

*New Idea***A paradigm for the evolution of human features: Apes trapped on barren volcanic islands****Allan G. Krill**

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**Abstract**

The *aquatic ape hypothesis* for human evolution can account for all the traits that distinguish humans from chimpanzees. This scientific paradigm has been considered impossible. It would require that human ancestors maintained a semiaquatic lifestyle for millions of years, whereas hominin fossils indicate relatively dry terrestrial environments. Here I propose a marine aquatic evolution that is speculative, but compatible with all the fossil and genetic evidence. In this hypothesis, hominins evolved from chimpanzee-like apes that became stranded on proto-Bioko—new volcanic islands with no terrestrial foods available. The apes were forced to eat shellfish and seaweed. From wading in water on two legs to obtain food, their bodies evolved to become bipedal. Naked skin, blubber, and protruding noses were also aquatic adaptations. Brain-size increase resulted from marine fatty acid DHA. Some of these hominins escaped to mainland Africa and their bipedal descendants are recorded at the famous fossil sites. The volcanic islands grew and evolved into Bioko, and the hominins that remained there evolved into *Homo sapiens*. They gave up their marine diet and semiaquatic habitat after food became available on the evolving island. Then, during one of the low sea-level stands in the Pleistocene epoch, humans walked to the mainland on the emergent Bioko land bridge. Unlike earlier aquatic ape ideas, the Bioko scenario can be tested by DNA. If the human genome includes a retrovirus that is otherwise only found in endemic animals on Bioko, it would show that our ancestors came from there. Unfortunately, Bioko and west-central Africa are not interesting to traditional paleoanthropologists, because they do not contain fossils.

**Why did humans evolve to be so different from all other primates?**

Genetic evidence shows that the last common ancestor of humans and chimpanzees lived about 6 million years ago (Lewin and Foley 2004). It was presumably arboreal, eating and sleeping mostly in trees, and no more human-like than modern apes. It is not known what ape species this ancestor was or if it is represented by existing fossils. It may have been *Pan troglodytes*, the chimpanzee.

A divergence resulted in two evolutionary branches: *panins*, that includes chimpanzees and bonobos, and *hominins*, that includes humans and extinct fossil species. Humans acquired many features that are unique among primates, such as two-legged running, large brain, naked body, and fat cells beneath the skin that are capable of producing a thick layer of blubber.

There is no consensus among scientists as to why any of the remarkable human features originally evolved (Tuomisto et al. 2018). The general question now is: Why did our branch evolve human features, and why did none of the other hundreds of primate species follow a similar evolutionary path? Paleoanthropologists, who are specialists in human fossils, seem to have little interest in this discussion (Morgan 2008).

**An unorthodox idea: evolution in the sea**

Perhaps human features evolved during a period of marine habitat—an idea referred to as the *aquatic ape hypothesis*. This suggestion was not made by paleoanthropologists. It was made by Sir Alister Hardy (1960), a marine zoologist. The idea was further supported by zoologist Desmond Morris in the best-selling books *The*

*Naked Ape* and *Manwatching* (Morris 1967, 1977). Neither of these scientists were especially concerned with fossils.

Elaine Morgan, a fiction-writer, made the aquatic ape hypothesis the central idea in her best-selling book *The Descent of Woman* (Morgan 1972). She followed that up with a more detailed popular-science work *The Aquatic Ape* (Morgan 1982) and a few more well researched books (Morgan 1990, 1994, 1997).

Bioko, a unique volcanic island 32 kilometers off the west coast of equatorial Africa, is shown here to be a plausible setting for an aquatic evolution. Proto-Bioko may have been the “Galapagos of human evolution.” Like iguanas on Galapagos, our ancestors may have gone from an arboreal habitat, to an aquatic habitat, to our present terrestrial habitat.

### **Human features and their aquatic explanations**

As discussed in the books by Morgan, each of the remarkable human features can be simply explained as an adaptation to an aquatic environment. Below are listed some of these features, and how they may have resulted from aquatic selection pressures.

***Bipedal gait.*** Humans and the extinct hominins seem to be the only mammals that have ever evolved to run on two legs. How did that happen? Chimpanzees and other primates walk on two legs while wading in water, to hold their heads as high as possible. Water gives them support while standing upright. Apes foraging for shellfish and seaweed in water could have gradually evolved the two-legged gait.

***Long legs.*** Humans have evolved longer legs than chimpanzees, allowing them to stand in deeper water. Wading birds also have long legs.

