Let’s talk about species, baby! Taxonomy and species concepts in the context of *Homo luzonensis*

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Abstract

Classifying an individual into a species is one of the first steps to better understand not only the individual in question, but also their evolutionary history and relationships. However, designating individuals into species can be a difficult process. It is particularly difficult in the field of paleoanthropology, where species designations must be made using only skeletal remains. A recent publication announced the reported discovery of a new hominin species, *Homo luzonensis*, from remains found at Callao Cave in the Philippines. However, this new species consists of only 13 skeletal specimens from three individuals. With such a small sample size, do the Callao Cave remains represent enough evidence to be called a separate species? In order to explore this question, I examine several species concepts and how they can and have been applied to fossil hominin species. I also utilise several comparable and recently discovered hominin taxa as case studies. The results of these analyses indicate that while the remains from Callao Cave can be designated as a new species, the low specimen count and lack of DNA evidence means that future criticism of this designation is likely. In addition, these cases studies highlight structural and human factors—such as pressure to publish and arguments over types of evidence—which influence the species designation process.

Introduction

On 11 April 2019, the field of paleoanthropology was set abuzz with an article announcing the discovery and description of a new hominin species, *Homo luzonensis*. The article, published in *Nature* (Detroit et al., 2019), described the bones from Callao Cave, on Luzon Island in the Philippines. In total, 13 skeletal elements were recovered, which came from an estimated minimum of three individuals (Detroit et al., 2019). One of the bones, a third metatarsal, has been directly dated using U-Series ablation to a minimum age of 66,700 years (Mijares et al., 2010). Stone tools and butchered animal remains dated between 777,000 and 631,000 years old have also been recovered on Luzon (Ingicco et al., 2018). These finds indicate that hominins have a deeper history in islands of Southeast Asia than initially thought, and raise challenging questions about human evolution, both in the region of Southeast Asia and the world at large.

However, while this is an exciting discovery, the decision to name the hominin remains from Callao Cave a new species may prove controversial. As noted, the finds comprise just 13 skeletal elements from three individuals. Is that enough evidence to call a population of hominins a separate species? And if not, then just what kind of evidence and how much of it do we need before we call a population a distinct taxon? In exploring these questions, this essay will first review issues surrounding taxonomies, species concepts, and related personal biases in paleoanthropology, before defining key aspects—namely morphology and genetics—used to identify distinct *Homo* taxa. The topic and key aspects will then be explored using several case studies, specifically discussing the recently discovered—and at times controversially designated and debated—species of *Homo floresiensis*, *Homo naledi*, and the Denisova hominins. The essay will then turn to the remains from Callao Cave, and evaluate whether they fit the criteria to be designated as a new *Homo* species. While the Callao Cave remains can be designated as a new species, they will likely face criticism based on their low specimen count and lack of DNA evidence.

Species concepts

In order to investigate the aforementioned questions regarding *H. luzonensis*, we must first address the following question: what is a species? It is beyond the scope of this essay to fully address all the issues regarding taxonomies, species concepts, and human personal biases within paleoanthropology. However, some discussion of the topic is required in order to contextualise the broader research questions of this essay.

Issues surrounding taxonomies and species concepts have always been contentious in paleoanthropology. This is characterised by the classic and infamous debate between 'lumpers' and 'splitters'. Lumpers, as the name suggests, prefer a taxonomy with fewer but more inclusive species; splitters, meanwhile, subscribe to a more speciose taxonomy (Wood & Lonergan, 2008). For instance, a splitter will recognise *Homo habilis* and *Homo rudolfensis* as separate species, while a lumper will collapse both into *H. habilis sensu lato* (for an example of both a lumping and splitting taxonomy for hominins, see Wood & Lonergan, 2008).

Intrinsically linked to the debate between lumpers and splitters are species concepts themselves. How one identifies a species will influence how many species one recognises. At least 22 species concepts have been identified (Mayden, 1997), although some models are more widely subscribed to than others. Species concepts used in paleoanthropology include the biological species concept, the evolutionary species concept, and the phylogenetic species concept (Conroy & Pontzer, 2012). Each species concept has its own advantages and drawbacks, although some are inherently more suitable when analysing fossil hominins.

