


2015

Dmanisi: A Taxonomic Revolution

Joshua L. Henderson

Western Oregon University, jhenderson11@mail.wou.edu

Follow this and additional works at: <https://digitalcommons.wou.edu/pure>

 Part of the [Archaeological Anthropology Commons](#), and the [Biological and Physical Anthropology Commons](#)

Recommended Citation

Henderson, Joshua L. (2015) "Dmanisi: A Taxonomic Revolution," *PURE Insights*: Vol. 4 , Article 4.

Available at: <https://digitalcommons.wou.edu/pure/vol4/iss1/4>

This Article is brought to you for free and open access by the Student Scholarship at Digital Commons@WOU. It has been accepted for inclusion in PURE Insights by an authorized editor of Digital Commons@WOU. For more information, please contact digitalcommons@wou.edu.

Dmanisi: A Taxonomic Revolution

Abstract

Over the past two decades, five different skulls have been found in the Dmanisi site located in the Republic of Georgia. These skulls are all very different in cranial features, but they are also some of the most complete and well preserved hominin skulls ever discovered. There is a major concern with these skulls, and with concern also comes controversy. We know that *Homo erectus* migrated from Africa into Eurasia. That is why some paleoanthropologists believe that, despite the cranial differences, the skulls found at the Dmanisi site all belong to *Homo erectus*. They claim that skeletal variations are common in a single species in multiple geographical locations. The opposing theory is that the remains seem to have both characteristics of *Homo habilis* and *Homo erectus*. They propose a new species called *Homo georgicus*, that fits between *Homo habilis* and *Homo erectus*. Using comparative analysis, I will demonstrate that the remains found at Dmanisi are in fact *Homo erectus*, and that the species as a whole contained many variable skeletal features throughout various populations, challenging current taxonomy and placing many species of *Homo* in the new *Homo erectus* spectrum.

Keywords

Dmanisi, Paleoanthropology, Archaeology, Biological Anthropology, *Homo erectus*, physical anthropology

Dmanisi: A Taxonomic Revolution

Joshua Henderson, Department of Anthropology, Western Oregon University

Over the past two decades, five different skulls have been found in the Dmanisi site located in the Republic of Georgia. These skulls are all very different in cranial features, but they are also some of the most complete and well preserved hominin skulls ever discovered. There is a major concern with these skulls, and with concern also comes controversy. We know that *Homo erectus* migrated from Africa into Eurasia. That is why some paleoanthropologists believe that, despite the cranial differences, the skulls found at the Dmanisi site all belong to *Homo erectus*. They claim that skeletal variations are common in a single species in multiple geographical locations. The opposing theory is that the remains seem to have both characteristics of *Homo habilis* and *Homo erectus*. They propose a new species called *Homo georgicus*, that fits between *Homo habilis* and *Homo erectus*. Using comparative analysis, I will demonstrate that the remains found at Dmanisi are in fact *Homo erectus*, and that the species as a whole contained many variable skeletal features throughout various populations, challenging current taxonomy and placing many species of *Homo* in the new *Homo erectus* spectrum.

Keywords: Dmanisi, Paleoanthropology, Archaeology, Biological Anthropology, *Homo erectus*, physical anthropology

Introduction

Imagine yourself in an abandoned medieval village in the Republic of Georgia. This village is located at the base of the Caucasus Mountains and is filled with the crumbled cobblestone ruins of a former medieval trade center. As with all historical sites, it often draws the attention of archaeologists to preserve its history. This was the case for this medieval village named Dmanisi. In 1936, archaeologists first excavated the remains of the city. Beyond finding medieval artifacts, the site seemed to be the average archaeological site. However in 1983 archaeologists discovered, beneath the ruins, sediment and faunal remains dating back to the Pleistocene. This new discovery invigorated archaeological efforts, which resulted in one of the most important finds in paleoanthropological history. Five skulls dating back to 1.8 million years ago were found in the sediment, each having different cranial characteristics. The brains associated with these skulls were quite small. The postcranial evidence found at the site suggests that the hominins to whom the skulls belonged were quite small as well. This seems to contradict what anthropologists previously believed, that the exodus out of Africa could only have occurred when hominin species were bigger brained with a larger physical frame. The remains found at Dmanisi are small brained with small physical frames, resembling *Homo habilis*, but also sharing many similarities to *Homo erectus*. The original research team concluded that the remains should be given their own species name; they patriotically named

