371

Hart, N., Nimphius, S., Rantalainen, T., Ireland, A., Siafarikas, A., Newton, R., 2017. Mechanical basis of bone strength, influence of bone material, bone structure and muscle action. J. Musculoskelet. Neuronal Interact. 17(3), 114–39.

.Hatala, K.G., Dingwall, H.L., Wunderlich, R.E., Richmond, B.G., 2013. Variation in foot strike patterns during running among habitually barefoot populations. PLoS One 8(1), e52548.

Hawkes, L., Kendall-Bar, J., 2025. A deep dive into oxygen sensing, seals directly detect blood oxygen to adjust time underwater. Science 387 (6740), 1256–1257.

Hayashi, S., Houssaye, A., Nakajima, Y., Chiba, K., Ando, T., Sawamura, H., Inuzuka, N., Kaneko, N., Osaki, T., 2013. Bone inner structure suggests increasing aquatic adaptations in Desmostylia (Mammalia, Afrotheria). PLoS One 8, e59146.

He, K., Eastman, T. G., Czolacz, H., Li, S., Shinohara, A., Kawada, S., Springer, M.S., Berenbrink, M., Campbell, K. L., 2021. Myoglobin primary structure reveals multiple convergent transitions to semi-aquatic life in the world's smallest mammalian divers. ELife 10, e66797. https://doi.org/10.7554/eLife.66797

Herries, A.I.R., Martin, J.M., Leece, A.B., Adams, J.W., Boschian, G., Joannes-Boyau, R., Edwards, T.R., Mallett, T., Massey, J., Murszewski, A., Neubauer, S., Pickering, R., Strait, D.S., Armstrong, B.J., Baker, S., Caruana, M.V., Denham, T., Hellstrom, J., Moggi-Cecchi, J., Mokobane, S., Penzo-Kajewski, P., Rovinsky, D.S., Schwartz, G.T., Stammers, R.C., Wilson, C., Woodhead, J., Menter, C., 2020. Contemporaneity of *Australopithecus*, *Paranthropus*, and early *Homo erectus* in South Africa. Science 368 (6486), eaaw7293.

Hilgen, S.L., Pop, E.L., Adhityatama, S., Veldkamp, A., Berghuis, H.W.K., Sutisna, I., Yurnaldi, D., Dupont-Nivet, G., Reimann, T., Nowaczyk, N., Kuiper, K.F., Krijgsman, W., Vonhof, H.B., Ekowati, D.R., Alink, G., Hafsari, M., Drespriputra, O., Verpoorte, A., Bos, R., Simanjuntak, T., Prasetyo, B., Joordens, J.C.A., 2023. Revised age and stratigraphy of the classic *Homo erectus* bearing succession at Trinil (Java, Indonesia). Quatern. Sci. Rev. 301, 107908.

Hiam, D., Voisin, S., Yan, X., Landen, S., Jacques, M., Papadimitriou, I., Munson, F., Byrnes, E., Brennan, S., Levinger, I., Eynon, N., 2019. The association between bone mineral density gene variants and osteocalcin at baseline, and in response to exercise: the gene SMART study. Bone 123, 23–27.

Hixson, S., Sharma, B., Kainz, M., Wacker, A., Arts, M., 2015. Production, distribution, and abundance of long-chain Omega-3 polyunsaturated fatty acids, a fundamental dichotomy between freshwater and terrestrial ecosystems. Environ. Rev. 23, 414–424.

Holm, B., Schagatay, E., Kobayashi, T., Masuda, A., Ohdaira, T., Honda, Y., 1998. Cardiovascular change in elderly male breath-hold divers (Ama) and their socioeconomical background at Chikura in Japan. Appl. Human Sci. J. Physiol. Anthropol. 17(5), 181–187.

Holmström, P., Mulder, E., Starfelt, V., Lodin-Sundström, A., Schagatay, E., 2020. Spleen size and function in Sherpa living high, Sherpa living low and Nepalese lowlanders. Front. Physiol. 11, 647.

Holmström, P., Pernett, F., Schagatay, E., 2022. Test-retest reliability of splenic volume assessment by ultrasonography. Sci. Rep. 12 (1), 18976.

Hora, M., Dattatreya, R., Struška, M., Pontzer, H., Sládek, V., 2025. Human energy expenditure and thermoregulation during persistence hunting in the Namib. J. Hum. Evol. 209, 103773.

Hora, M., Pontzer, H., Struška, M., Entin, P., Sládek, V., 2020. Comparing walking and running in persistence hunting. J. Hum. Evol. 172, 103247.

Houssaye, A., Botton-Divet, L. 2018. From land to water, evolutionary changes in long bone microanatomy of otters (Mammalia, Mustelidae). Biol. J. Linn. Soc. 125, 240–249.

Houssaye, A., de Buffrénil, V., 2021. Bone histology and the adaptation to aquatic life in tetrapods. In: de Buffrénil, V., de Ricqles, A., Zylberberg, L., Padian, K. (Eds.), Vertebrate Skeletal Histology and Paleohistology. CRC Press, Boca Raton, pp. 744–756.

Houssaye, A., Fish, F.E., 2016. Functional (secondary) adaptation to an aquatic life in vertebrates, an introduction to the symposium. Integr. Comp. Biol. 56, 1266–1270.

Hublin, J.J., Lefèvre, D., Perini, S., Muttoni, G., Skinner, M., Bailey, S., Freidline, S., Gunz, P., Rué, M., El Graoui, M., Geraads, D., Daujeard, C., Davies, T.W., Kupczik, K., Imbrasas, M., Ortiz, A., Falguères, C., Shao, Q., Bahain, J.-J., Queffelec, A., Gómez-Olivencia, A., Benazzi, S., Le Cabec, A., Sorrentino, R., Bergmann, I., Shibi-Alaoui, F.-Z., Gallotti, R., Raynal, J.-P., Mohib, A., 2026. Early hominins from Morocco basal to the *Homo sapiens* lineage. Nature 649, 902–908.

Hudson, M., 2022. Dragon divers and clamorous fishermen. Bronzization and transcultural marine spaces in the Japanese archipelago. In: Autiero, S., Cobb, M.A. (Eds.), Globalization and Transculturality from Antiquity to the Pre-Modern World. Routledge, New York, pp. 103–119.

Hurford, W.E., Hochachka, P., Schneider, R., Guyton, G., Stanek, K., Zapol, D., Liggins, G., Zapol, W., 1996. Splenic contraction, catecholamine release, and blood volume redistribution during diving in the Weddell seal. J. Appl. Physiol. 80(1), 298–306.

Hurford, W.E., Hong, S.K., Park, Y.S., Ahn, D.W., Shiraki, K., Mohri, M., Zapol, W.M., 1990. Splenic contraction during breath-hold diving in the Korean Ama. J. Appl. Physiol. 69, 932–936.

Ilardo, M., Ferreira dos Santos, M., Grote Beverborg, N., Rajan, M., Said, A., Verweij, N., van der Harst, P., van der Meer, P., Leibold, E., 2022. An erythropoietin-independent mechanism of erythrocytic precursor proliferation underlies hypoxia tolerance in Sea Nomads. Front. Physiol. 12, 760851.

Ilardo, M.A., Moltke, I., Korneliussen, T.S., Cheng, J., Stern, A.J., Racimo, F., de Barros Damgaard, P., Sikora, M., Seguin-Orlando, A., Rasmussen, S., van den Munckhof, I.C.L., Ter Horst, R., Joosten, L.A.B, Netea, M.G., Salingkat, S., Nielsen, R., Willerslev E., 2018. Physiological and genetic adaptations to diving in Sea Nomads. Cell 173 (3), 569–580.

