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Dmanisi

A Study of Species Hypotheses and Hominid
Variability

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I. Introduction

The taxonomic relationships between fossils have always been the primary concerns of paleoanthropologists. This topic is of such importance—arguably a core fundamental in paleoanthropology—that philosophical viewpoints in treating fossils are “developed”, subsequently causing debates and divides within the profession. Those who tend to “accept” variations within samples are “lumpers”, and those who are a little less inclined to accept variations are “splitters”. As such, new discoveries that present relatively unusual morphology, especially features that are considered “transitional”, sparks taxonomic debates that, at times, seem to nitpick at every little detail.

The Dmanisi site of the Former Soviet Republic of Georgia has yielded fossils that both record the earliest expansion of humans out of Africa, and have come under this same philosophical scrutiny. The presence of high variability, notably between the male Skull 5 (D4500/D2600) and the female skulls 2 and 3 (D2282/D211 and D2700/D2735 respectively), have been interpreted in various ways that lean towards either the presence of multiple species within the assemblage, or a single dimorphic species. The single-species interpretation also added implications that could potentially alter the way in which paleoanthropologists approach within-deme variations, especially in a critical time period (Late Pleistocene).

Indeed, while Dmanisi’s affinities with *H. erectus* and *H. habilis* have been examined by multiple authors (Gabunia & Vekua, 1995; Gabunia et al. 2000; Schwartz, 2000; Rightmire et al. 2006; Lordkipanidze et al. 2013; Spoor 2013; Rightmire et al. 2017), the question of whether the Dmanisi specimens represent a single or multiple

species has been the topic of intense analyses and debate. Metric, morphological, and geological analyses have been used to examine this query, with some authors finding either greater or lesser variation in the mandibles, dentition, and crania.

This paper aims to first evaluate these analyses and then look at their implications in determining variability in the hominid fossil record.

II. The Debate So Far: Mandibular Concerns

The presence of the large D2600 mandible in the Dmanisi sample is often the center of single or multiple species interpretations. Gabunia et al. (2002) initially referred to this specimen as a new species, *H. georgicus*, citing that its differences to the other specimens recovered at Dmanisi suggest that the site might represent multiple taxa. The other mandibles are more frequently grouped together. Indeed, Rightmire et al.'s (2006) analysis of the metric and anatomical similarities of the crania and mandibles also note that, while skulls 1-4 and their associated mandibles can appropriately be grouped together, D2600 might be an exception. A later analysis by Rightmire et al. (2009), however, mentioned that interpretations of D2600 is hampered by evidence of periodontal disease on the individual, and the authors argue that it has not been demonstrated that its corpus size, frequently seen as different from the other mandibles (Skinner et al. 2006; Rightmire et al. 2008; Gabunia et al. 2002; Bermúdez de Castro et al. 2014), precludes placing it with the others in a single paleodeme.

Skinner et al. (2006), looking at size and shape variation between D2600 and D211, highlighted the differences between the two mandibles compared to extant and extinct hominoids. As far as size variation, their pair-wise ratio analysis of corpus height

and breadth, and symphysis height and breadth between the two mandibles suggested that, for height measurements, the Dmanisi ratio is found in less than 5% of pair-wise comparisons with extant hominoids. Interestingly, maximum overall mandibular size (calculated with geometric mean) was higher in extant hominoids compared to D2600 and D211, with the exception of *P. paniscus*. However, they find that it was significantly unlikely to select two individuals of extant hominoids, barring *P. pygmaeus*, that had a ratio as high as Dmanisi. Overall mandibular size results, Skinner et al. (2006) argues, were driven largely by the difference in corpus height at M₁ between D2600 and D211, while corpus and symphysis breadth differences between the two were consistent with extant hominoids'.