it *Homo georgicus*. That designation was later retracted after further evidence showed similarities to samples of *Homo erectus* (Georgian National Museum 2013). Yet there are still some paleoanthropologists who believe these remains found at Dmanisi should belong to their own new species, and should still be named *Homo georgicus* (Schwartz et al. 2014), but the Georgian research team still holds true to their new classification as *Homo erectus*. If this is the case, we need to broaden our characteristics for *Homo erectus* and revise our current taxonomy to account for the variation among individuals (Mgeladze et al. 2011). By a comparison of the remains found at the Dmanisi site with African and Asian *Homo erectus* remains, I will demonstrate that the remains found at Dmanisi are in fact *Homo erectus*, and that the species as a whole contained many variable skeletal features throughout various populations, challenging current taxonomy and placing many species of *Homo* in the new *Homo erectus* spectrum.

Site and Setting

Located in the Caucasus Mountains in the Republic of Georgia, the town of Dmanisi sits quietly while archaeologists have been working diligently to uncover the remains of very early *Homo erectus*. In 1983, the discovery of a tooth from a Plio-Pleistocene rhinoceros prompted archaeologists to do more extensive digging. This led to the find of many simple Oldowan tools in 1984. The first real discovery of hominin occupation came in 1991 when the research team led by Dr. David

Lordkipanidze unearthed a complete mandible (D211) with its full set of dentition. In 1999, two craniums, D2280 and D2282, were found. A third cranium (D2700) was then discovered in 2001, the fourth and toothless cranium (D3444) was found in 2002, and the fifth and final cranium (D4500) found to date was found in 2005. Cranium number five (D4500) is the most complete cranium representing the genus *Homo* from Dmanisi. All of the skulls and postcranial evidence found at Dmanisi dates to around 1.8 million years ago (Georgian National Museum 2013). These remains suggest that *Homo erectus* left Africa much sooner than previously thought.

The Controversy

The discovery of the remains at Dmanisi has generated some very different viewpoints on the designation of species. After discovering the fifth cranium, Lordkipanidze and colleagues published a paper to which some opposing theorists responded (Lordkipanidze et al. 2013). Schwartz, Tattersal and Chi argue that the mandibles, dentition and cranial vaults of the skulls found at Dmanisi have too many differences between them, and compared to other *Homo erectus* specimens the differences could not be the result of within-species variation. These morphological differences provide sufficient evidence for the new species *Homo georgicus* and possibly other new species designations, pending further research (Schwartz et al. 2014).

The research team at the Dmanisi site led by Lordkipanidze recently published a paper documenting the anatomical features of skull five and the implications they have on the theory of variability within *Homo erectus*. In their article "A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early Homo," they demonstrate how the fifth skull exemplifies their theory of the variability of the *Homo erectus* paleodeme (Lordkipanidze et al. 2013). The endocranial volume of skull five is very small compared to the other remains found at Dmanisi. The brain was estimated to be around 546 cc with a wide and elongated cranium. These features matched closely with those of African *Homo habilis*. Contrasting to the brain case, the face is one of the largest and most prognathic of all *Homo* species. The postcranial evidence indicated that the individual stood about 146-166 cm tall and weighed around 47-50 kg. This range, along with the shape of the mandible and face, closely resembles early *Homo erectus* found in both Africa and Asia (Lordkipanidze et al. 2007).