Irvine, L., Palacios, D., Urban, J., Mate, B., 2017. Sperm whale dive behavior characteristics derived from intermediate-duration archival tag data. Ecol. Evol. 7 (19), 7822–7837.

Johansson, O., Schagatay, E., 2014. Sara Campbell, world champion in deep diving after 9 months of training – How is this possible? Hum. Evol. 29(1–3), 67–73.

Joordens, J.C.A., d'Errico, F., Wesselingh, F.P., Munro, S., de Vos, J., Wallinga, J., Ankjærgaard, C., Reimann, T., Wijbrans, J.R., Kuiper, K.F., Mücher, H.J., Coqueugniot, H., Prié, V., Panuel, M., van der Haas, V., Lustenhouwer, W., Joosten, I., Schulp, A., van Os, B., Reijmer, J.J.G., Roebroeks, W., 2015. *Homo erectus* at Trinil on Java used shells for tool production and engraving. Nature 518, 228–231.

Joordens, J.C.A., Feibel, C.S., Vonhof, H.B., Schulp, A.S., Kroon, D., 2019. Relevance of the eastern African coastal forest for early hominin biogeography. J. Hum. Evol. 131, 176–202.

Joordens, J.C.A., Kuipers, R.S., Wanink, J.H., Muskiet, F.A.J., 2014. A fish is not a fish, patterns in fatty acid composition of aquatic food may have had implications for hominin evolution. J. Hum. Evol. 77, 107–116.

Joordens, J.C.A., Wesselingh, F.P., de Vos, J., Vonhof, H.B., Kroon, D., 2009. Relevance of aquatic environments for hominins, a case study from Trinil (Java, Indonesia). J. Hum. Evol. 57 (6), 656–671.

Kaifu, Y., Aziz, F., Indriati, E., Jacob, T., Kurniawan, I., Baba, H., 2008. Cranial morphology of Javanese *Homo erectus*, new evidence for continuous evolution, specialization, and terminal extinction. J. Hum. Evol. 55(4), 551–580.

Kay, D., Taaffe, D.R., Marino, F.E., 2010. Whole-body precooling and heat storage during self-paced cycling performance in warm humid conditions. J. Sports Sci. 17 (12), 937–944.

Kennedy, G.E., 1986. The relationship between auditory exostoses and cold water, a latitudinal analysis. Am. J.

Phys. Anthropol. 71 (4), 401–415
Knechtle, B., Dalamitros, A.A., Barbosa, T.M., Sousa, C.V., Rosemann, T., Nikolaidis, P.T., 2020. Sex differences in swimming disciplines—can women outperform men in swimming? Int. J. Environm. Res. Publ. Health 17 (10), 3651, 1-17.
Koops, K., Wrangham, R.W., Cumberlidge, N., Fitzgerald, M.A., van Leeuwen, K.L., Rothman, J.M., Matsuzawa, T., 2019. Crab-fishing by chimpanzees in the Nimba Mountains, Guinea. J. Hum. Evol. 133, 230–241.
Kooyman G.L., 1989. Diverse Divers. Physiology and Behavior. Zoophysiology 23, Springer Nature, New York.
Kooyman, G.L., 2009. Marine mammal diving physiology. In: Steele, J., Thorpe, S., Turekia, K. (Eds.), Marine Biology. Elsevier Academic Press, Oxford, UK, pp. 458–464.
Kuliukas, A.V., Morgan, E., 2011. Aquatic scenarios in the thinking on human evolution, what are they and how do they compare? In: Vaneechoutte, M., Kulikukas, A., Verhaegen, M., (Eds.), Was Man More Aquatic In The Past, Fifty Years After Alister Hardy Waterside Hypotheses of Human Evolution. Bentham Books, Singapore, pp. 106–119.
Kusuma, P. Brucato, N., Cox, M., Letellier, T., Manan, A., Nuraini, C., Grangé, P., Sudoyo, H., Ricaut, F.-X., 2017. The last sea nomads of the Indonesian archipelago, genomic origins and dispersal. Eur. J. Hum. Genet. 25, 1004–1010.
Kyriacou, D., Blackhurst, D., Parkington, J., Marias, A., 2016. Marine and terrestrial foods as a source of brain-selective nutrients for early modern humans in the southwestern Cape, South Africa. J. Hum. Evol. 97, 86–96.
Langdon, J., 1997. Umbrella hypotheses and parsimony in human evolution, a critique of the Aquatic Ape Hypothesis. J. Hum. Evol. 33, 479–494.
Lee, J.-Y., Lee, H.-H., Kim, S., Jang, Y.-J., Baek, Y.-J., Kang, K.-Y., 2016. Diving bradycardia of elderly Korean women divers, Haenyeo, in cold seawater, a field report. Industr. Health 54 (2), 183–190.
Levin, N.E., 2015. Environment and climate of early human evolution. Ann. Rev. Earth Planet. Sci. 43, 405–429.
Lewis, M., O'Riain, J., 2017. Foraging profile, activity budget and spatial ecology of exclusively natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa. Int. J. Primatol. 38, 751–779.
Li, X., Yang, Y., Zhang, B., Lin, X., Fu, X., An, Y., Zoy, Y., Wang, J.-X., Wang, Z., Yu, T., 2022. Lactate metabolism in human health and disease. Signal Transduct. Target. Ther. 7, 305.
Lieberman, D., Mahaffey, M., Cubesare Quimare, S., Holowka, Wallace, I., Baggish, A., 2020. Running in Tarahumara (Rarámuri) culture, persistence hunting, footracing, dancing, work, and the fallacy of the athletic savage. Curr. Anthropol. 61 (3), 356–368.
Lindström, S., Sanei, H., van de Schootbrugge, B., Pedersen, G.K., Lesher, C.E., Tegner, C., Heunisch, C., Dybkjær, K., Outridge, P.M., 2019. Volcanic mercury and mutagenesis in land plants during the end-Triassic mass extinction. Sci. Adv. 5, eaaw4018.
Lodin-Sundström, A., Schagatay, E., 2010. Spleen contraction during 20 min normobaric hypoxia and 2 min apnea in humans. Aviat. Space Environ. Med. 81, 545–549.
Lone, K., Kovacs, K.M., Lydersen, C., Fedak, M., Andersen, M., Lovell, P., Aars, J., 2018. Aquatic behaviour of polar bears (*Ursus maritimus*) in an increasingly ice-free Arctic. Sci. Rep. 8, 9677.
Longman, D., Merzbach, V., Pinto, J., Atkinson, L., Wells, J., Gordon, D., Stock, J., 2022. Alternative metabolic strategies are employed by endurance runners of different body sizes; implications for human evolution. Adapt. Hum. Behavior Physiol. 8, 79–97.
Lopes-Marques, M., Serrano, C., Cardoso, A., Salazar, R., Seixas, S., Amorim, A., Azevedo, L., Prata, M., 2020. GBA3: a polymorphic pseudogene in humans that experienced repeated gene loss during mammalian evolution. Sci. Rep. 10, 11565.
López-Rey, J., García-Martínez, D., Martellie, S., Beyer, B., Palancar, C., Torres-Sanchez, I., García-Río, F., Bastir, M., 2023. Estimation of the upper diaphragm in KNM-WT 15000 (*Homo erectus* s.l.) and Kebara 2 (*Homo neanderthalensis*) using a *Homo sapiens* model. J. Hum. Evol. 185, 103442.
López-Rey, J., Crevecoeur, I., May, H., Nadel, D., Palancar, C., Gómez-Recio, M., García-Martínez, D., Bastir, M., 2025. Fossil ribcages of *Homo sapiens* provide new insights into modern human evolution. Comm. Biol. 8, 1038.
Lorentz, K., Casa, B., 2021. External auditory exostoses, repetitive aquatic activity and increasing social complexity in Chalcolithic Cyprus: specialists of the sea? Int. J. Osteoarchaeol. 31 (4), 605–620.
Malm, T., 1999. Shell Age Economics, Marine Gathering in the Kingdom of Tonga, Polynesia. Ph.D. Dissertation. Lund University.
Malm, T., 2007. Searching for clues in the lagoon, Is marine gathering a reflection of our evolutionary past? SPC Women in Fish. Inf. Bull. 20, 10–16.
Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thompson, E., Watts, I., Williams, H.M., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature 449(7164), 905–908.
Marean, C.W., Cowling, R.M., Franklin, J., 2020. The Palaeo-Agulhas Plain, temporal and spatial variation in an extraordinary extinct ecosystem of the Pleistocene of the Cape Floristic Region. Quatern. Sci. Rev. 235(106161), 1–17.
Marino, F., Sibson, B., Lieberman, D., 2022. The evolution of human fatigue resistance. J. Comp. Physiol. B 192, 411–422.
Matsuda, I., Tuuga, A., Akiyama, Y., Higashi, S., 2008. Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. Am. J. Primatol. 70, 1097–1101.
Matsuda, I., Tuuga, A., Bernard, H., 2011. Riverine refuging