Comparison of the two mandibles with extinct hominoid taxa, on the other hand, shows that the degree of size dimorphism in the Georgian specimens is variably present among the comparative samples, similar to the extant hominoid analysis. While comparisons with *H. habilis sensu lato* and *H. erectus sensu lato* showed that Dmanisi fell within the maximum ratios of these comparative groups, comparisons with the "longer" taxonomic interpretation of the specimens (eg. *H. habilis s. l.* broken into *H. habilis* and *H. rudolfensis*), showed that differences between D2600 and D211 exceeded most of the pairs in the comparative taxa. Indeed, the overall size of the mandibles and corpus height and breadth were rarely found in all other comparisons. The degree of dimorphism in Dmanisi was also shown to be moderately to highly unlikely seen in the hominid fossil record, depending on the taxonomic interpretation used. Again, mandibular corpus height drove these results. It is worth noting, however, that the presence of Sangiran 6 (an *H. erectus* mandible from Java, Indonesia) in the

comparative samples also lead to contrasting outcomes. Without the Sangiran 6 mandible, *H. erectus sensu lato* comparisons with Dmanisi showed that the maximum ratios in *H. erectus* would have fallen below that of Dmanisi's.

On the other hand, shape variation analysis of D2600 and D211 using average Euclidean distances suggested that the pattern of variation in Dmanisi does not resemble that of most extinct and extant hominoids, with the interesting exception of *H. sapiens*. Skinner et al. (2006) found that the shape differences between male and female orangutans and gorillas were not as extreme as D2600 and D211, but Dmanisi fell within the top end of shape variation compared to modern humans. In addition, Skinner et al. (2006) finds that the large difference in height between the two mandibles was not matched by a proportional difference in breadth, which Skinner et al (2006) argues to be a difference in shape. These authors also find that shape analysis on the two mandibles suggests that shape differences may actually serve to reduce overall size dimorphism.

Skinner et al. (2006) proposed two interpretations to their analyses. Dmanisi could represent a single species, but its degree of sex dimorphism exceeds expectations, warranting the need to reconsider its inclusion in *Homo*. On the other hand, a multiple-species interpretation, Skinner et al (2006) argues, fits with the fossils' geologic context, as well as the similarities of D211 with the other Dmanisi hominids.

In their 2008 paper, Rightmire et al questions the results of Skinner et al (2006). These authors argue that the condition of the mandibles, may have skewed the results of Skinner et al's (2006) analysis, and propose alternative metric approaches, such as

using corpus heights at P₃ instead of M₁. Using the same resampling method used by Skinner et al. (2006) but with corpus heights at P₃, Rightmire et al (2008) find that the resulting ratios are consistent with Skinner et al.'s (2006) claims, but when gorillas are the standard, differences comparable to those measured at Dmanisi are not significantly rare (P = 0.06). Furthermore, since Skinner et al.(2006) used corpus proportions of D2600 that were affected by pathology, neither the overall mandibular size findings or Euclidean shape distance analysis done by Skinner et al (2006) were useful. Rightmire et al (2008) also suggest that the gap in ages for D211 and D2600 may be substantial, and it would be likely that growth-related changes would have decreased the corpus size difference between the two mandibles. Citing Van Arsdale's (2006) analysis, Rightmire et al. (2008) also argues that the single-species hypothesis may not hold when humans are used as the comparative standard, but the hypothesis cannot be rejected based on comparisons with highly dimorphic apes.

Van Arsdale and Lordkipanidze (2012)'s analysis further supports a single-species interpretation of Dmanisi mandibles D211, D2735, and D2600. Comparing the index of relative difference between Dmanisi pairs with that of extant hominoids, the authors find that while for some metrics Dmanisi's variation is greater than expected, (most notably when D2600 is considered) when individual characteristics are considered jointly in a nested resampling analysis, Dmanisi fits well in a single species. That is, the Dmanisi pairs often show magnitudes of variation not readily seen in extant hominoids, but the expected level of variability (how many traits they are varying in) is not greater than that of gorillas, chimpanzees, and modern humans. The geological and stratigraphic settings of the fossils also suggest that a multiple taxic interpretation is not

parsimonious, Van Arsdale and Lordkipanidze (2012) argues. In addition, the authors cite that Dmanisi has consistent traits that are either distinct to early *Homo* or unique to the Dmanisi specimens, and while the degree of variation is high, where Dmanisi is varying is similar to where other hominids vary.