***Large brain.*** Humans are the only land mammals with a remarkably large brain. Docosahexaenoic acid (DHA) is an omega-3 fatty acid that is known to be a limiting nutrient for mammalian brain growth. It is rare on land, but richly available in the marine food chain, due to algae that produce it. A marine diet could account for the human brain evolution (Crawford 2010).

***Human teeth.*** Hominins have teeth with thick enamel and reduction of sharp canines. These traits may have evolved from a unique marine diet, and from having no adversaries to threaten.

***Naked skin.*** Fur on mammals is useful. It keeps the skin cooler in direct sun, and keeps the body warmer at night. Fur protects the skin from damaging rays of the sun. It helps protect against abrasions and some biting insects. Fur has disadvantages in water and mud, and has been

lost by some aquatic-, semiaquatic-, and wallowing mammals, such as the whale, dolphin, manatee, walrus, hippopotamus, elephant, rhinoceros, and pig. Human swimming competitors shave their bodies to swim faster, and wear smooth caps on their heads.

***Subcutaneous fat.*** Fat cells directly beneath the skin allow overweight humans to accumulate an immense layer of fat, which in aquatic mammals would be called blubber. It provides buoyancy and thermal insulation in water. Overweight chimpanzees can produce visceral fat around the internal organs, but do not have any cells for subcutaneous fat.

***Swimming babies.*** Human infants stay relaxed under water. They keep their eyes open and look around. They can quickly learn to swim. Chimpanzee infants panic in water. Their bodies are more dense, and rapidly sink.

***Weak neck at birth.*** A baby’s neck is too weak to support the large and heavy head. However, if the birth occurs in water, and if the baby remains in water for the first few months of life, the neck is sufficiently strong.

***Chubby infants.*** Chimpanzees are born with only about 3% body fat and remain lean and strong, whereas humans are born with about 15% body fat. Human milk has nearly twice as much fat as chimpanzee milk (Hinde and Milligan 2011), and human babies rapidly plump out with subcutaneous fat after birth.

***Infant grasping reflex.*** Chimpanzee infants cling to their mother’s hair while she climbs. Human infants have the same grasping reflex, but are too weak and fat to hang in the air. However, they can float in seawater, grasping the long head hair of parents and siblings.

***Long oily head hair.*** An infant’s parents and siblings have long sebum-coated head hair that floats. Sebaceous glands are mainly located on the scalp and face, and contribute to acne. The elevated position of head hair while swimming and wading makes it appropriate for babies to hold on to.

***Protruding nose.*** The human nose deflects water during swimming and diving, and while an infant floats on its back. The exposed nostrils of chimpanzees are ill-suited for swimming. The most aquatic living primate is the proboscis monkey, with a human-like nose.

***Streamlined body and paddle-shaped feet and hands.*** A chimpanzee-shaped body could never compete in swimming or diving against a human-shaped body.

***Descended larynx.*** The human windpipe opens into the back of the mouth. This is an awkward design, because it

allows the accidental inhalation of food or drink. This positioning is an advantage for the walrus, manatee, sea lion, and for human swimmers. It allows rapid full inhalation through the mouth before a dive.

**Voluntary breath control.** Humans have little control of their heart rate, just as chimpanzees have little control of their breath. The ability to take a deep breath and release it slowly evolved among mammals that dive. Breath control is also a prerequisite for human speech.

**Salty fluid expenditure.** Humans are unique among primates in having eccrine sweat glands over most of the body. On a hot day, humans will lose more than a liter of salty sweat per hour, yet they can only drink about a liter at a time. The human thermoregulation strategy of sweating to prevent overheating, and the excretion of copious salty urine, seem unlikely to have evolved in a dry terrestrial climate.

Morgan (1997) discussed these and many other human features. Anthropologists would try to explain each of these unique human features independently. The aquatic explanations are parsimonious, because all features are related to a single cause. But the explanations are all unacceptable, if one rejects the premise of an aquatic human evolution.

### **The aquatic ape hypothesis has been considered disproven**

Some scientists have debated the aquatic ape hypothesis (Roede et al. 1991), and some have modified it to include possible freshwater environments (Vanechoutte et al. 2011).

Most paleoanthropologists have flatly rejected the aquatic ape hypothesis. John H. Langdon has been a leading opponent. He introduced the term *umbrella hypothesis* to describe a “simple idea that overspreads and appears to resolve many scientific questions” (Langdon 1997). He argued that the aquatic hypothesis was unnecessary, because non-aquatic explanations are available for each of the human features.