by proboscis monkeys (*Nasalis larvatus*) and sympatric primates, implications for adaptive benefits of the riverine habitat. Mammal. Biol. 76, 165–171.

Maxwell, S.J., Hopley, P.J., Upchurch, P., Soligo, C., 2018. Sporadic sampling, not climatic forcing, drives observed early hominin diversity. Proc. Nat. Acad. Sci., U.S.A. 115 (19), 4891–4896.

Mazin, J.-M., de Buffrénil, V. (Eds.), 2001. Secondary Adaptation of Tetrapods to Life in Water. Verlag Dr. Friedrich Pfeil, München.

McKnight, J.C., Mulder, E., Ruesch, A., Kainerstorfer, J.M., Wu, J., Hakimi, N., Balfour, S., Bronkhorst, M., Horschig, J.M., Pernett, F., Sato, K., Hastie, G.D., Tyack, P., Schagatay, E., 2021. When the human brain goes diving, using near-infrared spectroscopy to measure cerebral and systemic cardiovascular responses to deep, breath-hold diving in elite freedivers. Phil. Trans. R. Soc. B 376(1831), 20200349.

McKnight, J.C., Bønnelycke, E.-M., Balfour, S., Milne, R., Moss, S., Armstrong, H., Downie, C., Hall, A., Kershaw, J., 2025. Cognitive perception of circulating oxygen in seals is the reason they don't drown. Science 387, 1276–1280.

Mirceta, S., Signore, A.V., Burns, J.M., Cossins, A.R., Campbell, K.L., Berenbrink, M., 2013. Evolution of mammalian diving capacity traced by myoglobin net surface charge. Science 340 (6138), 1234192.

Mitsunaga, B., Lupien, R., Ouertani, S., Stubbs, B., Deino, A., Kingston, J., Stockhecke, M., Brown, E. Russel, J., 2023. High-latitude, Indian ocean, and orbital influences on eastern African hydroclimate across the Plio-Pleistocene boundary. Paleoceanogr. Paleoclimatol. 38, e2023PA004671.

Mizushima, S., Suwa, G., Hirata, K., 2016. A comparative analysis of fetal to subadult femoral midshaft bone distribution of prehistoric Jomon hunter-gatherers and modern Japanese. Anthropol. Sci. 124(1), 1–15.

Montgomery, H., Marshall, R., Hemingway, H., Myerson, S., Clarkson, P., Dollery, C., Hayward, M., Holliman, D., Jubb, M., World, M., Thomas, E., Brynes, A., Saeed, N., Barnard, M., Bell, J., Prasad, K., Rayson, M., Talmud, P., 1998. Human gene for physical performance. Nature 393, 221-222. https://doi.org/10.1038/30374

Moore, R., Schuman, T., Scott, T., Mann, S., Davidson, M., Labadie, R., 2010. Exostoses of the external auditory canal in white-water kayakers. Laryngoscope 120 (3), 582–590.

Morin, E., Winterhalder, B., 2024. Ethnography and ethnohistory support the efficiency of hunting through endurance running in humans. Nat. Hum. Behav. 8, 1065–1075.

Mortola, J.P., Wilfong, D., 2016. Hematocrit and hemoglobin levels of nonhuman apes at moderate altitudes, a comparison with humans. High Alt. Med. Biol. 17(4), 323–335.

Muhammad, R., Kaikaew, T., Panjan, S., Meesawat, S., Thabthimthong, W., Payungporn, S., Apipattarachaiwong, J., Kanthaswamy, S., Luncz, L., Malaivijitnond, S., 2024. Influence of COVID-19 on the emergence of stone-tool use behavior in a population of common long-tailed macaques (*Macaca fascicularis fascicularis*) in Thailand. Am. J. Primatol. 86, e23580.

Mulder, E., Schagatay, E., and Sieber, A., 2021. First evaluation of a newly constructed underwater pulse oximeter for use in breath-holding activities. Front. Physiol. 12, 649674.

Mussi, M., Skinner, M.M., Melis, R.T., Panera, J., Rubio-Jara, S., Davies, T.W., Geraads, D., Bocherens, H., Briatico, G., Le Cabec, A., Hublin, J.-J., Gidna, A., Bonnefille, R., Di Bianco, L., Mendez-Quintas, E., 2023. Early *Homo erectus* lived at high altitudes and produced both Oldowan and Acheulean tools. Science 382(6671), 713–718.

Myers, M.J., Steudel, K., 1985. Effect of limb mass and its distribution on the energetic cost of running. J. Experiment. Biol. 116, 363–373.

Nabais, M., Dupont, C., Zilhão, J., 2023. The exploitation of crabs by Last Interglacial Iberian Neanderthals. The evidence from Gruta da Figueira Brava (Portugal). Front. Environ. Archaeol. 2, 1097815.

Nieminen, P., Finnilä, M., Hämäläinen, W., Lehtiniemi, S., Jämsä, T., Tuukkanen, J., Kunnasranta, M., Henttonen, H., Mustonen, A.-M., 2024. Osteological profiling of femoral diaphysis and neck in aquatic, semiaquatic, and terrestrial carnivores and rodents: effects of body size and locomotor habits. J. Comp. Physiol. B 194, 473–492.

Ntoumani, M., Dugué, B., Rivas, E., Gongaki, K, 2023. Thermoregulation and thermal sensation during whole-body water immersion at different water temperatures in healthy individuals. A scoping review. J. Therm. Biol. 112, 103430.

Okerblom, J., Fletes, W., Patel, H.H., Schenk, S., Varki, A., Breen, E.C., 2018. Human-like CMAH inactivation in mice increases running endurance and decreases muscle fatigability, implications for human evolution. Proc. R. Soc. B 285, 20181656.

Okumura, M., Boyadjian, C., Eggers, S., 2007. Auditory exostoses as an aquatic activity marker: a comparison of coastal and inland skeletal remains from tropical and subtropical regions of Brazil. Am. J. Phys. Anthropol. 132, 558–567.