One species concept is the biological species concept. This species concept is popular in biology (Hublin, 2014), particularly with mammalogists and ornithologists (Holliday, 2003). Simply put, in this concept species are defined as 'groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups' (Mayr, 1970, p. 12). While this species concept can be tested on extant taxa (Holliday 2003), this obviously is not the case with fossil taxa (Derricourt, 2009; Holliday, 2003; Hublin, 2014). There are further drawbacks to this model. For instance, how would a first-generation hybrid of two species be classified (Holliday, 2003)? This species concept also stresses maintaining genetic isolation, rather than highlighting characters that conspecific individuals have in common (Wood & Lonergan, 2008). That being said, while most applications of the biological species concept to fossil hominins have to be inferential (Tattersall & Mowbray, 2005), recent DNA analyses (e.g. Reich et al., 2011; Sankararaman, 2012) have proven that past populations of hominins did interbreed with each other, thus fulfilling the criteria for the biological species concept to be applied.

Another species concept is the evolutionary species concept. Under this concept, species are 'a lineage (an ancestral descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies' (Simpson, 1961, p. 153). This model was an attempt to add a temporal dimension to species concepts, particularly the biological species concept (Holliday, 2003; Wood & Lonergan, 2008). Under this model, a lineage is separated into segments called 'chronospecies', and the boundaries of these chronospecies can be discontinuities in this fossil record (Wood & Lonergan, 2008). This notion of chronospecies has been met with opposition, with some saying that chronospecies inflate taxic diversity and the divisions between chronospecies are arbitrary (White, 2014).

In the phylogenetic species concept, species are defined as 'an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent' (Cracraft, 1989, pp. 34–35). This concept is therefore independent of the reproductive isolation criterion of other concepts (Holliday, 2003) and combines genealogical and morphological aspects (Tattersall & Mowbray, 2005). Given that morphology is the only physical attribute that survives fossilisation which can provide any information on potential species recognition (Tattersall & Mowbray, 2005), it is perhaps unsurprising that the phylogenetic species concept is the favoured species concept of those who study hominin taxonomy (Holliday, 2003; Wood & Lonergan, 2008). However, given the rise of ancient DNA analysis, this paradigm may begin to shift in the future.

Paleoanthropologists are human too …

Paleoanthropologists may have their own agendas for wanting to call a distinct population of hominins a new species. Paleoanthropologists, like most academics, are under intense pressure to 'publish or perish'. That is, in order to be competitive in a market where 6,000 people a year (in Australia alone) will graduate with a PhD in science, scientists are under extreme pressure to publish their work, ideally in top-tier journals like *Nature* or *Science* (Barbour, 2015). This factor, combined with restricted access to both funding and materials (i.e. the fossils themselves), creates an environment where there is both obvious motivation and substantial opportunity for researchers to 'create' new species (White, 2013). To quote Derricourt (2009), 'the classic "moment" in palaeoanthropology has become the announcement in the pages of a journal such as the weekly *Nature* or *Science* of a new discovery, together with its naming—and the immediate reporting of this announcement in the international print and electronic media' (p. 195). It should also be noted that publication in a top-tier journal like *Nature* or *Science* can increase a scholar's ability to secure grant funding and achieve tenure (Levi-Kraus, 2019). Perhaps unsurprisingly, paleoanthropology is probably affected by the above factors more frequently than other scientific fields (Bruner, 2013). As can be seen, the structural and human-driven factors of publish or perish, limited access to fossil materials, and the renown that follows the naming of a new species have a potentially profound effect on species designation and the field of paleoanthropology overall.

In addition to gaining access to materials, funding, and general career advancement, researchers may also have nationalistic reasons for naming a new species. This can relate to the nationality of the find location or nationality of the excavation team, and national pride can also influence the naming of the new species itself—which makes things difficult if the same taxon is later found in another country (Derricourt, 2009). While these points are quite pessimistic of paleoanthropology as a whole, it is nevertheless important to remain cognisant of such potential biases. Clearly, paleoanthropologists are human too, and are subject to personal biases that influence how they interpret the fossil record.