Through comparison with remains from the Turkana boy KNM-WT15000 (1.6 mya) and the remains of adolescent *Homo habilis* KNM-ER1813 (1.9 mya), Lordkipanidze and colleagues (2007) conclude that the fifth cranium and the postcranial evidence belonging to the

same individual have morphological skeletal characteristics that fall between KNM-ER1813 and KNM-WT15000. This suggests that the remains do not belong to *Homo habilis*, and supports the idea that the remains found at Dmanisi are in fact early *Homo erectus* and that *Homo erectus* may have varied greatly as it was still evolving en route to Eurasia. The team also concludes that *Homo erectus* made it into Europe much sooner than previously thought (Lordkipanidze et al. 2013). They conclude by stating that further analysis will have to take place in order to further confirm the degree of variation among *Homo erectus* and to understand "mechanisms of evolution and geographic dispersal of early *Homo*" (Lordkipanidze et al. 2013: 330).

The Fossils

In order to truly understand the theories that surround Dmanisi, one must thoroughly examine all the evidence that has been found at the site. At this time, I would like to review cranial (See Figure 1) and postcranial features found at Dmanisi and possibly shed some light on the key ideas behind Lordkipanidze's position.

Skull 1 D2280

The first skull was discovered in 1999. Much of the facial morphology is missing on this skull. The skull has a small endocranial volume, like all the Dmanisi remains, at 775 cc. The individual is to be considered male. By looking at Figure 1, it is easy to see the very pronounced thickened supraorbital ridge and a strong angular torus, which are both characteristics of *Homo erectus* (Rightmire et al. 2006: 118-119).

Skull 2 D2282

This skull probably belonged to a young adult according to the unfused cranial sutures. The cranium has gracile muscle attachment areas, which also suggest female. The skull's cranial vault is very much intact, but unfortunately the face was deformed post-mortem, which prevents us from viewing the facial characteristics. Skull D2282 has an endocranial volume of 660 cc. The skull was found with its mandible (D211), which contains 16 intact teeth showing very slight wear (Rightmire et al. 2006:121-122).

Skull 3 D2700

The third skull is considered to be an adolescent. This is due to its partially erupted third molar. The skull has very pronounced supraorbital ridges and a zygomatic arch that coincides with D2282. Skull D2700 has an endocranial volume of 600 cc (Rightmire et al. 2006: 124-126).



Figure 1 Computer generated view of all five craniums found at Dmanisi. Picture: Marcia Ponce de León and Christoph Zollikofer, University of Zurich, Switzerland

Skull 4 D3444

This skull is very complete and offers many distinctly *Homo* features. We know this skull to be a male who was of older age. The mandible lacks teeth, suggesting old age and the possibility that this individual survived for several years like this before death. His diet was likely modified to compensate for lacking teeth and possibly indicates the fact that he may have received help from others for finding suitable food. The supraorbital ridge is very pronounced, much like the other skulls. The skull has a very broad face with a large zygomatic arch. The endocranial volume is around 650 cc (Rightmire et al. 2006:139).

Skull 5 D4500

The fifth skull is the most complete hominin skull found to date. This individual was a male who was of an adult age. It exhibits some of the most robust features of all the skulls, such as a very large supraorbital ridge. It has a very broad zygomatic arch and a very long face and maxilla. Despite the robust physical features of the skull, the fifth skull had the smallest endocranial volume out of the Dmanisi sample. The volume of the skull is 546 cc. The teeth associated with the skull are very worn, probably the result of a tough diet. There is evidence that the mandibular joint was deformed due to a persistent arthritis (Lordkipanidze et al. 2013:326-328).

Postcranial Evidence

In 2007, the postcranial remains of one adolescent and three adult individuals were unearthed in close proximity to the five skulls found in previous years.

Adolescent Remains of Skull D2700

The postcranial remains of the adolescent individual are thought to belong to cranium D2700 due to their close proximity in the stratigraphic layers. The remains of the adolescent consist of a left clavicle D2724, right and left first rib (D2716/D2855), an 11th rib (D217), five vertebrae

(D2673/D2674/D2721/D2713/D2672), right and left humeri (D2715/D2680), a left femur (D3160), two distal phalanges of the hand (D2679/D3480), two right metatarsals (D2671/D2669), and the first distal phalanx of the right foot.