Örnhagen, H., Schagatay, E., Andersson, J., Bergsten, E., Gustafsson, P., Sandström, S., 1998. Mechanisms of "buccal pumping"("lung packing") and its pulmonary effects. In: Genser, M. (Ed.), Diving and Hyperbaric Medicine Collection of Manuscripts for the XXIV Annual Scientific Meeting of the European Underwater and Baromedical Society, Stockholm, Sweden, August 12-15, 1998. FOA Report: FOA-B--98-00342--721—SE.

Pacini, N., Harper, D., 2008. Aquatic, semi-aquatic and riparian vertebrates. In: Dudgeon, D. (Ed.), Tropical Stream Ecology, Academic Press, Cambridge, MA, pp. 147–197.

Peri, S., Kulkarni, A., Feyertag, F., Berninsone, P.M., Alvarez-Ponce, D., 2018. Phylogenetic distribution of CMP-Neu5Ac hydroxylase (CMAH), the enzyme synthetiz-

ing the proinflammatory human xenoantigen Neu5Gc. Genome Biol. Evol. 10, 207–219.

Persson, G., Lodin-Sundström, A., Linér, M.H., Andersson, S.H.A., Sjögreen, B., Andersson, J.P.A., 2023. Splenic contraction and cardiovascular responses are augmented during apnea compared to rebreathing in humans. Front. Physiol. 14, 1109958.

Pickering, T.R., Bunn, H.T., 2007. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. J. Hum. Evol. 53, 434–438.

Pollen, A.A., Kilik, U., Lowe, C.B., Camp, J.G., 2023. Human-specific genetics, new tools to explore the molecular and cellular basis of human evolution. Nat. Rev. Genet. 24, 687–711.

Ponganis, P., 2015. Diving Physiology of Marine Mammals and Seabirds. Cambridge University Press, Cambridge, UK.

Pontzer, H., 2017. Economy and endurance in human evolution. Curr. Biol. 27(12), R613-R621.

Ponzetta, M.T., Hauser, G., Vienna, A., 1997. Auditory hyperostosis and the environment: an update. Int. J. Anthropol. 12, 29–42.

Pop, E.L., Hilgen, S.L., Adhityatama, S., Berghuis, H., Veldkamp, A., Vonhof, H.B., Sutisna, I., Alink, G., Noerwidi, S., Roebroeks, W., Joordens, J.C.A., 2023. Reconstructing the provenance of the hominin fossils from Trinil (Java, Indonesia) through an integrated analysis of the historical and recent excavations. J. Hum. Evol. 176 (103312), 1–26.

Pop, E.L., Noerwidi, S., Spoor, F., 2024. Naming *Homo erectus*, a review. J. Hum. Evol. 190, 103516.

Rahn, H., Yokoyama, T., 1965. Physiology of breath-hold diving and the Ama of Japan. Symposium paper presented 31 August-1 September 1965, Tokyo, Japan.

Rhys-Evans, P., Cameron, M., 2017. Aural exostoses (surfer's ear) provide vital fossil evidence of an aquatic phase in Man's early evolution. Ann. R. Coll. Surg. Engl. 99 (8), 594–601.

Rhys-Evans, P., 2020. The Waterside Ape: An Alternative Account of Human Evolution. CRC Press Taylor and Francis, Boca Raton.

Ríos, L., Sleeper, M., Danforth, M., Murphy, H., Kutinsky, I., Rosas, A., Bastir, M., Gómez-Cambronero, J., Sanjurjo, R., Campens, L., Rider, O., Pastor, F., 2023. The aorta in humans and African great apes, and cardiac output and metabolic levels in human evolution. Sci. Rep. 13, 6841.

Rizal, Y., Westaway, K.E., Zaim, Y., van den Bergh, G.D., Bettis, E.A., Morwood, M.J., Huffman, O.F., Grün, R., Joannes-Boyau, R., Bailey, R.M., Sidarto, Westaway, M.C., Kurniawan, I., Moore, M.W., Storey, M., Aziz, F., Suminto, Zhao, J., Aswan, Sipola, M.E., Larick, R., Zonneveld, J.-P., Scott, R., Putt, S., Ciochon, R.L., 2020. Last appearance of *Homo erectus* at Ngandong, Java, 117,000–108,000 years ago. Nature 577, 381–385.

Roach, N.T, Hatala, K.G., Ostrofsky, K.R., Villmoare, B., Reeves, J.S., Du, A., Braun, D.R., Harris, J.W.K., Behrensmeyer, A.K., Richmond, B.G., 2016. Pleistocene footprints show intensive use of lake margin habitats by *Homo erectus* groups. Sci. Rep. 6(26374), 1–9.

Roberts, P., Prendergast, M. E., Janzen, A., Shipton, C., Blinkhorn, J., Zech, J., Crowther, A., Sawchuk, E. A., Stewart, M., Ndiema, E., Petraglia, M., Boivin, N. 2020. Late Pleistocene to Holocene human paleoecology in the tropical environments of coastal eastern Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 537, 109438.

Robinson, J.R., Rowan, J., Campisano, C.J., Wynn, J.G., Reed, K.E., 2017. Late Pliocene environmental change during the transition from *Australopithecus* to *Homo*. Nat. Ecol. Evol. 1, 0159.

Rodriguez, J., Cuales, J., Herrera, M., Zubiri, L., Muallil, R.N., Ishmael, A., Jimenez, E.B., Stoneking, M., De Ungria, M.C.A., 2022. Ethical challenges in genetic research among Philippine Indigenous Peoples, insights from fieldwork in Zamboanga and the Sulu Archipelago. Front. Genet. 13,901515.

Rodríguez-Zamora, L., Engan, H., Lodin-Sundström, A., Schagatay, F.S., Iglesias, X., Rodríguez, F., Schagatay, E., 2018. Blood lactate accumulation during competitive freediving and synchronized swimming. Undersea Hyperb. Med. 45(1), 55–63.

Roede, M., Wind, J., Patrick, J., Reynolds, V. (Eds.), 1991. The Aquatic Ape, Fact or Fiction? The First Scientific Evaluation of a Controversial Theory of Human Evolution. Souvenir Press, London.

Rooney, R., 2020. The Cenozoic magmatism of East Africa, Part IV – the terminal stages of rifting preserved in the Northern East African Rift System. Lithos 360–361, 105381.

Ruby, B.C., Cuddy, J.S., Hailes, W.S., Dumke, C.L., Slivka, D.R., Shriver, T.C., Schoeller, D.A., 2015. Extreme endurance and the metabolic range of sustained activity is uniquely available for every human not just the elite few. Comp. Exerc. Physiol. 11(1), 1–7.

Ruff, C.B., Burges, M.L., Ketcham, R., Kappelman, J., 2016. Limb bone structural proportions and locomotor behavior in A.L. 288-1 ("Lucy"). PLoS One 11(11), e0166095.

Ruff, C.B., McHencry, H., Thackeray, J.F., 1999. Cross-sectional morphology of the SK 82 and 97 proximal femora. Am. J. Phys. Anthropol. 109, 509–521.

Ruff, C.B., Sylvester, A.D., Rahmawati, N.T., Suriyanto, R.A., Storm, P., Aubert, M., Joannes-Boyau, R., Berghuis, H., Pop, E., Batenburg, K.J., Coban, S.B., Kostenko, A., Noerwidi, S., Renema, W., Adhityatama, S., Joordens, J.C.A., 2023. Two Late Pleistocene human femora from Trinil, Indonesia, implications for body size and behavior in Southeast Asia. J. Hum. Evol. 172, 103252.

Ruff, C.B., Trinkaus, E., Walker, A., Larsen, C.S., 1993. Postcranial robusticity in *Homo*, I, temporal trends and mechanical interpretation. Am. J. Phys. Anthropol. 91, 21–53.