More importantly, the aquatic ape hypothesis seemed to be disproven by fossil evidence. Fossils and geological deposits where hominin fossils are found commonly indicate dry environments. Fossils also show that human features appeared over a time span of several million years, with bipedalism evolving first, followed much later by brain-size increase. Therefore, the aquatic ape hypothesis would require several periods of aquatic habitats, for which there is no fossil evidence. In his recent textbook on human evolution, Langdon (2016) used the aquatic ape hypothesis as an example of an appealing, yet deceptive, paradigm.

### **Alternative paradigms are not welcome in science**

Within the field of paleoanthropology, the aquatic ape hypothesis is rarely discussed. As noted in a leading textbook by Lewin and Foley (2004, p. 283): “most textbooks on human evolution—this one included—simply ignore the aquatic ape model.” In a recent survey, many life scientists reported that they had never heard of the aquatic ape hypothesis (Tuomisto et al. 2018).

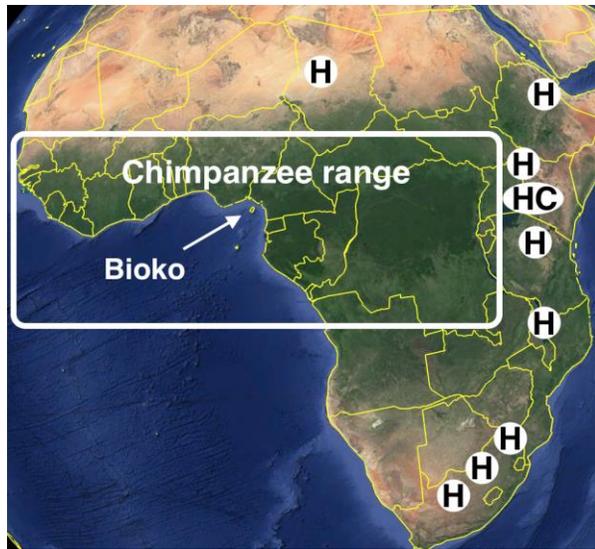
My own expertise is in the history of plate tectonics in geology, where the unorthodox *continental drift hypothesis* might also be called an umbrella hypothesis. Alfred Wegener showed that it covered a wide range of seemingly unrelated features. Although it was well researched and presented in a few respectable books by Wegener and other scientists, it was ridiculed by geologists and fossil experts. The strong evidence for it was kept out of geology textbooks and scientific journals for 40 years (Krill 2014). Then continental drift was corroborated by a new type of data—the magnetic record of rocks on the seafloor. The hypothesis helped give geophysicists instant success. Continental drift quickly developed into a powerful paradigm for earth science, with the fresh new name *plate tectonics*. The scandalous four-decade denial of continental drift was played down, and no lessons were learned. Science can indeed deny a correct hypothesis for decades.

Both the continental drift hypothesis and the aquatic ape hypothesis are more than simple hypotheses—they are scientific paradigms. There is a natural tendency for scientists and scientific journals to work only within the established paradigm, while disregarding any others (Kuhn 1962).

The evidence for the aquatic ape paradigm does not have much to do with fossils and fossil sites, which are the bread and butter of paleoanthropology. The aquatic paradigm focuses on living humans and chimpanzees: their anatomy, physiology, and genetics. Textbooks of human evolution do not give much attention to these features, because they cannot be preserved as fossils. Textbook authors have considered the aquatic paradigm to be a distraction that should be avoided by students who need to learn how fossils have been interpreted.

### **All hominin species may have originated on proto-Bioko islands**

Fossils show that there were several branches of hominins in Africa and Asia, some living concurrently (Lewin and Foley 2004). Many species have been named, but it is not known if any of them is the ancestor of another species, or of *Homo sapiens*. The fossils are scanty and the identifications are uncertain. Each of the species became extinct, except for *Homo sapiens*.



**Figure 1.** Range of chimpanzees in historic times. (None on Bioko or other islands of the Cameroon Volcanic Line.) Letters H and C indicate hominin and chimpanzee fossil sites, all of which are outside the current range of chimpanzees. Base map from Google Earth.

The aquatic paradigm proposed here offers a simple explanation for all hominin fossils and their ages and interpretations. Bipedalism may have evolved among semiaquatic apes on the volcanic islands of proto-Bioko. All known hominin species may have descended from those bipedal apes.

Unfortunately, there is probably not a single mammalian fossil on Bioko. Fossils only occur where climate conditions and geological deposits were suitable for fossilization. Those conditions are rare. Fossil experts acknowledge this fact with the adage: “Absence of evidence is not evidence of absence.” The absence of fossils on Bioko does not discredit it as an evolutionary site. But with no possibility of fossils on Bioko or nearby parts of Africa, these areas are uninteresting to paleoanthropologists.