Applying species concepts to hominins

Applying species concepts to fossil hominins is not a clear or easy process. The previous discussion highlighted the issues and controversies in paleoanthropology surrounding taxonomies and species concepts. The discussed species concepts also hinted at the kind of evidence that a researcher may require in order to name a population a new taxon. For example, a researcher who follows the biological species concept will require DNA evidence to support claims to taxic diversity, and will also likely place greater weight on DNA evidence. Conversely, a researcher who subscribes to the phylogenetic species concept will place more weight on morphological traits present in the fossils of extinct hominins. Therefore, it follows that in a perfect world, we would call a population a separate species if it is both genetically and morphologically distinct and has many samples for analysis and replicability.

In practice, however, this is rarely the case. While they are becoming more common, DNA analyses on hominins are still comparatively rare, owing to both the poor preservation of DNA in ancient remains and the destructive nature and prohibitive cost of analysis (Geigl & Grange, 2018). Contamination of samples can also pose a problem to ancient DNA analysis (Marx, 2017). Morphological analyses also have their own issues. Although many new fossils have been found since the 1990s (Trinkaus, 2018), such fossils are still generally rare and often fragmentary (Derricourt, 2009; White, 2014). This rarity of fossil resources in turn causes replicability issues in the discipline, with finds sometimes taking years to appear in published journals (Derricourt, 2009).

With all of this in mind, we will now discuss several newly discovered *Homo* species in the context of taxonomy and species concepts and consider whether or not they fit as separate taxa, and if they do, how they fit. The case studies are *Homo floresiensis*, *Homo naledi*, and the Denisova hominins. These taxa were chosen because they are all relatively recent finds, are all late Pleistocene *Homo*, and each has had its own controversy and subsequent taxonomy dilemmas.

Case study one: *Homo floresiensis*

Homo floresiensis is a small-bodied hominin found at Liang Bua on the Indonesian island of Flores, first reported in October 2004 (Brown et al., 2004). The type specimen of the species is LB1, a partially complete skeleton of an adult female (Brown et al., 2004). More remains from the same site were later found and described, bringing the total number of identified individuals to nine (Morwood et al., 2005). Although the remains were initially reported to be 18,000 years old, newer absolute dating methods indicate that the skeletal remains at the site are between 100,000 and 60,000 years old (Sutikna et al., 2016). Currently, all attempts to retrieve DNA from any of the skeletal samples have failed (Jones, 2011; Marx, 2017).

LB1 was attributed to a new species based on analysis of its morphology, which represented a unique combination of primitive and derived characters (Brown et al., 2004). Specifically, LB1 has primitive wrist bones similar to the great apes or australopithecines (Tocheri et al., 2007), but a face which is morphologically closer to members of the *Homo* genus (Brown et al., 2004). They also have comparatively shorter legs and a different body shape compared to modern humans (Jungers & Baab, 2009). Furthermore, a recent Bayesian analysis of craniodental features rejected the hypothesis that the Liang Bua remains represent a pathological individual or population of *H. sapiens* (Dembo, Matzke, Mooers, & Collard, 2015), further strengthening the argument that these remains from Liang Bua constitute a distinct taxon.

In spite of the morphological evidence indicating that the Liang Bua remains constitute a distinct taxon, controversy emerged, with some researchers believing that the remains were simply a modern *H. sapiens* individual with an abnormal pathology (Groves, 2007). Some have argued that the remains represent a modern human with a significantly smaller head and brain size (microcephaly), with the endocranial volume of LB1 falling within range of a modern microcephalic sample (Jacob et al., 2006; Martin et al., 2006; Weber, Czarnetzki, & Pusch, 2005). However, subsequent reanalysis of the Liang Bua remains rejected this hypothesis, with a cranial morphometric comparison indicating that LB1 is unlikely to represent a microcephalic *H. sapiens* individual (Argue, Donlon, Groves, & Wright, 2006). This result was supported by analysis indicating that the brain shape of LB1 is non-pathological and contains multiple derived features, despite its small size (Falk et al., 2009). Furthermore, geometric morphometric studies of skulls have indicated that not only is LB1 separate from all *H. sapiens*, but all microcephalic samples fall within range of modern humans (Lyras, Dermitzakis, Van der Geer, Van der Geer, & De Vos, 2009), in turn supporting the conclusion that the Liang Bua remains represent a taxon separate from *H. sapiens*.