The articular processes of the five vertebrae have a downward slope to them, thus resembling vertebrae found in the australopithecine which dates back to 2.7-4 million years (Berger et al. 2002: 193). The spinal process is short and narrow and the canal shape is very wide transversely. What makes the adolescent vertebrae so interesting is that the spinal process and the canal shape resemble the *Homo erectus* fossil found in Nariokotome KNMWT15000, and those found in modern *Homo sapiens*. The humeri of the adolescent are very straight and the position of the epicondyle is much higher than the lateral condyle. These characteristics resemble the morphology of the australopithecine.

Adult Postcranial Remains of Cranium D4500

The robust postcranial fossils (See Figure 2) are thought to belong to the larger of the three adult fossils, cranium D4500. The remains consist of a right scapula (D4166), right and left clavicles (D4162/D4161), the right second rib (D4063), left humerus (D4507), right femur (D4167), right patella (D3418), right tibia (D3901), left talus (D4110), two right metatarsals (D2021/D4165), a left metatarsal (D4508), and one distal phalanx of the foot (D3877).

The glenoid cavity of the right scapula (D4166) is more cranially oriented, resembling scapulae found in australopithecines. If you look at the shape of the conoid tubercle of the clavicles (D4162/D4161), you can see that they resemble the shape of modern *Homo sapiens*. The humerus of the adult (D4507) is also very straight and contains the same characteristics as the adolescent fossil. The femur (D4167), tibia (D3901), and patella (D3418) are the most complete lower extremities found among the genus *Homo*. The medullary canal of the femur is narrow and resembles that of samples found in African and Asian *Homo erectus*. The tibia (D3418) is the first complete tibia found among the hominins. The tibia is very robust and has a degree of torsion that resembles that of modern *Homo sapiens* (Lordkipanidze et al. 2007).

Other Adult Postcranial Remains

The other two adults are very small in contrast with those associated with cranium D4500. The postcranial remains are also very few. The first of the smaller adults is believed to belong to the older cranium (D344). The remains consist of a right medial cuneiform (D4111), and a right metatarsal (D3442). The only evidence that has been found of the third smaller adult is one right metatarsal

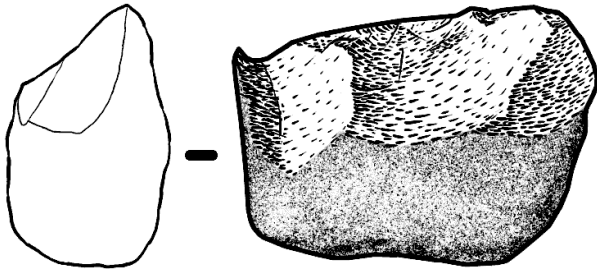


Figure 2. Drawing of Oldowan chopper found at Dmanisi
 Photo: Chopper of Dmanisi by Locutus Borg/ Public Domain

(D3479). Currently, there is not have enough evidence to demonstrate which individual this metatarsal belongs to (Lordkipanidze et al. 2007).

Tool Assemblage

In all stratigraphic layers, roughly 8,000 Oldowan tools have been found (Georgian National Museum 2013).



Figure 4. Anterior lateral view of Turkana Boy Cranium with attached mandible. Photo: Hominid_Skull-Homo_Ergaster-KNM-WT-15000-TurkanaBoy_004 by North Carolina School of Science and Mathematics/CC BY-NC-SA 2.0



Figure 5. Skull D2700. Photo: Cropped from *Homo georgicus* by Rama/Public Domain



Figure 3. Replica of Oldwan stone tool found at Dmanisi.
 Photo: Cropped from Dmanisi stone tool 2 by Gerbil/ CC BY-

The tools that are found at Dmanisi fall under two different categories. There are manuports, which are tools that are unmodified, and tools that have been strategically modified to achieve a specific purpose. The manuports include unmodified cobbles, broken cobbles, cobble fragments, and cobbles with single flake scars and percussion marks. It is believed that these cobbles were taken out of the Mashavera and Pinezauri rivers that lie only 100 meters below the occupation site. The tools that show signs of modification include cores, choppers (See Figure 2), and various flake tools (See Figure 3) (Ana Mgeladze et al. 2010: 571-572).