Ruxton, G., Wilkinson, D., 2011. Thermoregulation and endurance running in extinct hominins, Wheeler's models revisited. J. Hum. Evol. 61(2), 169–175.

Schagatay, E., 1991. The significance of the human diving reflex. In: Roede, M., Wind, J., Patrick, J., Reynolds, V. (Eds.), The Aquatic Ape, Fact or Fiction? The First Scientific Evaluation of a Controversial Theory of Human Evolution. Souvenir Press, London, pp. 247–254.

Schagatay, E., 1996. The Human Diving Response - Effects of Temperature and Training. Ph.D. Dissertation. Lund University, Sweden, ISRN, LUNBDS/(NBZF/1043)/1-108.

Schagatay, E., 2009. Review, Predicting performance in competitive apnea diving, Part I, static apnea. Diving Hyperb. Med. 39(2), 88–99.

Schagatay, E., 2010. Review, Predicting performance in competitive apnea diving. Part II, dynamic apnea. Diving Hyperb. Med. 40(1), 11–22.

Schagatay, E., 2011a. Review, Predicting performance in competitive apnea diving. Part III, depth. Diving Hyperb. Med. 41(4), 216–228.

Schagatay, E., 2011b. Human breath-hold diving ability suggests a selective pressure for diving during human evolution. In: Vaneechoutte, M., Kuliukas, A., Verhaegen, M. (Eds.), Was Man More Aquatic in the Past? Fifty Years After Alister Hardy Waterside Hypotheses of Human Evolution, Bentham Science Publishers, Amsterdam, pp. 120–147.

Schagatay, E., 2014. Human breath-hold diving ability and the underlying physiology. Hum. Evol. 29(1–3), 125–140.

Schagatay, E., Andersson, J., 1998. Diving response and apneic time in humans. Undersea Hyperb. Med. 25(1), 13–19.

Schagatay, E., Andersson, J.P.A., Hallén, M., Pålsson, B., 2001. Physiological and genomic consequences of intermittent hypoxia —selected contribution, role of spleen emptying in prolonging apneas in humans. J. Appl. Physiol. 90, 1623–1629.

Schagatay, E. , Holmström, P. , Mulder, E. , Limbu, P. , Schagatay, F.S. , Engan, H., Lodin-Sundström, A., 2020a. Spleen volume and contraction during apnea in Mt. Everest climbers and Everest Base Camp trekkers. High Alt. Med. Biol. 21(1), 84–91.

Schagatay, E., Joordens, J.C.A., 2024. What characterizes a diving mammal? – A comparison between humans and other shallow divers. Abstract 10th SECAD Meeting, Liège (Belgium).

Schagatay, E., Lodin-Sundström, A., Abrahamsson, E., 2011. Underwater working times in two groups of traditional apnea divers in Asia, the Ama and the Bajau. Diving Hyperb. Med. 41(1), 27–30.

Schagatay, E. , Lunde, A. , Nilsson, S. , Palm, O., Lodin-Sundström, A. 2020b. Spleen contraction elevates hemoglobin concentration at high altitude during rest and exercise. Eur. J. Appl. Physiol. 120, 2693–2704.

Schagatay, E., Richardson, M., Lodin-Sundström, A., 2012. Size matters, spleen and lung volumes predict performance in human apneic divers. Front. Physiol. 3(173), 1–8.

Schagatay, F.S., 2022. Freediving for Shellfish, A Comparative Study of the Gathering of Molluscs in Modern Japan and During the Jomon-Period. BSc Thesis. Uppsala University.

Scholander, P.F., 1940. Experimental investigations on the respiratory function in diving mammals and birds. Hvalrådets Skr. 22, 1–131

Scholander, P. F., 1963. The master switch of life. Sci. Am. 209, 92–106.

Schoorl, J.M., Veldkamp, A., Claessens, L., van Gorp, W., Wijbrans, J.R., 2014. Edifice growth and collapse of the Pliocene Mt. Kenya, evidence of large-scale debris avalanches on a high-altitude glaciated volcano. Glob. Planet. Change 123, 44–54.

Semaw, S., Rogers, M.J., Simpson, S.W., Levin, N.E., Quade, J., Dunbar, N., McIntosh, W.C., Cáceres, I., Stinchcomb, G.E., Holloway, R.L., 2020. Co-occurrence of Acheulian and Oldowan artifacts with *Homo erectus* cranial fossils from Gona, Afar, Ethiopia. Sci. Adv. 6, eaaw4694.

Seymour, R.S., Bosiocic, V., Snelling, E.P., 2017. Correction to 'Fossil skulls reveal that blood flow rate to the brain increased faster than brain volume during human evolution'. R. Soc. Open Sci. 4, 170846.

Shao, Y., Zhou, L., Li, F., Zhao, L., Zhang, B.-L., Shao, F., Chen, J.-W., Chen,, C.-Y., Bi, X., Zhuang, X.-L., Zhu, H.-L., Hu, J., Sun, Z., Li, X., Wang, D., Rivas-González, I., Wang, S., Wang, Y.-M., Chen, W., Li, G., Lu, H.-M., Liu, Y., Kuderna, L.F.K., Farh, K.K.-H., Fan, P.-F., Yu, L., Li, M., Liu, Z.-J., Tiley, G.P., Yoder, A.D., Roos, C., Hayakawa, T., Marques-Bonet, T., Rogers, J., Stenson, P.D., Cooper, D.N., Schierup, M.H., Yao,, Y.-G., Zhang, Y.-P., Wang, W., Qi, X.-G., Zhang, G., Wu, D.-D., 2023. Phylogenomic analyses provide insights into primate evolution. Science 380(6648), 913–924.

Shave, R., Lieberman, D., Drane, A., Brown, M., Batterham, A., Worthington, S., Atencia, R., Feltrer, Y., Weiner, R., Wasfy, M., Baggish, A., 2019. Selection of endurance capabilities and the trade-off between pressure and volume in the human heart. Proc. Nat. Acad. Sci., U.S.A. 116(40), 19905–19910.

Shurer, C., Chin-Hun Kuo, J., Monet Roberts, L., Gandhi, J., Colville, M., Enoki, T., Pan, H., Su, J., Noble, J., Hollander, M., O'Donnell, J., Yin, R., Pedram, K., Möckl, L., Kourkoutis, L., Moerner, W., Bertozzi, C., Feigenson, G., Reesink, H., Paszek, M., 2019. Physical principles of membrane shape regulation by the glycocalyx. Cell 177, 1757–1770.

Smail, I., Rector, A., Robinson, J., Reed, K., 2025. Pliocene climatic change and the origins of *Homo* at Ledi-Geraru, Ethiopia. Ann. Hum. Biol. 52(1), 2462255.

Smith, T.S., Partridge, S.T., 2004. Dynamics of intertidal foraging by coastal brown bears in southwestern Alaska. J. Wildl. Manag. 68(20), 233–240.

Spoor, F., Wood, B., Zonneveldt, F., 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. Nature 369, 645–648.

Stander, P.E., 2019. Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. Namib. J. Environ. 3A, 1–10.

Steele, J., Clegg, M., Martelli, S., 2013. Comparative morphology of the hominin and African ape hyoid bone, a possible marker of the evolution of speech. Hum. Biol. 85 (5), 639–672.

Steudel-Numbers, K., Wall-Scheffler, C., 2009. Optimal running speed and the evolution of hominin hunting strategies. J. Hum. Evol. 56(4), 355–360.