Similarly, it has also been suggested that the Liang Bua remains represent modern *H. sapiens* individuals with conditions which cause stunted growth, such as endemic cretinism (Obendorf, Oxnard, & Kefford, 2008; Oxnard, Obendorf, & Kefford, 2010), Laron Syndrome (Hershkovitz, Kornreich, & Laron, 2007), or even Down Syndrome (Henneberg, Eckhardt, Chavanaves, & Hsü, 2014; Eckhardt, Henneberg, Chavanaves, Weller, & Hsü, 2015). However, these hypotheses have been rejected by subsequent analyses (Baab et al., 2016; Brown, 2012; Falk et al., 2009; Westaway, Durband, Groves, & Collard, 2015). Some have proposed that the strong controversy surrounding *H. floresiensis* and LB1 relates to continuing academic disputes regarding the evolutionary importance of brain size as opposed to neurological reorganisation (Falk et al., 2009). As such, most paleoanthropologists now accept the validity of *H. floresiensis* as a distinct taxon (Groves, 2007).

In summary, *H. floresiensis* was declared a new taxon based on the morphometric analysis of the incomplete remains of nine individuals (Morwood et al., 2005). Currently, no attempts to retrieve DNA from the remains have been successful (Jones, 2011; Marx, 2017). Without DNA, *H. floresiensis* cannot be a proven species under the biological species concept. It can, however, still be considered a separate taxon under the phylogenetic species concept. Its status as a valid taxon has been disputed, mainly by those who consider the Liang Bua remains to be modern *H. sapiens* individuals with various pathologies. However, despite these claims, most consider *H. floresiensis* to be a valid taxon, due to its unique morphology. This claim could potentially be bolstered by the discovery of more skeletal examples of the species.

Case study two: *Homo naledi*

The fossils comprising *Homo naledi* were found in the Dinaledi Chamber of the Rising Star Cave system of South Africa and were announced publicly in September 2015 (Berger et al., 2015). Using a combination of Uranium series ESR and Uranium-Thorium dating, the fossils in the Dinaledi chamber were dated to between 236,000 and 335,000 years old (Dirks et al., 2017). The fossil assemblage contained over 1,500 specimens representing almost every skeletal element of the body and comprised at least 15 individuals (Berger et al., 2015). A few years later, a further 131 specimens were recovered from the nearby Lesedi Chamber (Hawks et al., 2017). To date, all attempts to obtain DNA from *H. naledi* remains have been unsuccessful (Berger, Hawks, Dirks, Elliott, & Roberts, 2017).

Similar to *H. floresiensis*, *H. naledi* was also attributed to a new species based on analysis of its unique morphology. More specifically, the morphology of the cranium and mandible is similar to that found in *Homo*, while its small brain size is closer to the range of australopithecines (Berger et al., 2015). However, the brain shape of *H. naledi* shares aspects of its structure with *Homo*, despite its smaller size (Holloway et al., 2018). The pelvis, meanwhile, resembles that of an australopithecine more than it resembles *Homo* (VanSickle et al., 2018), while its feet are predominantly closer to modern humans (Harcourt-Smith et al., 2015). The hands of *H. naledi* are also unique, with derived wrist morphology similar to humans, but long curved manual phalanges similar to those found in australopithecines (Kivell et al., 2015). This mosaic of derived, primitive, and unique features—combined with the incredibly homogenous nature of the assemblage of *naledi* fossils—led to the attribution of the Dinaledi chamber remains as a separate taxon (Berger et al., 2015).

There was some critique of the attribution of the fossil to a new taxon, in spite of its unique morphology and large sample size. Some have suggested that the fossils in the chamber represent more than one species (Callaway, 2015); however, most critics argue that the fossils belong to *Homo erectus*, with the proponents of this hypothesis chiefly being Chris Stringer (Stringer, 2015) and Tim White (Handwek, 2015; Lents, 2016). John Hawks replied to these criticisms on his personal blog, where he reiterated the differences between *H. naledi* and *H. erectus*, along with the homogenous nature of the finds (Hawks, 2015). Given the discovery of *H. naledi* was widely publicised to the general public (Williams, 2016), it is perhaps unsurprising these criticisms were mainly communicated through newspapers, magazines, and other similar sources, and that the response came from a personal blog. Furthermore, it should be noted that as of December 2019, there has been no published academic criticism of the new species attribution of the Dinaledi and Lesedi Chamber fossils. As such, it appears that most paleoanthropologists accept *H. naledi* as a separate taxon.