### **Primate fossils do not exist in the main primate habitats**

Fossils of mammals are not found in warm humid climates, because the bones decay before they can become fossilized. No primate fossils are known from the tropical rainforests of central and western Africa where chimpanzees currently live (Figure 1). Based on the current population of chimpanzees, one can calculate that over the past few million years, at least a billion panins must have lived and died there.

The only chimpanzee fossils ever reported are three teeth that were lying loose on the ground in the East African Rift Valley (McBrearty and Jablonski 2005). The semiarid climate and geological deposits of the Rift Valley are suitable for fossils. Hominin fossils are also found there, but the preservation of fossils does not imply that the Rift Valley was the main habitat for hominins or chimpanzees.

### **Physical isolation by rafting**

Consider now a chance event that might have resulted in peripatric speciation—the evolution of a new species from founders that had become physically isolated. I imagine that about six million years ago, a few chimpanzee-like apes, or a pregnant female (“Chimp Eve”), were in a tree beside a river of coastal Nigeria or Cameroon. Floodwater from a tropical storm eroded the riverbank and carried the tree out to the Atlantic Ocean. Like modern chimpanzees, the apes were unable to swim. They clung to the floating tree.

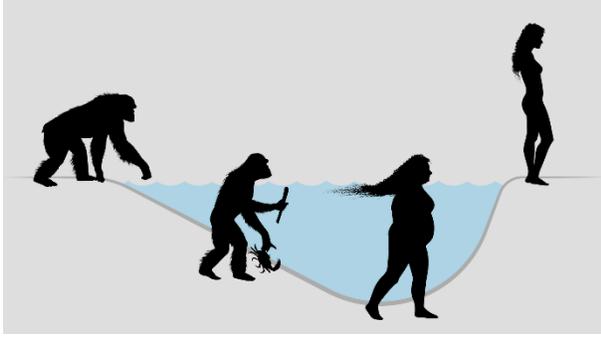
The apes drifted to proto-Bioko, which consisted of one or more young volcanic islands, at least 32 kilometers offshore. When a new volcanic island forms by eruptions in the sea, it has no flora or fauna. The biodiversity of proto-Bioko was presumably still very limited when the apes arrived. There was no possibility of an arboreal lifestyle. The steep, rocky, and naked islands would have been as different from the African mainland as humans are different from other primates.

### **Similarities between the proto-Bioko islands and Galapagos islands**

The situation is similar to the Galapagos Islands, 900 kilometers from South America. There are 18 major islands in the Galapagos archipelago, with a total land area about four times that of Bioko.

The only native land mammal on Galapagos is the rice rat, of which there are seven different species that evolved on different islands. The one or more founders are thought to have arrived on a raft of vegetation in a single colonization event about three million years ago (Harris and Macdonald 2007.)

The most relevant example of speciation in Galapagos is the semiaquatic iguana ([https://en.wikipedia.org/wiki/Marine\\_iguana](https://en.wikipedia.org/wiki/Marine_iguana) retrieved Nov 3 2019; Macleod et al. 2015). In all of South America, Central America, and southern Mexico, there is only one species of iguana. It is the Green Iguana, which lives in trees. It seems likely that a female Green Iguana, pregnant with many eggs, rafted on a tree to Galapagos about eight million years ago. The iguana and its descendants survived on a diet of seaweed. As with humans, they evolved distinctive new features. There were dramatic changes to the teeth, face,



**Figure 2.** Four possible stages of human peripatric speciation. Chimpanzee-like ape, semiaquatic ape, semiaquatic *Homo sapiens*, terrestrial *Homo sapiens*. Intermediate hominins, bipedal but with relatively small brains, are not shown. Illustration by Alex Krill.

hands, feet, skin, and strategy of thermoregulation. Different islands now have different species or subspecies of this Marine Iguana. They are the only lizards in the world with a marine diet.

Some Marine Iguanas eventually found food on land and abandoned the semiaquatic habitat. Their descendants evolved due to the new selection pressures. So now there are three species of terrestrial iguanas on the Galapagos Islands ([https://en.wikipedia.org/wiki/Galapagos\\_land\\_iguana](https://en.wikipedia.org/wiki/Galapagos_land_iguana) retrieved Nov 3 2019). They are similar to the Marine Iguana, and quite unlike the Green Iguana of South America. Such a path from arboreal habitat, to semiaquatic habitat, to terrestrial habitat, is what may have caused the evolution of humans.