Suntsova, M.V., Buzdin, A.A., 2020. Differences between human and chimpanzee genomes and their implications in gene expression, protein functions and biochemical properties of the two species. BMC Genom. 21(S7), 535.

Steegmann, T., Cerny, F., Holliday, T., 2002. Neandertal cold adaptation, physiological and energetic factors. Am. J. Human Biol. 14(5), 556–583.

Takenaka, M., Hayashi, K., Yamada, G., Ogura, T., Ito, M., Milner, A.M., Tojo, K., 2022. Behavior of snow monkeys hunting fish to survive winter. Sci. Rep. 12, 20324.

Taylor, A., Berke, M., Castañeda, I., Koutsodendris, A., Campos, H., Hall, I., Hemming, S., LeVay, L., Cartagena Sierra, A., O'Connor, K., Expeditions 361 Scientists, 2021. Plio-Pleistocene continental hydroclimate and Indian ocean sea surface temperatures at the southeast African margin. Paleoceanogr. Paleoclimatol. 36(3), e2020PA004186.

Timmons, J.A., 2011. Variability in training-induced skeletal muscle adaptation. J. Appl. Physiol. 110.3, 846–853.

Thompson, M.A., 2017. Physiological and biomechanical mechanisms of distance specific human running performance. Integr. Compar. Biol. 57(2), 293–300.

Thordarson, T., Self, S., 2003. Atmospheric and environmental effects of the 1783-1784 Laki eruption, a review and assessment. J. Geophys. Res. 108 (D1 4011), 7-1 to 7-29.

Tobias, P., 1998. Water and human evolution. Out There 3, 38–44.

Tobias, P., 2011. Revisiting water and hominin evolution. In: Vaneechoutte, M., Kuliukas, A., Verhaegen, M. (Eds.), Was Man More Aquatic in the Past? Fifty Years After Alister Hardy Waterside Hypotheses of Human Evolution, Bentham Science Publishers, Amsterdam, pp. 3–16.

Toyota, B., Kitagawa, K. 1974. The ear of the Ama. J. Jap. Assoc. Rural Med. 23(1), 15–19.

Trauth, M.H., Asrat, A., Berner, N., Bibi, F., Foerster, V., Grove, M., Kaboth-Bahr, S., Maslin, M.A., Mudelsee, M., Schäbitz, F., 2021. Northern hemisphere glaciation, African climate and human evolution. Quatern. Sci. Rev. 268, 107095.

Trinkaus, E., Ruff, C.B., 2012. Femoral and tibial diaphyseal cross-sectional geometry in Pleistocene Homo. PaleoAnthropology 2012, 13–62.

Trinkaus, E., Samsel, M., Villotte, S., 2019. External auditory exostoses among western Eurasian late Middle and Late Pleistocene humans. PLoS One 14(8), e0220464.

Tuomisto, H., Tuomisto, M., Tuomisto, J., 2018. How scientists perceive the evolutionary origin of human traits, results of a survey study. Ecol. Evol. 8(6), 3518–3533.

Tye, A., Jones, A., 2025. An overlooked early report of chimpanzees using tools to forage for oysters. Afr. J. Ecol. 63 (1), e70010.

Tyler, D.E., Krantz, G.S., Sartono, S., 1995. The taxonomic status of the '*Meganthropus*' cranial (Sangiran 31) and the '*Meganthropus*' occipital fragment III. In: Bower, J., Sartono, S. (Eds.), Evolution and Ecology of *Homo erectus*. Pithecanthropus Centennial Foundation, Leiden University, Leiden, pp. 189–201.

Ubelaker, D.H., Wu, Y., Zeidler, J.A., 2022. Auditory exostoses and *Spondylus* diving in ancient Ecuador. In: Beekman, C.A., McEwan, C. (Eds.), Waves of Influence: Pacific Maritime Networks Connecting Mexico, Central America, and Northwestern South America. Dumbaryon Oaks, Washington, D.C., pp. 457–468.

Vaill, M., Kawanishi, K., Varki, N., Gagneux, Varki, A., 2023. Comparative physiological anthropogeny, exploring molecular underpinnings of distinctly human phenotypes. Physiol. Rev. 103, 2171–2229.

Van de Schootbrugge, B., Wignall, P.B., 2016. A tale of two extinctions, converging end-Permian and end-Triassic scenarios. Geol. Mag. 153(2), 332–354.

Van der Lubbe, H.J.L., Hall, I.R., Barker, S., Hemming, S.R., Baars, T.F., Starr, A., Just, J., Backeberg, B.C., Joordens, J.C.A., 2021. Indo-Pacific Walker circulation drove Pleistocene African aridification. Nature 598, 618–623.

Vellers, H.L., Kleeberger, S.R., Lightfoot, J.T., 2018. Inter-individual variation in adaptations to endurance and resistance exercise training: genetic approaches towards understanding a complex phenotype. Mamm. Genome 29, 48–62.

Verhaegen, M., Munro, S., 2011. Pachyosteosclerosis suggests archaic *Homo* frequently collected sessile littoral foods. Homo - J. Comp. Hum. Biol. 62(4), 237–247.

Vermeij, G.J., Motani, R., 2018. Land to sea transitions in vertebrates, the dynamics of colonization. Paleobiol. 44(2), 237–250.

Villa, P., Soriano, S., Pollarolo, L., Smriglio, C., Gaeta, M., D'Orazio, M., Conforti, J., Tozzi, C., 2020. Neandertals on the beach, use of marine resources at Grotta dei Moscerini (Latium, Italy). PLoS One 15(1), e0226690.

Villotte, S., Knüsel, C.J., 2016. External auditory exostoses and prehistoric aquatic resource procurement. J. Archaeol. Sci. Rep. 6, 633–636.

Vrba, E., 2007. Role of environmental stimuli in hominid origins. In: Henke, W., Tattersall, I. (Eds.), Handbook of Paleoanthropology Volume III, Phylogeny of Hominids. Springer-Verlag, Berlin, pp. 1441–1481.

Wall, W.P., 1983. The correlation between high limb-bone density and aquatic habits in recent mammals. J. Paleontol. 57(2), 197–207.

Wallace, I., Toya, C., Peña Muñoz, M., Meyer, J., Busby, T., Reynolds, A., Martinez, J., Thompson, T., Miller-Moore, M., Harris, A., Rios, R., Martinez, A., Jahashvili, T., Ruff, C.B., 2023. Effects of the energy balance transition on bone mass and strength. Sci. Rep. 13, 15204.

Wegener, F., Wegner, M., Weiss, N., 2022. External auditory exostoses in wind-dependent water sports partici-

pants: German wind- and kitesurfers. Eur. Arch. Otorhinolaryngol. 279, 2353–2361.

Westaway, M., Durband, A., Lambert, D., 2015. Human evolution in Sunda and Sahul and the continuing contributions of Professor Colin Groves. In: Behie, A., Oxenham, M. (Eds.), Taxonomic Tapestries, The Threads of Evolutionary, Behavioural and Conservation Research. ANU Press, Canberra, pp. 249–276.

Widianto, H., Noerwidi, S., 2020. It's time to look to the west, a new interpretation on *Homo erectus* findings distribution of Java. Berkala Arkeologi 40(2), 153–178.

Will, M., 2020. Neanderthal surf and turf, did our closest relatives adapt to the sea in the same way as early humans? Science 367(6485), 1422–1423.

Williams, C., Williams, M., Eynon, N., Ashton, K., Little, J., Wisloff, U., Coombes, J., 2017. Genes to predict VO-2max trainability, a systematic review. BMC Genom. 18(Suppl 8), 831.

Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le Boeuf, B.J., Horning, M., Calambokidis, J., Croll, D., 2000. Sink or swim, strategies for cost-efficient diving by marine mammals. Science 288, 133–136.

Willie, C.K., Ainslie, P.N., Drvis, I., MacLeod, D.B., Bain, A.R., Madden, D., Maslov, P.Z., Dujic, Z., 2015. Regulation of brain blood flow and oxygen delivery in elite breath-hold divers. J. Cereb. Blood Flow Metab. 35, 66–73.

Wood, B., 2020. Birth of *Homo erectus*. Evol. Anthropol. 29, 293–298.

Work, P., Lewis, R., Bourque, B., 2025. A multidisciplinary approach to resolve the taxonomy of the historically extinct sea mink (*Neogale macrodon*) (Maine, USA). Quatern. Res. 126, 55–70.

Yuan, Y., Zhang, Y., Zhang, P., Liu, C., Wang, J., Gao, H., Hoelzel, R., Seim, I., Lvc, M., Lin, M., Dong, L., Gao, H., Yang, Z., Caruso, F., Lin, W., da Fonseca, R.R., Wang, D., Wang, X., Rasmussen, M.H., Liu, M., Zheng, J., Zhao, L., Campos, P.F., Kang, H., Iversen, M., Song, Y., Guo, X., Guo, J., Qin, Y., Pan, S., Xu, Q., Meng, L., A, Y., Liu, S., Ming-Yuen Leeo, S., Liu, X., Xu, X., Yang, H., Fan, G., Wang, K., Lia, S., 2021. Comparative genomics provides insights into the aquatic adaptations of mammals. Proc. Natl. Acad. Sci., U.S.A. 118(37), e2106080118.

Zilhão, J., Angelucci, D.E., Igreja, M.A., Arnold, L.J., Badal, E., Callapez, P., Cardoso, J.L., d'Errico, F., Daura, J., Demuro, M., Deschamps, M., Dupont, C., Gabriel, S., Hoffmann, D.L., Legoinha, P., Matias, H., Monge Soares, A.M., Nabais, M., Portela, P., Queffelec, A., Rodrigues, F., Souto, P., 2020. Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. Science 367(6485), eaaz7943.

Zohar, I., Alperson-Afil, N., Goren-Inbar, N., Prévost, M., Tütken, T., Sisma-Ventura, G., Hershkovitz, I., Najorka, J., 2023. Evidence for the cooking of fish 780,000 years ago at Gesher Benot Ya'aqov, Israel. Nat. Ecol. Evol. 6, 2016–2028.

Supplement 1 to Dive First, Run Later? The Role of Endurance Diving in Human Evolution

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SUPPLEMENT 1
This supplement contains: Supplementary Tables S1–S2.

PaleoAnthropology **2027:1** **supplement to Joordens and Schagatay 2027:1** **ISSN 1545-0031**
Paleoanthropology Society & European Society for the study of Human Evolution
OPEN ACCESS
Early View available online 17 September 2026

Supplementary Table S1.

Cortical area (%) at 50% (midshaft) and 80% section of the femur (data compiled by Christopher Ruff)

Specimen	Taxon	Section (%)	N	TA	CA	%CA	Section (%)	N	TA	CA	%CA	Sources cortical area	Age (range) in Ma	Sources age
A.L. 288-1	*Australopithecus afarensis*	50	1	330	198	**59.9**	80		332	198	59.5	Ruff et al. 2016	3.2	Ruff et al. 2016
Stw 99	*A. africanus*	50	1	484	356	**73.6**	80		634	552	87.1	Ruff et al. 2020	2.6-2.0	Bleuze et al. 2022
Stw 121	*A. africanus*	50	1	363	292	**80.4**	80					Ruff et al. 2020	2.6-2.0	Bleuze et al. 2022
SK 82	*Paranthropus robustus*		1				80		577	490	84.9	Ruff et al. 1999		
SK 97	*P. robustus*		1				80		593	457	77.1	Ruff et al. 1999		
ER 1500d	*P. boisei*		1				80		417	299	71.7	Ruff et al. 2016		
OH 80-2	*P. boisei*		1				80		611	524	85.8	Dominguez-Rodrigo et al. 2013		
ER 1472	*Homo sp.*	50	1	464	400	**86.2**	80		502	424	84.5	Trinkaus and Ruff 2012	2.0	Joordens et al. 2013
ER 1481a	*H. sp.*	50	1	391	332	**84.9**	80		529	414	78.3	Trinkaus and Ruff 2012	2.0	Joordens et al. 2013
OH 62	*H. habilis*	50	1	265	220	**83.0**	80					Ruff 2009	1.8	Bleuze et al. 2022
OH 28	*H. erectus*	50	1	576	410	**71.2**	80		685	446	65.1	Trinkaus and Ruff 2012	0.8-0.6	Bleuze et al. 2022
ER 737	*H. erectus*	50	1	586	441	**75.3**	80		738	510	69.1	Trinkaus and Ruff 2012	1.6	Bleuze et al. 2022
ER 803a	*H. erectus*	50	1	626	504	**80.5**	80		706	542	76.8	Trinkaus and Ruff 2012	1.5	Bleuze et al. 2022
ER 1808mn	*H. erectus*	50	1	551	478	**86.8**	80		629	498	79.2	Trinkaus and Ruff 2012	1.7	Bleuze et al. 2022
BOU-VP-2/15	*H. erectus*	50	1	589	497	**84.4**	80					Ruff, pers. comm.	1.0	Asfaw et al 2002
BOU-VP-19/63	*H. erectus*	50	1	664	587	**88.4**	80					Ruff, pers. comm.	1.0	Asfaw et al 2002
Kresna 11	*H. erectus*	50	1	590	454	**76.9**	80		692	453	65.5	Puymerail et al. 2012	0.9	Bleuze et al. 2022
Trinil II	*H. erectus*	50	1	559	406	**72.7**	80		587	389	66.3	Ruff et al. 2015	0.8	Hilgen et al. 2023; Pop et al. 2023
Trinil III	*H. erectus*		1				80		563	408	72.5	Ruff et al. 2015	0.8	Hilgen et al. 2023; Pop et al. 2023
Trinil V	*H. erectus*	50	1	521	393	**75.6**	80		586	409	69.8	Ruff et al. 2015	0.8	Hilgen et al. 2023; Pop et al. 2023
Trinil IV	*H. erectus*	50	1	491	349	**70.9**						Ruff et al. 2015	0.8	Hilgen et al. 2023; Pop et al. 2023
Pecos + E. Af.	*H.s. sapiens*	50	100			**69.8 ± 8.4**	80	100			58.9 ± 8.0	Ruff 1995	Holocene	
Europ. Holocene	*H.s. sapiens*	50	1791			**74.0 ± 7.1**						Ruff 2018	Holocene	
Europ. UP	*H.s. sapiens*	50	37			**80.7 ± 6.6**						Ruff 2018	Upper Pleistocene	
Pan 1	*Pan troglodytus*	50	23			**67.7 ± 8.2**	80	23			67.7 ± 8.2	Ruff 2002		
Pan 2	*Pantroglodytus*	50	99			**65.6 ± 7.8**						Burgess 2018		
Gorilla 1	*Gorilla gorilla*	50	20			**65.5 ± 9.9**	80	20			65.7 ± 6.5	Ruff 2002		
Gorilla 2	*Gorilla gorilla*	50	137			**65.7 ± 6.5**						Ruff et al. 2018		
						mean ± SD					mean ± SD			

N = Number of specimens
TA = Total Area
CA = Cortical Area

Supplementary Table S2.