Comparing Dmanisi Hominins with African and Asian *Homo erectus*

In order to clearly demonstrate that the Dmanisi hominins are in fact *Homo erectus*, one must compare them to the cranial, postcranial, and tool assemblages of African and Asian *Homo erectus* fossils.

Turkana Boy KNM-WT15000

The Turkana Boy KNM-WT15000 is a complete set of remains of a 1.6 mya *Homo erectus* adolescent that was found in the west Turkana region of Kenya (Tattersal 2000:56-57). If one were to examine the skulls of KNM-WT15000 (See Figure 4) and the adolescent male skull D2700 (See Figure 5) one could see many similarities. Both skulls have very pronounced supraorbital ridges and zygomatic bones. The brain cases of the two skulls are very long relative to their height. The brain size of KNM-WT15000 is about 880 cc whereas the cranium of D2700 was around 600 cc. If you look at the tops of the two craniums, you can see that both D2700 (See Figure 5) and KNM-WT15000 have a sagittal keel, which is a distinctive trait of *Homo erectus*. Both skulls have a very flat nasal cavity and a flat maxilla. The mandibles of each are very similar in shape with small, rectangular incisors.

The postcranial evidence found for both the adolescent at Dmanisi and the Turkana boy also shares many of the same characteristics. The vertebrae of both fossils have large open canals that resemble modern human vertebrae. The tubercular shape of the clavicles

also resemble each other. The humeral torsion in the adolescent Dmanisi remains is very low compared to modern humans. The Turkana boy has a similar angle of humeral torsion. KNM-WT has a humeral torsion of 111.5 degrees, and the adolescent Dmanisi fossil has an angle of 104 degrees. Both have low humeral torsion because the species of *Homo erectus* had not developed throwing tools such as spears yet (Hawks 2007).

The Peking Man of Zhoukoudian

In Zhoukoudian, China, anthropologists discovered Peking man, which dates to 750,000 years old (Rincon 2009). This fossil is quite a bit younger than fossils found at Dmanisi but it still shares some of the same characteristics (Doray 2013). If you look at the Peking Man skull reconstruction (See Figure 6) and compare it to the nearly complete Dmanisi skull D4500 (See Figure 7), it can clearly be seen that the cranial and facial structures all



Figure 6. Anterior lateral view of Peking Man Skull. Photo: Hominid_Skull-Homo Erectus_Peking_Man_003 by NCSSM/CC BY-NC-SA 2.0

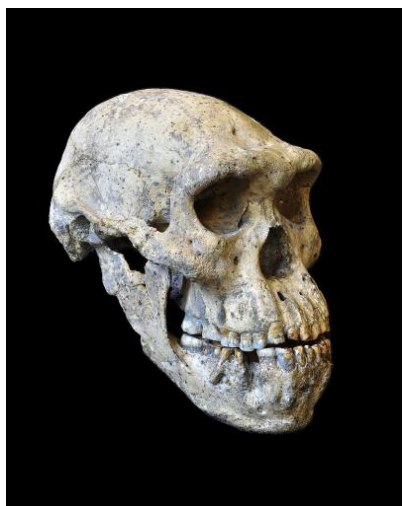


Figure 7. Anterior Lateral view of Skull D4500. Photo: Dmanisi Skull 5 by Guram Bumbiashvili, Georgian National Museum at EurekAlert.org

