Commentary

Have we already tested the aquatic ape hypothesis?

Yuichi Nakazawa

Yuichi Nakazawa (ynakazawa@med.hokudai.ac.jp), Faculty of Medicine, Hokkaido University, Sapporo, Japan

Krill (2020) proposes a new idea of human origins, in favor of the aquatic ape hypothesis (AAH) that Alister Hardy originally proposed, followed by its resurrection (Morgan 1982, 1997). In the first part of the paper, the author concisely summarizes the characteristics of AAH, and then makes a comparison of AAH and the continental drift hypothesis which was at first mostly dismissed by the scientific community but eventually proved by plate tectonics. This is probably the most significant part of the paper. Paradigmatic bias sometimes alters the views and thoughts of scientists in a scientific community (e.g., Clark 1993, Clark and Lindly 1991), in which researchers may share the implicit perception that it is better to avoid addressing a big question.

For exploring explanations of behavioral and cultural adaptations in the origin of human evolution (e.g., Foley and Lahr 2014), the AAH provides an intriguing framework intending to explain a causal relationship between ecological condition (i.e., water) and human adaptive response (physiological and behavioral changes). The explanatory framework of AAH is evolutionary and adaptationistic, notably seen in traits of human anatomy and physiology seemingly adapted to the aquatic environment, such as the paranasal sinuses (Keir 2009; Rae and Koppe 2014). Another adaptationist model on the origin of hominins is represented by the savanna-based hypothesis (e.g., Dart 1925; Wheeler 1991; Wolpoff 1980) which is also a causal explanatory model embraced by scholars in favor of the significance of human fossil record (Morgan 1997). However, even the savanna-based hypothesis is not entirely supported because a group of the earliest hominin, notably *Ardipithecus ramidus* lived in the woodland environment, not in the savanna (Reed 1997, White et al. 2009). This implies that given environment and emergence of bipedalism are not necessarily correlated. If the latter were the case, unanswered questions remain.

A new finding can support the hypothesis, but it can also urge to revise the frame of hypothesis. Indeed, the well-recognized textbook of evolution by Zimmer and Emlen (2013: 561) considers that bipedal locomotion may have adapted early hominins for living in open-savanna habitat in Africa without mentioning the environment where bipedal locomotion first emerged. Given this understanding, it is fair to say that both the AAH and savanna-based hypotheses are still in the process of being tested.

The AAH has a characteristic of an “umbrella hypothesis” (Langdon 1997: 479) in which a simple idea explains many questions. Explanations in AAH, however, are not explicit, or as the author says, “parsimonious”. They are rather regarded as interpretations (statements that are not yet explicitly tested) because potential processes for how apes adopted terrestrial lifeways (after earlier adaptation to an aquatic environment) are not yet explicitly tested against systematically collected data sets (but see Rae and Koppe 2014). In addition to its paradigmatic nature, the AAH is complicated by its dual structure: it involves a series of hypotheses that are testable against multiple sources of data (e.g., comparative physiology among primates, human anatomy), while attempting to explain the causal scenario of human origins.

An interesting part of this paper is the proto-Bioko in coastal Cameroon as the candidate for the “Eden” where aquatic ape evolved to bipedal hominin. Although the author does not clearly mention, groups of ape could have refuted to an island in response to some sort of exogenous events (e.g., disaster, inter-specific competition). Referring to the global sea-level changes, the author assumes that land bridges between the island and the African continent appeared at 2.5 Ma and the proto-Bioko experienced a cycle of island and part of land for 20–30 times by 1.3 Ma. I assume that readers working

outside of Africa have seldom heard about Bioko. It is my hope that Krill tells more about the geological background of Bioko, in particular to make sure that this island was present at least during the Early Pleistocene to allow apes perceive it as the island to visit. Also, the author estimated the bridge formation only based on the present shelf depth. This estimation may not be correct, considering local tectonic uplift and subsidence, as well as volcanic eruptions that could have accumulated thick volcanic sediments along the coast of Cameroon. It would be helpful for readers to know what the coastal features and paleo-environment were like during the Early Pleistocene.