The data in this table are from Table 1 in **Wall, W.P.. 1983. The correlation between high limb-bone density and aquatic habits in recent mammals. J. Paleontol. 57 (2). 197-207.**

		Limb bone density in g/cm3								
Species	**Common name**	**Humerus**	**Radius-Ulna**	**Femur**	**Tibia-Fibula**	**Category**	**Environment**	**N**	**Provenance**	**Accession number(s)**
Rhinocerus unicornus	Indian rhinoceros	1.31	1.27	1.3	1.25	Terrestrial		2	zoo	NMNH 33695
Cerathoterium simum	White rhinoceros	1.29	1.3	1.3	1.37	Terrestrial		3	wild	AMNH 238245. NMNH 164592
Diceros bicornis	Black rhinoceros	1.33	1.41	1.31	1.41	Terrestrial		2	wild	NMNH 162931
Didermoceros	Sumatran rhinoceros	1.24	1.26	1.25	1.35	Terrestrial		2	zoo	NMNH 49561
Bison americanos	Bison	1.19	1.19	1.14	1.27	Terrestrial		3	zoo	AMNH 19175. NMNH 49760
Equus burchelli	Zebra	1.18	1.26	1.18	1.19	Terrestrial		2	wild	NMNH 162959
Phacocoerus aethiopicus	Wart hog	1.19	1.15	1.13	1.06	Terrestrial		2	wild	NMNH 36864
Sus scrofa	European wild hog	1.02	1.04	1.03	0.98	Terrestrial		2	wild	NMNH 15184
Lama guanoco	Guanaco	1.19	1.37	1.16	1.31	Terrestrial		2	wild	NMNH 92137
Tayassu peccari	White-lipped peccary	1.22	1.32	1.21	1.31	Terrestrial		2	wild	NMNH 257318
Rangifer tarandus	Caribou	1.21	1.35	1.28	0.96	Terrestrial		1	zoo	AMNH 24206
Cervus eldi	Eld deer	1.12	1.33	1.24	1.23	Terrestrial		1	zoo	AMNH 35704
Tragelaphus strepsiceros	Greater kudu	1.21	1.27	1.09	1.19	Terrestrial		1	zoo	AMNH 79328
Hippotragus equinus	Roan antelope	1.27	1.26	1.27	1.23	Terrestrial		1	zoo	AMNH 80134
Taurotragus oryx	Eland	1.22	1.3	1.18	1.29	Terrestrial		1	zoo	AMNH 80189
Alces alces	Moose	0.96	1.12	1.18	0.98	Terrestrial		1	zoo	AMNH 16868
Connochaetes gnu	White-lipped gnu	1.14	1.21	1.19	1.24	Terrestrial		1	zoo	AMNH 14138
Gazella dorcas	Gazelle	1.19	1.21	1.06	1.26	Terrestrial		1	zoo	AMNH 17416
Tapirus terrestris	Brazilian tapir	1.25	1.37	1.25	1.35	Terrestrial		4	zoo	AMNH 10025. NMNH 261025. UMA 24
Okapia johnstoni	Okapi	1.26	1.28	1.1	1.36	Terrestrial		1	zoo	AMNH 149148
Aplodontia rufa	Mountain beaver	0.97	1.16	1.08	1.12	Terrestrial		2	wild	UMA 1319
Didelphis virginiana	Opossum	1.14	1.21	1.24	1.1	Terrestrial		2	wild	UMA1319
Procyon lotor	Raccoon	1.16	1.29	1.13	1.14	Terrestrial		15	wild	UMA 1709. 1777. 2649.3361. 3481. 3482. 3483. 3484
Felis leo	Lion	1.29	1.38	1.27	1.37	Terrestrial		2	wild	NMNH 172677
Macaca mulata	Rhesus macaque	1.32	1.31	1.26	1.14	Terrestrial		2	zoo	UMA 2304
Ursus arctos	Alaskan brown bear	1.29	1.38	1.32	1.21	Terrestrial		2	wild	NMNH 123386
Ursus maritiumus	Polar bear	1.39	1.65	1.33	1.65	Semi-aquatic	Marine	1	wild	NMNH 275124
Ondatra zibeticus	Muskrat	1.68		1.37		Semi-aquatic	Freshwater	2	wild	UMA 2238
Castor canadensis	North American beaver	1.72	1.73	1.61	1.57	Semi-aquatic	Freshwater	11	wild	UMA 1274. 1775.2062. 2063. 2065. 2237
Lutra canadensis	North American river otter	1.54	1.71	1.32	1.41	Semi-aquatic	Freshwater/Marine	1	wild	UMA 2290
Enhydra lutris	Sea otter	1.65	1.82	1.46	1.6	Semi-aquatic	Marine	5	wild	NMNH 21336. 49492. 263315
Hydrochoerus hydrochoerus	Capybara	1.49	1.58	1.51	1.48	Semi-aquatic	Freshwater	2	wild	NMNH 241103
Hippopotamus amphibius	Hippopotamus	1.53	1.63	1.51	1.63	Semi-aquatic	Freshwater	9	zoo/wild	AMNH 15898 (zoo). NMNH 254987 (zoo). NMNH 162976. 162977. 162980 (wild)
Choeropsis liberiensis	Pygmy hippopotamus	1.51	1.74	1.53	1.62	Semi-aquatic	Freshwater	3	zoo	AMNH 148452. NMNH 31406
Pusa hispida	Ring seal	1.62	1.71	1.55	1.81	Semi-aquatic	Marine	2	wild	NMNH 504208
Otaria flavescens	South American sea lion	1.39	1.49	1.42	1.65	Semi-aquatic	Marine	1	wild	AMNH 73120
Eumetopias jubatus	Steller sea lion	1.35	1.46	1.39	1.54	Semi-aquatic	Marine	2	wild	AMNH 77883
Hydrurga leptonix	Leopard seal	1.44	1.48	1.55	1.45	Semi-aquatic	Marine	1	wild	AMNH 36200
Monachus monachus	Monk seal	1.39	1.45	1.42	1.45	Semi-aquatic	Marine	2	wild	AMNH 73607
Erignathus barbatus	Bearded seal	1.35	1.64	1.67	1.43	Semi-aquatic	Marine	2	wild	AMNH 75248
Arctocephalus australis	South American fur seal	1.34	1.67	1.47	1.55	Semi-aquatic	Marine	2	wild	NMNH 23331
Trichechus manatus	Manatee	2.00	2.35			Aquatic	Freshwater/Marine	3	zoo/wild	AMNH 14161 (zoo). NMNH 527909 (wild)
Callorhinus ursinus	Northern fur seal	1.58	1.69	1.7	1.63	Semi-aquatic	Marine	2	wild	NMNH 258588
Cystophora cristata	Hooded seal	1.27	1.27	1.46	1.45	Semi-aquatic	Marine	1	wild	AMNH 184659
Leptonychotes weddelli	Weddell seal	1.31	1.3	1.34	1.4	Semi-aquatic	Marine	2	wild	NMNH 504875
Odobenus rosmarus	Walrus	1.26	1.31	1.35	1.35	Semi-aquatic	Marine	2	wild	NMNH 500254
Mirounga angustirosris	Elephant seal	1.15	1.25	1.08	1.23	Semi-aquatic	Marine	2	wild	NMNH 260867
Cetacea indet.	Whale (unidentified sp.)	1.16	1.26			Aquatic	Marine	1	wild	GC 574

AMNH = American Museum of Natural History. New York
NMNH = National Museum of Natural History. Washington DC
GC = Georgia College. Milledgesville

All species in blue font are semi-aquatic, except for *Trichechus manatus* and *Cetacea* indet. that are aquatic.