Isolated volcanic islands, like Galapagos and Bioko, can be ideal for speciation, sometimes better than large continents like South America and Africa. Also within a continent, isolation by a body of water can lead to primate speciation. It seems that some chimpanzees (*Pan troglodytes*) became isolated by the Congo River, and evolved into bonobos (*Pan paniscus*.) The river has apparently formed an effective barrier to gene flow for a very long time (Prüfer et al. 2012).

### Compulsory marine diet and two-legged walking

The postulated apes that were trapped on proto-Bioko survived by eating crabs, shellfish, and seaweed. Gathering food at low tide was easy. At high tide, it required wading in the water. Like modern apes, they waded on two legs, as upright as possible. When the semiaquatic apes came out of the water, perhaps carrying a crab and a tool to crack it, it was natural to walk on two legs.

Because proto-Bioko lacked predators, it would have been a safe place for apes to practice bipedalism. Even modern Bioko has no leopards or other large predators.

Over time, evolution of bones and ligaments made it completely natural for the semiaquatic apes on proto-Bioko to run on only two legs (Figure 2).

### Proto-Bioko was uniquely suited for aquatic evolution

Bioko is not the first island that has been suggested for the aquatic ape hypothesis. La Lumiere (1981) and Morgan (1982) looked for possible ancient coastlines near the dry hominin fossil sites. They suggested that the aquatic ape venue might have been the Danakil Alps, near the Red Sea and the site of the famous fossil Lucy. The Danakil highlands may have been an island surrounded by seawater at an earlier time. But apes there would not have been trapped or forced to adopt a marine diet.

I felt that the aquatic ape venue was more likely an extant island within the current range of chimpanzees. I discovered Bioko on May 14, 2017, through a simple check on Google Earth. It is perfectly situated geographically, and further study showed it to be perfectly suited geologically as well. No other African island is appropriate.

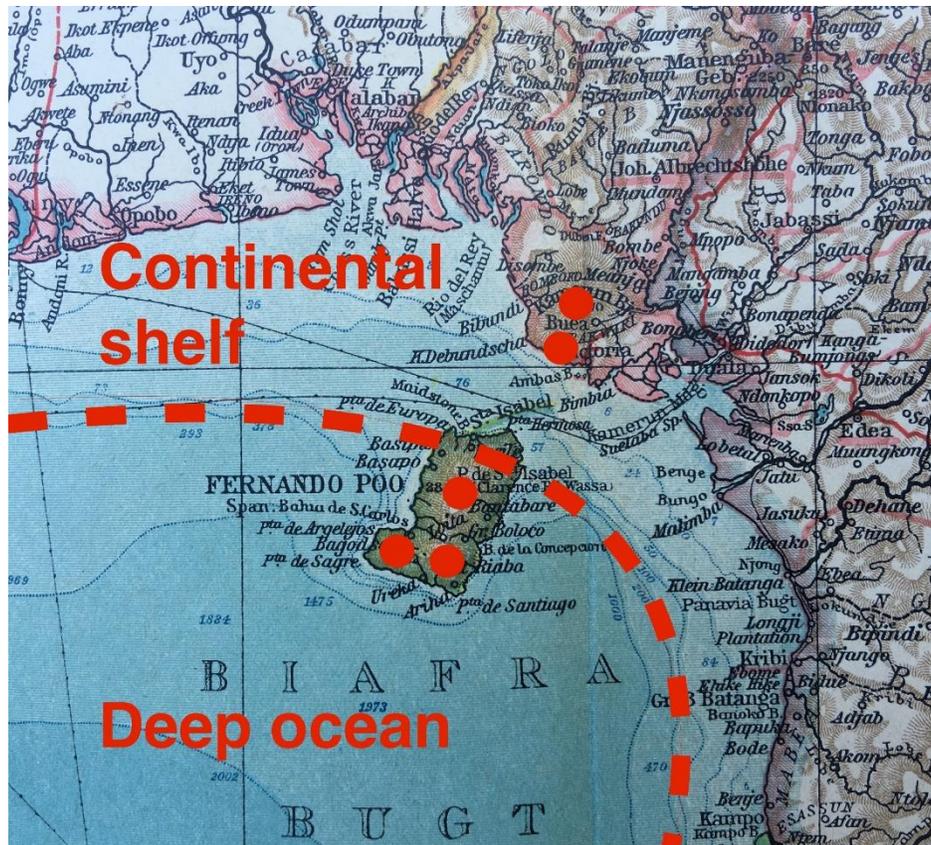
Bioko is a volcanic island of the Cameroon Volcanic Line. Volcanoes on that line have been sporadically active for up to thirty million years (Fitton 1987). There are three known volcanoes on Bioko (Figure 3). Pico Basilé is the highest, rising 3000 meters above sea level in the northeastern part of the island. It last erupted in 1923. The volcano Gran Caldera, 35 km further away on the southwestern side of Bioko, is 2000 meters high. On the nearby mainland, Mount Cameroon is 4000 meters high.