Bermúdez de Castro et al.'s (2014) approach to the Dmanisi mandibles focused on morphological aspects related to growth and development, independent of size or sexual dimorphism. The authors argue that the differences between D2600 and the other mandibles are not only significant, but are established early in ontogeny. For instance, differences in corpus height were originally attributed to age (Rightmire et al 2008), but Bermúdez de Castro et al. (2014) argue that growth in the “smaller” Dmanisi mandibles in this area would be small, not enough to make the difference. Comparing with the Atapuerca-SH fossils, the authors also find that pattern of variation also suggests that Dmanisi follows primitive/derived conditions rather than sexual dimorphism, where D2600 shows a “mosaic” of primitive features shared with the D211 and D2735 and features unique to D2600, as well as homoplastic features related to Neandertals. These features, the authors argue, cannot be attributed to variability in a single paleodeme that includes the “smaller” mandibles, which both exhibit the same molar size sequence that differs from D2600. In addition, Bermúdez de Castro et al. (2014) also consider if variation in the mandibles *could* be a result of different diets (not ontogeny). Due to the differences in wear patterns of the D2600 mandible compared to the other specimens, Bermúdez de Castro et al (2014) suggest that D2600 is adapted to different niches, further supporting two different paleodemes at Dmanisi.

III. The Debate So Far: Dental Analyses

Comparative analysis of the dental remains done by Martinon-Torres et al. (2008) affirms the morphological and metric similarities between D211/D2282 (skull 2) and D2700/D2735 (skull 3), and considers the differences of D2600 with the rest of the sample. While the Dmanisi teeth were found to be generally primitive and the degree of size difference between the fossils can be found in Olduvai *H. habilis* material, Martinon-Torres et al (2008) find that the D2600 dentition is quite larger, with different size sequences, root systems, and derived contour in its molars compared to the other two mandibles. To this extent, Martinon-Torres et al (2008) suggests that there are 2 paleodemes in the Dmanisi sample.

Conversely, Macaluso (2010)'s metric assessment stands in contrast to Martinon-Torres et al's (2008) analysis. According to Macaluso (2010), maximum pair-wise size ratio comparisons for Dmanisi, *P. troglodytes*, *G. gorilla*, *H. sapiens*, and *A. boisei* (whose taxonomy is not contentious) suggests that Dmanisi does not have excessive size variation for most dental dimensions, including pairs with D2600, after size corrections. Maxillary dental size differences between D2282 and D2700 also show lower levels of variation versus the other comparative taxa. Macaluso et al (2010) do note that D2600's standing is still questionable, however. Morphological analysis is hard to interpret, as the crowns of D2600 are worn. Premolar root assessment of D2600 shows that it is different from the other mandibles, but differences in this area is also variable in other taxa, and might have been the result of sexual dimorphism.

IV. The Debate So Far: Cranial Variability

Along the same lines, numerous studies have also been done with the Dmanisi crania. For instance, besides questioning Dmanisi's affinities with *H. erectus*, Schwartz (2000) noted that the D2280 and D2282 crania indicate metric and morphological differences that could suggest intertaxic difference, rather than intrapopulational variation. Gabunia et al. (2000; same paper as Schwartz) responded to this by stressing that the geological context of the two skulls suggests that they were members of a single population. In addition, Gabunia et al. (2000) mentioned that the morphological variation of the specimens can instead be attributed to individual variation, sexual dimorphism, or differences in ages. This view was shared by Vekua et al. (2002) regarding the D2700/D2735 complete skull, citing its resemblances to the earlier crania and the D211 mandible.