The taxa of *H. naledi* and *H. floresiensis* share similarities when it comes to explorations into species concepts. Both were declared new species based on morphometric analyses, and no DNA attempt has yet been successful. However, the combined assemblage of fossils from the Dinaledi and Lesedi Chambers dwarfs the number found in Flores. The sheer quantity of fossil samples—over 1,500—has worked in favour of *H. naledi*. It is far harder to dispute the validity of a new species when there is such a large number of available samples, all of which are homogenous. Consequently, there have been no formal academic challenges as of December 2019 to *H. naledi*'s status as a valid taxon.

Case study three: The Denisova hominins

Our third case study is the hominins from Denisova Cave, Siberia. At present, five specimens have been identified as belonging to this group of hominins. A phalanx and three molars were recovered from Denisova Cave (Slon et al., 2017), while a mandible from Baishiya Cave, China was later found to also form part of the Denisovan population (Chen et al., 2019). A sixth specimen was found at Denisova Cave, but this individual was later found to be a first-generation hybrid between a Denisovan and a Neanderthal (Slon et al., 2018). As only five identified specimens belong to the Denisovans, morphological analysis is virtually impossible.

However, DNA analysis has proven to be a game-changer with the Denisova hominins. Analysis of the mitochondrial genome of one of the Denisovan individuals was undertaken in 2010 (Krause et al., 2010), with the results indicating that the individual was genetically distinct from other hominins, including humans. Other samples from the site were analysed, with both mitochondrial and nuclear DNA being found in multiple samples (Reich et al., 2010; Sawyer et al., 2015; Slon et al., 2017). Later analyses found that not only were Denisovans distinct from humans, but they had interbred with both humans (Browning, Browning, Zhou, Tucci, & Akey, 2018) and Neanderthals (Slon et al., 2018).

When it comes to species concepts, assigning a species to the Denisovans becomes difficult. With virtually no specimens available for morphometric analysis, they cannot truly be classified as a species under the phylogenetic species concept. Furthermore, given that Denisovans interbred with *H. sapiens*, under the biological species concept they would be classed as *H. sapiens*. However, it is not that straightforward. For instance, Neanderthals also interbred with humans (Sankararaman, 2012), thus some have argued they should also be classed as a subspecies of *H. sapiens* (e.g. Gunbin, Afonnikov, Kolchanov, Derevianko, & Rogaev, 2015). However, Neanderthals are morphologically distinct from humans (Harvati 2003; Tattersall & Schwartz, 1998), and therefore are most often considered a separate species (Harvati, 2003; White, Gowlett, & Grove, 2014). Perhaps because of this, the taxonomic status of the Denisova hominins seems to be uncertain, with these hominins being given placeholder names such as *Homo sapiens denisova* (Gunbin et al., 2015), and *Homo sp. altai* (Malyarchuk, 2011).

Homo luzonensis

With these case studies in mind, we turn back to *H. luzonensis*. A total of 13 skeletal elements were recovered from Callao Cave, which came from an estimated minimum of three individuals (Detroit et al., 2019). The elements included maxillary teeth, manual and pedal phalanges, a femoral shaft, and a third metatarsal. These specimens were designated to a new species based on morphological analysis, and so far, no attempts to retrieve DNA from the specimens have been successful (Detroit et al., 2019). As stated earlier, *H. luzonensis* is argued to be a new species, based on a unique combination of primitive and derived morphological traits. The following section will outline the evidence present in Detroit et al. (2019), which they argue supports the conclusion that the Callao Cave remains constitute a new species.

The teeth found in Callao Cave further support the notion that they represent a new species. For example, the premolars are relatively large compared to the molars, which are unlike any other hominins, except for *Paranthropus*. Furthermore, the premolars have multiple roots, which is a primitive trait found in *Australopithecus*, *Paranthropus*, and early *Homo* (Detroit et al., 2019, p. 182). The molars, meanwhile, have more derived features, such as a reduced number of cusps and simplified occlusal morphology. This is similar to more modern *Homo* such as *H. neanderthalensis*, *H. floresiensis*, and *H. sapiens*. However, the molars are incredibly small. They are smaller than those of *H. sapiens* and even *H. floresiensis*, which is argued to be strong evidence for a new species (Detroit et al., 2019, p. 182). The mix of primitive and derived features of the teeth of the Callao Cave specimens suggest that the remains are unique, and possibly represent a new taxon.