No rocks on Bioko have been shown to be older than about 1.3 million years (Yamgouot et al. 2015). This is only a minimum age. We can assume that proto-Bioko consisted of separate volcanic islands, much lower than today, and that they had merged into the single island by 1.3 million years ago. In order to determine where the first Bioko volcanoes were located, one would need to get samples of older rocks by drilling to sea level in various parts of the present island. There is no economic incentive to do such drilling.

### Pleistocene land bridges

Bioko is centered just off the edge of the African continental shelf, which is only about 60 meters deep between the island and mainland Africa (Figure 3). The center of the island is built up from the ocean floor, which is over one thousand meters deep.

During the Pleistocene epoch, glacial ice accumulations on the northern continents caused sea levels to drop as much as 120 meters. These sea-level fluctuations temporarily exposed much of the world's continental shelves. Each time the sea level dropped



**Figure 3.** Map of Bioko (Fernando Póo) and the margin of the African continental shelf. The northeastern point of the island is 32 kilometers from mainland Africa. Bathymetric contours are 20, 50, 100, 200, 1000, and 2000 meters. The red dashed line marks the probable 200 meter contour early in the history of proto-Bioko. Red spots show recent volcanic centers. Map from Andree (1923).

below about 60 meters, the African continental shelf would have been exposed. This exposure formed a land bridge to Bioko.

If proto-Bioko islands were touching the continental shelf, the first land bridge may have appeared about 2.5 million years ago (Figure 4). After that, the land bridge would have been submerged and re-exposed about 20 to 30 times (Figure 4). It seems more likely that all the proto-Bioko volcanoes were beyond the shelf, so the first land bridge came later. In any case, the island probably had its present size about 1.3 million years ago, and land bridges appeared periodically after that time. The most recent land bridge became submerged about 10,000 years ago.

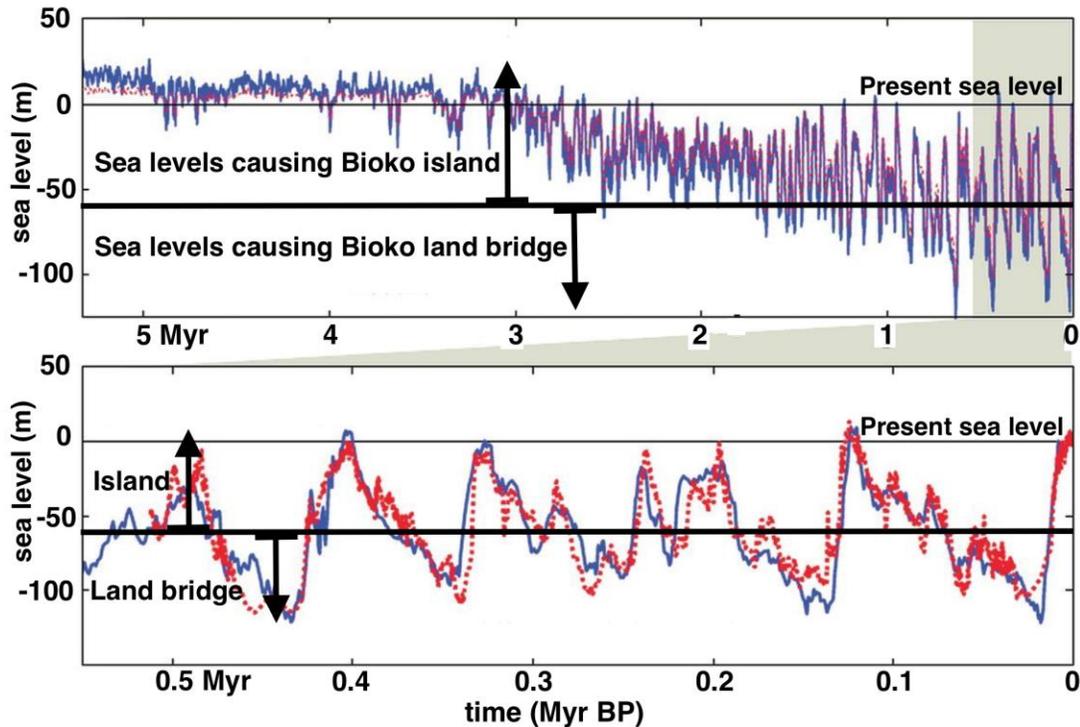
The diversity of flora and fauna of the isolated island must have dramatically increased when the first land bridge appeared. Plants and animals would invade the island across the exposed continental shelf. But Bioko was steep and rocky, and not suitable for some types of plants and animals.