Contrary to the superior idea to introduce Bioko as the “Eden” of hominin evolution, an unclear part of this paper is the description regarding the *Homo sapiens*. It was not *Homo sapiens* who first acquired bipedal style of walking from the quadrupedal. The evidence of upright walking by hominins is at least found from *Australopithecus afarensis*, evolving during 3.7–2.9 Ma, probably along a different lineage from genus *Homo*. *Australopithecus afarensis* has a complete fossil record including the well-known “Lucy” (a nearly complete skeleton), suggesting upright walking (Haile-Selassie et al. 2010). We also know that human footprints in Laetoli were left by *Australopithecus afarensis*. Therefore, upright walking likely appeared among *Australopithecine*, not first among genus *Homo*. In contrast, brain sizes of hominins significantly increase with the appearance of *Homo erectus* (1.8–1 Ma) (Aiello and Wheeler 1995), evolved later than the *Australopithecine* (Klein 2009). Given this observation, the author’s interpretation that acquisition of DHA contributed to increase the brain size that is sympathetic to AAH needs to be reconsidered. Brain expansion may be correlated to an increasing proportion of meat in the hominin diet (Aiello and Wheeler 1995), and the use of fire that saved the cost of digestion and enhanced nutrition and calories intake (Wrangham 2010). Regarding the diet effect on the increasing brain size, the author may be better to consult the critical role of aquatic diet including macrophytes for hominins and pongids (Verhaegen et al. 2002, Wrangham et al. 2009).

In the last part of paper, Krill mentions that Bioko as the origin of human evolution is potentially tested by contributions from genetic study. DNA obtained from the indigenous Bubi people may possess evidence of genetic isolation, but the result may be opposite: recent origin of indigenous people who migrated from somewhere outside the local region. Similar situations are found in other indigenous populations. For example, although living in far distance, Siberians (northeastern Asian) and Europeans have genetic affinity (e.g., Lamnidis et al. 2018, Wong et al. 2017). Generally speaking, genetic

studies give superior pictures of human migrations, and they may reveal that gene flows in and between current ethnic groups were more frequent than expected. Surely, I would not negate the possibility that the present Bubi people maintain some signature of isolation in their ancient genetic codes. Just as genetic diversity of modern *Homo sapiens* was reduced by population contraction during the Last Glacial Maximum in Europe (Posth et al. 2016), I expect that some degree of genetic bottleneck could also have occurred among the small population trapped on Bioko island.

If one wants to evaluate the evolution of aquatic ape in the small island of Bioko in a scientific manner, it will eventually come to demand some evidence. Physiological evidence potentially supporting aquatic lifeways is the presence of auditory exostoses, which is seen among fishermen who routinely dive deep into sea water (Katayama 1998). Habitual diving to gather shellfish in the Pacific regions is common (e.g., Irimoto 1973, Kuchikura 1975), and auditory exostoses caused by cold water and deep diving habit are identified in fossil specimens from a wide range of prehistoric populations, from Neandertals (Trinkaus et al. 2019) to the Neolithic Jomon (Katayama 1998). If a specimen of hominin cranium having auditory exostoses or similar traumatic feature is found from Bioko, it will give supportive evidence of AAH.

While the author sees the AAH is mainly concerned with anatomy, physiology and genetics, I would like to add the archaeological point of view. Wading in the shallow offshore environment to gain aquatic foods would have needed spears and hooked sticks to catch small to medium fish and gather shellfish along shorelines and coral reefs. Because such tools are intended to be designed to carry during their underwater fishing and gathering, wood and bamboo implements would be appropriate as opposed to stone tools. These organic tools are rarely preserved in the terrestrial condition, but if any, they may be found from archaeological sites buried by underwater deposits.

Under the situation that no hard evidence of early hominin fossils from Bioko is yet given, as the author knows, not many paleoanthropologists, especially hominin fossil experts would seriously treat the author’s vision on the origin of hominins from aquatic environment. This will also relate to research bias, since the western coast of Central Africa is outside the regions where most paleoanthropologists have been working. On the other hand, it is important for scholars in paleoanthropology and its related disciplines to realize that Krill (2019) proposes new testable ideas that may help to evaluate the AAH. It is thought-provoking with a criticism to ignored status of AAH in the research community of hominin origins.

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