have a similar shape. Just like the adolescent Dmanisi skull, the Peking man and has a very prominent supraorbital ridge and zygomatic bone. The brain case for the Dmanisi skull D4500 is very small at 546 cc. The Peking Man had a brain case of 915 cc (Doray 2013). The discrepancy in brain size is believed to be the result of evolution over time, considering that Dmanisi was an early form of *Homo erectus* 1.8 million years ago (Lordkipanidze et al. 2007). Both crania have a sagittal keel and a large flat maxilla. The mandibles and dentition are quite large. This could be due to selection by the tough food sources both consumed. The main difference between the Peking man and D4500 is the size variation in brain volume. The postcranial remains associated with skull D4500 contain a complete tibia. The tibia has a similar torsion to modern humans, which could suggest efficient locomotion and the ability to travel long distances (Lordkipanidze et al. 2007). The leg bones of the Peking man closely resemble those of modern *Homo sapiens* (Wu and Lin 1983: 89).

Modern Human Variation

Darwin states that, through natural selection, differences are selected for and accumulated over generations and generations. That is how we evolved as a species. These differences are accelerated when a population changes habitat or food source (Darwin 1859:132). Over the course of just a few thousand years, a population can have many different characteristics than their ancestors and other populations. Different populations can accumulate different characteristics due to regional selective forces. That is why our modern human population is so diverse.

If you walk around any public place that people frequent and just take a moment to observe the people around you, you might observe that some people are taller than others. The people around you may all have a different cranial shape. Some people have very high cheek bones, and some may even have a large protruding chin. The skeletal features among modern humans are very diverse. In knowing how diverse our own species is, we should be able to accept that *Homo erectus* was most likely a diverse species as well, given its large distribution across Africa and Eurasia.

According to biological anthropologist Dr. Christopher Ruff of Johns Hopkins University, variation in modern human body shape and size is differentiated by geographical region and access to resources. Populations today that live in areas where they have access to food and health care are often much bigger in size. We should also include climate as well. A change in climate can drastically alter body shape and size over time (Ruff 2002: 225-227).

According to J.B. Anderson and William S. Politzer, 70-80% of bone structure is based on genetics. The other 20-30% is based on environmental factors. The environmental factors they attribute this to are the different mineral intakes that humans receive from their food and water resources based on their geographical location. One of the biggest reasons for genetic variation in different populations is gene flow (Anderson and Politzer 1994:129-130). Gene flow "is a collective term that includes all mechanisms resulting in the movement of genes from one population to another" (Slatkin 1985:393). This often occurs when one population migrates and interbreeds with another population. This explains how genetic variability has become so diverse over a geographical area.

If you consider that *Homo erectus* traveled a vast distance out of Africa into Eurasia, it is reasonable to think that the species experienced some amount of variation over time. Migrating across that vast distance, *Homo erectus* would have experienced a change in environmental factors, such as a change in climate and nutritional intake. They would have experienced an evolutionary force of gene flow resulting from interbreeding. Over the life span of *Homo erectus*, many variations would have occurred. That is how we can account for the lower brain size in the Dmanisi skulls, along with various other morphological differences.

Conclusion

The Dmanisi fossils are the key to supporting a change in our current taxonomy regarding variation within the *Homo erectus* paleodeme. In this paper I have reviewed the controversy, examined the fossil evidence, and briefly articulated the multidimensional forces of variation. In doing so, I have shown that compared to African and Asian *Homo erectus*, the Dmanisi fossils show many cranial and postcranial similarities, with some subtle differences. In addition I have demonstrated that the Dmanisi remains are, in fact, consistent with those of *Homo erectus* and as such, should be further studied to fully understand the concurrent diversity of early *Homo erectus*. Thus, the Dmanisi remains clearly indicate that we must review our current taxonomy to account for the natural variation that occurs over time and space. I support that Lordkipanidze and colleagues' new theory of variation within *Homo erectus* will revolutionize our current taxonomy. The Dmanisi fossils provide sufficient support to the idea that there are many other species in our taxonomy that should be included in the *Homo erectus* spectrum. With further research and future discoveries, we will be able to more accurately place our ancient ancestors where they belong, furthering our knowledge of what it means to be human.