### Early hominins could have swum to Africa

Even before the first possible land bridge, semiaquatic hominins on proto-Bioko could have seen the towering Mount Cameroon on mainland Africa, and some could have swum there. It is a shorter distance than swimming the English Channel, and there are no tidal cross currents and no danger of hypothermia. The goal would be clearly visible from the water. Occasional volcanic eruptions on Mount Cameroon might have aroused the apes' curiosity.

When hominins arrived on forested Africa, those who survived attacks from unfamiliar predators could adopt a non-marine diet. Bipedal hominins could have spread to many different environments, including the semiarid East African Rift Valley, and the region with limestone caves in South Africa. Hominin fossils were preserved in those places.

Paleoanthropologists have identified many species of bipedal small-brained hominins that they are trying to understand. It is not known where or why they speciated.



**Figure 4.** Estimates of sea levels over the past 5.3 and past 0.55 million years. Diagrams modified from Hansen et al. (2013)

It is possible that all these species inherited their bipedalism from semiaquatic apes on proto-Bioko. Different species could have evolved on different islands, as we see on Galapagos. Bipedal hominins that swam to Africa could have hybridized with African apes, or otherwise evolved due to the new terrestrial selection pressures. All of these species are now extinct.

#### ***Homo sapiens* on Bioko may have abandoned the semiaquatic habitat**

Proto-Bioko evolved geologically by the addition of more lava, and biologically by the arrival of more plant and animal species. Once the Bioko forest could provide sufficient terrestrial foods, some *Homo sapiens* would have abandoned their semiaquatic lifestyle.

Terrestrial humans on Bioko would not have coexisted with semiaquatic humans. Having large brains, the two groups would have different languages, different cultures, and different gods. They would have conflicts involving weapons, and people fighting from land would have all the advantages. They would quickly eliminate

any semiaquatic holdouts. Never again would there be semiaquatic humans.

#### **Early fossils of *Homo sapiens***

Each time the Pleistocene sea level dropped, the shore habitats would not have changed much where the ocean was deep. Semiaquatic or terrestrial *Homo sapiens* on southwestern Bioko could have continued living mainly on seafood. On the northeastern side, however, the shoreline would have disappeared, and the land bridge would have made it natural for those humans to walk to mainland Africa.

It is not known when the first *Homo sapiens* emerged in Africa. The oldest fossil discoveries are from Morocco, thought to be about 300,000 years old (Hublin et al. 2017). Humans may have been on Bioko or other places much earlier, without appropriate conditions for preservation of fossils.

About 165,000 years ago, humans seem to have made paintings in a cave in South Africa. They also left piles of discarded seashells (Marean et al. 2007). Those

humans may have lived mainly on a marine diet, but they are not thought to have been semiaquatic.

### **Evolutionary changes take time**

Human features today seem to mostly reflect a semiaquatic evolution, and not so much the more recent terrestrial lifestyle. In comparison with a chimpanzee, the human body seems better suited for life on Bioko than in places such as the East African Rift Valley.

Fur would not be needed for warmth or for sun protection on Bioko. Both the air and seawater there are warm year round, and the nights are never cold. The sun is not strong. Malabo, the capital, is ranked as one of the cloudiest cities in the world.

Human drinking capacity is relatively low, and in dry places people need to carry water in containers. Humans on Bioko could drink fresh water that was always available. Southern Bioko is known as one of the rainiest places on Earth.

Human features are still evolving. Variations in the color of human skin and hair must have evolved after human fur was lost. Although there is no fossil evidence for skin or body hair, humans may be hairier now than shortly after the postulated semiaquatic evolution.

Fossils show that the brains of early *Homo sapiens* were larger than brains of humans living today (Lewin and Foley 2004). The return to a terrestrial diet with less DHA might explain this reduction in brain size.

### **Genetics of living humans may be able to test the Bioko hypothesis**

To make this aquatic hypothesis less speculative, one might look for durable fossils, such as human teeth or stone tools. But one-time discoveries of human fossils, announced with great fanfare by scientists, are not a convincing type of evidence. They might be a hoax perpetrated by non-scientists, as we know from Piltdown Man and other examples. Irreproducible evidence is often accepted in paleoanthropology, because of the keen public interest and paucity of good evidence. For scientific evidence to be considered good, it should be repeatable and testable by independent and impartial scientists.