The other morphological evidence comes from hand and foot bones. One pedal phalanx (CCH4) demonstrates a number of primitive features, including a distinct curvature of the shaft and well-developed flexor sheath attachments, which are similar to what is found in *Australopithecus* (Detroit et al., 2019, pp. 183–184). The second foot bone (CCH3), an intermediate pedal phalanx, cannot tell us much, as this bone is highly variable in hominins. However, visually, it seems closer to *H. sapiens* than to *A. afarensis* (Detroit et al., 2019, p. 184). There was also a third metatarsal (CCH1), which demonstrated a feature of the proximal articular facet, which is very uncommon in hominins but has been seen in *A. sediba* (Detroit et al., 2019, p. 184).

One intermediate manual phalanx (CCH2) also has primitive features, such as well-developed flexor sheath attachments and an elongated and dorso-palmarly compressed shaft. These features are typically seen in *Australopithecus*, and somewhat in *H. habilis* (Detroit et al., 2019, p. 182). The other hand bone, a distal manual phalanx (CCH5), has proportions which fall within the range of variation for *H. sapiens* and *Australopithecus* but outside the range for *H. neanderthalensis* and *H. floresiensis* (Detroit et al., 2019, p. 183).

It is this unique mix of primitive and derived traits that Detroit et al. (2019) argue constitutes a new species. However, can the hominin remains from Callao Cave truly be classified as a new taxon? The short answer is yes. Morphometric analysis indicates that these remains are unlike any other hominin fossil yet found. As such, they can be called a new taxon under the phylogenetic species concept. In practice, however, this would probably be an uphill battle. With few specimens and no DNA, the designation of the Callao Cave remains to a new species will likely face substantial criticism. For example, the taxon of *H. floresiensis* comprises nine individuals and dozens of skeletal samples from both the cranium and post cranium (Morwood et al., 2005), yet still faces criticism in the academic literature. Given that the species designation *H. floresiensis* is still disputed by some, it is almost certain that *H. luzonensis* will be subjected to similar scrutiny.

Functionally, the only way to put the species argument for *H. luzonensis* to rest is to unearth more specimens. Although this represents a formidable challenge, finding more samples could assist with resolving other species debates. For instance, finding substantial Denisovan remains could help assist in resolving their species debate. Analyses of their morphology could inform us not only about the hominins themselves, but about taxonomies and species concepts. Fundamentally, paleoanthropology is data poor (White, 2014) and needs more samples to help elucidate the evolution of and relationships between extinct taxa.

It should also be remembered that designation of a population to a new 'species' is a rather arbitrary endeavour from the outset. Names are just that: names. We can call a population a new species, but functionally, calling it something different tells us absolutely nothing about it (Derricourt, 2009). Conversely, lumping many distinct populations into single species is also unproductive, as it does little to clarify the history of human evolution (Hublin, 2014). For the record, past studies seem to suggest that hominins were taxonomically diverse (Schwartz & Tattersall, 2015; Wood & Boyle, 2016). However, not all taxa are equally as convincing (Wood & Boyle, 2016), and trends indicate that many new 'species' of hominin eventually get subsumed into larger taxa over time (Derricourt, 2009). Ultimately, taxonomies are just hypotheses, and are to some degree subjective (Wood & Lonergan, 2008). Moreover, the only true use of a taxonomy is to communicate and share information (Bruner, 2013). Ultimately, a taxonomy is only useful if it can effectively communicate the ideas behind it.

Conclusion

In summary, while the Callao Cave remains can be designated as a new species (*H. Luzonensis*), this decision will likely face academic criticism and challenges over time. The small number of specimens—combined with a lack of DNA analysis—means that this species attribution remains tenuous. Additionally, several structural and human factors—including pressure to publish, restricted access to funding and materials, and nationalistic ties—were also identified as processes which influence species designations. Finally, the case studies presented demonstrate that species concepts and taxonomies are ultimately hypotheses when applied to fossil taxa, and more specimens will be required before any definitive statements can be made. However, there is no denying that the finds at Callao Cave are significant to our understanding of human evolution. Given that Luzon—similar to Flores—has never been connected to mainland Southeast Asia via a land bridge (Voris, 2000), this has implications for understanding the behavioural complexity of hominins in human evolution.

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