Dr. Robin Smith served as faculty sponsor for the submission of this article to PURE Insights.

Sources

- Anderson, JB and William S Politzer
1994 Ethnic and Genetic Differences in Susceptibility to Osteoporotic Fractures. *Advances in Nutritional Research* 9:129-149.
- Berger, Lee, Lacruz, Rodrigo, and Darryl J. de Ruiter
2002 Brief Communication: Revised Age Estimates of Australopithecus-Bearing Deposits at Sterkfontein, South Africa. *American Journal of Physical Anthropology* 119: 192-197.
- Darwin, Charles
1859 *On the Origin of Species by Means of Natural Selection*. London, UK: John Murray
- Doray, Fran
2013 *Homo erectus*. Australian Museum. Accessed November 5th 2014 <http://australianmuseum.net.au/Homo-erectus>.
- Georgian National Museum
2013 Hominins. Accessed November 5th 2014 <http://dmanisi.ge/page?id=12&lang=en>.
- Hawks, John
2007 Hands Down, Palms Forward. John Hawks web blog. Accessed November 8th http://johnhawks.net/weblog/fossils/lower/dmanisi/palms_forward_2007.html
- Hawks, John
2013 The New Skull From Dmanisi. John Hawks web blog. Accessed November 8th 2014 <http://johnhawks.net/weblog/fossils/lower/dmanisi/d4500-lordkipanidze-2013.html>
- Humphreys, Stuart
2013 Turkana Boy *Homo ergaster* skull. Australian Museum. Accessed November 5th 2014 <http://australianmuseum.net.au/Homo-erectus>.
- Lordkipanidze, David
2007 Dmanisi Early Human Reconstructed. National Geographic. Accessed November 8th 2014 http://ngm.typepad.com/blog_central/2007/09/dmanisi-early-human-reconstructed.html
- Lordkipanidze, David, Marcia S. Ponce de León, Ann Margvelashvili, Yoel Rak, G. Philip Rightmire, Abesalom Vekua, and Christoph P. E. Zollikofer
2013 A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early *Homo*. *Science* 342(6156):326-331.
- Lordkipanidze, David, Tea Jashashvili, Abesalom Vekua, Marcia S. Ponce de Leon, Christoph P. E. Zollikofer, G. Philip Rightmire, Herman Pontzer, Reid Ferring, Oriol Oms, Martha Tappen, Maia Bukhsianidze, Jordi Agustí, Ralf Kahlke, Gocha Kiladze, Bienvenido Martínez-Navarro, Alexander Mouskhelishvili, Medea Nioradze, and Lorenzo Rook
2007 Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449(7160):305-310.

- Mgeladze, Ana, David Lordkipanidze, Marie-Hélène Moncelb, Jackie Despriebe, Rusudan Chagelishvilia, Medea Nioradzea, and Giorgi Nioradzea
2011 Hominin occupations at the Dmanisi site, Georgia, Southern Caucasus: Raw materials and technical behaviours of Europe's first hominins. *Journal of Human Evolution* 60(5):571-596.
- Rightmire, Phillip, David Lordkipanidze, and Abesalom Vekua
2006 Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *Journal of Human Evolution* 50(2):115-141.
- Rincon, Paul
2013 Peking Man Older Than Thought. BBC News. Accessed November 5th 2014
<http://news.bbc.co.uk/2/hi/science/nature/7937351.stm>
- Ruff, Christopher
2002 Variation in Human Body Size and Shape. *Annual Review of Anthropology* 31:211-232.
- Schwartz, J, I Tattersal, and Z Chi
2014 Comment on "A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early *Homo*." *Science* 344(6182):360.
- Slatkin, Montgomery
1985 Gene Flow in Natural Populations. *Annual Review of Ecology and Systematics*. 16:393-430.
- Tattersal, Ian
2000 Once We Were Not Alone. *Scientific American* 282(1):56-62
- Wu Rukang and Lin Shenglong
1983 Peking Man. *Scientific American* 248(6): 86-94.