The research tools of human evolution now include the DNA of living humans and apes. Such evidence can be tested and reproduced. It was genetic evidence, not fossils, that showed that the divergence of humans and chimpanzees took place no more than about 6 million years ago. Eager paleoanthropologists had interpreted primate fossils to indicate a much earlier divergence.

To test the Bioko hypothesis, one might study the genetics of the indigenous Bubi people that live in isolated places on Bioko. There are many types of genetic study possible. These include the well known

Mitochondrial DNA and Y-chromosomal DNA, and the DNA of tiny parasites that live in the hair follicles of humans (Palapoli et al. 2015).

Endogenous retroviruses make up a few percent of the human genome. These retroviruses may be passed down to descendants for as much as a million years. Most of the apes and monkeys of Africa were infected by the simian immunodeficiency virus (SIV) at some undetermined time in the past. Genomes of primates outside of Africa do not include this retrovirus. A few African ape species also avoided contracting SIV: humans (*Homo sapiens*), two chimpanzee subspecies (*Pan troglodytes ellioti*, *Pan troglodytes versus*), and bonobos (*Pan paniscus*) (Locatelli 2016). Our human ancestors may have been isolated on Bioko when SIV was spreading among African primates.

Retroviruses carried by the monkeys on Bioko show that they are related to monkeys on mainland Africa, but evolved in isolation (Worobey et al. 2010). Retroviruses might be able to prove the Bioko hypothesis: If the genome of the world's human population includes a retrovirus that is otherwise only found in endemic animals on Bioko, it would show that our ancestors had contact with them there.

### **A testable version of the aquatic ape hypothesis**

If an aquatic human evolution really happened, it most likely happened on Bioko. No other place would have involved the reproductive isolation and the lack of forest foods that would force chimpanzee-like apes to adopt a semiaquatic habitat.

Unlike other versions of the aquatic ape hypothesis, the Bioko version is testable by the study of DNA of humans, other primates, and other animals that are still isolated on Bioko.

Paleoanthropology textbooks have avoided previous versions of the aquatic ape hypothesis, mainly because the hypothesis does not involve fossils. Since no fossils will likely be found on Bioko or nearby parts of Africa, traditional paleoanthropologists will still not be able to play this aquatic-ape sport, any more than professional basketball players could play on a wet grassy field.

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## Response to referee

I thank Dr. Yuichi Nakazawa (2020) for both reviewing and publishing commentary on this article.

Although initially surprised, I appreciate his comment that the most significant part of the paper may be the comparison of the aquatic ape paradigm with the continental drift / plate tectonic paradigm of geology, a comparison first made by Morgan (1985, 1990). It was my fascination with continental drift history that led me to challenge the rejection of the aquatic ape paradigm and look for an extraordinary marine location such as Bioko. For most scientists, it must be almost unthinkable that an alternative paradigm could be worth considering, after having been brushed aside by experts and publicly ridiculed for decades.

Dr. Nakazawa is concerned that the oldest known volcanic rocks on Bioko are only about 1.3 million years old, much younger than hominin speciations. This situation is similar to that on Galapagos: the marine iguana and other endemic species on Galapagos are thought to have been living on Galapagos islands much earlier than any of the available volcanic rocks (Rassmann 1997, Macleod et al. 2015). The first rocks of proto-Bioko and of proto-Galapagos are nowhere exposed.

Dr. Nakazawa correctly points out an oversimplification: I assumed that the surface of the continental shelf near Bioko has not changed over the past few million years. The black 60-meter line of Figure 4 is based on that assumption. More likely, the shelf between Bioko and the mainland was many meters lower and has been built up by the addition of extra sediment. Erosion from the high volcanic mountains of Cameroon and Bioko probably provides more sediment than elsewhere along the African continental shelf. Bioko blocks some incoming waves, so more sediment is left in the shadow-zone between Bioko and the mainland. Erupted volcanic lava or ash may also have added to the shelf between Bioko and Mount Cameroon. Furthermore, the shelf could now be uplifted some meters due to thermal expansion in the mantle below the modern volcanoes.

If the shelf was significantly lower, animals would not have been able to walk between proto-Bioko and the mainland as early as 1.3 million years ago. The ancestors of most of the endemic animals of Bioko probably migrated there by walking on land bridges. To test when the first land bridge occurred, one might study the genetics of endemic animals on Bioko and their relatives on the mainland (see Worobey et al. 2010).

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