Variations in Dmanisi's cranial capacity were examined to determine whether individual variation or sexual dimorphism could explain differences between the crania. Comparing the cranial capacity ratios of D2280, D2282, and D2700 to extant hominoids, Lee (2005) found that the largest difference between any two of the Dmanisi pairs were within distributions of male-male pairs of chimpanzees and gorillas, but were not likely to be found in male-male pairs of modern humans or female-female pairs of the three comparative taxa. Indeed, Lee (2005) cited that the largest variation between the Dmanisi specimens was more likely observed between male-female pairs of *G. gorilla*, *P. troglodytes*, and modern humans, which suggests that a single species hypothesis cannot be rejected with regards to Dmanisi's cranial capacities. Rightmire et al. (2006)'s assessment of metric and anatomical similarities of D2280/D211, D2282, D2700/D2735

and the edentulous Skull 4 suggests similar interpretations. These authors' analysis notes that all four Dmanisi specimens share a common bauplan, which warrants putting the four individuals into one species.

Experimentation and analysis by Rightmire et al. (2009) also compared the Dmanisi specimens to *H. sapiens* and extinct hominids, including *H. erectus*, *H. habilis*, and *H. rudolfensis*. The authors find that Dmanisi endocranial volume variability (using coefficients of variation) does not exceed that of all comparative taxa, but some dimensions of Dmanisi's braincases are more variable than expected, approaching the variation seen in a larger sample of African and Asian *H. erectus*. The authors noted that these measurements were not subject to masticatory strain and therefore have low CV's in extant hominoids such as *H. sapiens*. Substantial variation was also seen in some dimensions of the face, but Rightmire et al (2009) notes that these dimensions are usually variable in ancient *Homo* and *H. sapiens* (eg. Cheek height) due to the high magnitude of mechanical strain in the area. Dmanisi also exhibited less than the anticipated variation for areas such as biorbital breadth, nasal breadth, and some angles of subnasal protrusion.

With the results of their analysis, Rightmire et al (2009) considers some explanations as to why, for some measurements, Dmanisi does not conform to the variability in other taxa. They suggest that either the Dmanisi specimens represent more than one species given their comparatively greater neurocranial size and shape variation, that Dmanisi's pattern of variability is different from modern humans and apes, or that CV analyses of the specimens are unreliable due to its small sample size. Rightmire et al (2009) notes that, as far as these interpretations go, statistical problems

cannot be ruled out, but the understanding of variation in comparative fossil samples are also incomplete, and some groups might show inter individual variation unrecorded in extant hominoids. The authors also argue that the totality of evidence (cranial volume and face dimensions) in Dmanisi does not support a multiple-species interpretation of the specimens, and that previous bootstrap analyses of craniofacial and mandibular measurements indicate that size differences in Dmanisi are, while large compared to chimpanzees and modern humans, not significantly greater than other ape taxa. Rightmire et al. (2009) further comments that Dmanisi's geologic context, in paleontological terms, documents a single paleodeme.

The discovery of the D4500 cranium, associated with the D2600 mandible, brought more interpretations of the variation in Dmanisi. Apart from citing the geological conditions of the Dmanisi site (spatially and temporally constrained setting), Lordkipanidze et al. (2013) comments that geometric-morphometric analysis of Dmanisi (including D4500) and extant and extinct hominoids shows that craniomandibular shape variation among the Georgian specimens show overall similar patterns and ranges of variation with those seen in *Pan* demes and modern humans. Nonmetric analysis of the crania, on the other hand, show that Dmanisi varies in maxillofacial features interpreted as evidence for taxonomic diversity, but Lorkipanidze et al. (2013) argue that, generally, within-deme variations are more substantial and wider than previously recognized. Indeed, these authors comment that Dmanisi presents evidence that intrademic and intraspecific variation tend to be misinterpreted as species diversity.

Conversely, Spoor (2013) questions Lordkipanidze et al.'s (2013) findings. Spoor (2013) mentions that the latter authors should have analyzed the individual differences

of the Dmanisi specimens instead of their overall similarity, as species are defined by specific morphological features, not overall cranial shape. Spoor (2013) also comments that Lordkipanidze et al. (2013) did not discuss primitive and derived traits, and made no reference to non-cranial fossil evidence in Dmanisi, which could suggest behavioral differences similar to how biomechanical analyses of *H. habilis* and *H. erectus* post-crania suggested as such.

Schwartz et al. (2014) commented on Lordkipanidze et al.'s (2013) analysis as well. Schwartz et al. (2014) remarked that since the Dmanisi fossils were found in a spatially and temporally constrained setting which suggests a single population interpretation, Lordkipanidze et al. (2013) saw differences in the crania as intraspecies variation, focusing on general shape and morphology. Schwartz et al. (2013) also criticized Lordkipanidze et al.'s (2013) claims of a gorilla-level mandibular variation but human and *Pan* cranial variation in Dmanisi, as these cannot both be correct, Schwartz et al. argues. Furthermore, Schwartz et al. (2014) criticizes the notion that gorilla variability was used to affirm single-deme interpretations when variation in Dmanisi exceeded humans and chimps. These authors also commented that the geometric-morphometric analyses by Lordkipanidze et al. (2013) might have been faulty, and that species-distinguishing features are also present in the Dmanisi crania, such as vault size and supraorbital detail. Finally, Schwartz et al. (2014) commented that Dmanisi dental differences, such as those seen in Dmanisi's premolar roots and the presence/lack of metaconids, did not support single-species interpretations.

Zollikofer et al. (2014) responded to Schwartz et al.'s (2014) criticisms, remarking that the geologic setting of the Dmanisi fossils was necessary to test a single-species

hypothesis, but not to preclude its falsification. Thus, geometric-morphometric analysis done by Lordkipanidze et al. (2013) was then used to assess the hypothesis, which showed that a single-species hypothesis could not be rejected. Zollikofer et al (2014) also clarifies Schwartz et al.'s (2014) misconceptions about Dmanisi's dentition; premolar root variation aside, Schwartz et al. (2014) had reported different premolar root numbers for D2600 and D2735 than what is actually seen in the two mandibles, and metaconid presence was consistent for D211 and D2735.

More recently, Rightmire et al. (2017) also examined the variability of the Dmanisi crania, including the relatively recently-found D4500 cranium. In their analysis, Rightmire et al. (2017) compared the CV's of Dmanisi to *A. boisei*, *H. erectus sensu lato*, and *H. sapiens* to determine the crania's variability, and used principal components analysis to explore the relationship of Dmanisi to early *Homo* and *H. erectus*. The results of these analyses suggest that the Dmanisi crania and D4500 are probably conspecific with each other. Several Dmanisi variables, such as ECV's, most measurements of the braincase, and several facial measurements, do not show excessive variation relative to other hominids. But some, like parietal arc length and cranial height, show more variability. Interestingly, compared to modern humans, Dmanisi notably exceeds *H. sapiens* for bimaxillary chord, but falls within a modern human range of variability in all other variables, including midfacial measurements. It is worth noting, however, that Rightmire et al. (2017) comments that the D2600 mandible, which Rightmire et al. (2017) associates with the D4500 cranium, is shown to be different from the other mandibles, and only the KNM – ER 60000 fossil attributed to *H.*

rudolfensis presents overall proportions that approximate D2600. Resemblances between the two are less apparent in other features, however.

Rightmire et al.'s (2017) principal components analysis, on the other hand, showed that for principal components looking at 42.9% and 31.2% of total variance, the Dmanisi crania cluster together at about the same extent that the *H. erectus* Zhoukoudian crania cluster together. In conclusion, Rightmire et al. (2017) summarizes that both the CV'S and the PC analyses supports the taxonomic integrity of the Dmanisi assemblage, arguing that variation due to growth and dimorphism is to be expected among individuals.

V. Review and Conclusions

With all these analyses in mind, it is extremely hard to “pick a side” on Dmanisi’s multiple/single species argument. Bermúdez de Castro et al.’s (2014) paper, for instance, shows compelling evidence of speciation based on ontogeny. Indeed, if those variable traits within the Dmanisi specimens are shown earlier on in growth, then Dmanisi would, in a sense, show some signs of genetic divergence. After all, if vast ontogenetic differences between species are established earlier on in ontogeny, this may show species isolation.

However, if not for their comment that D2600’s traits *can potentially be* developments due to diets, which shows adaptations to different ecological niches, rather than just pure ontogeny, their assessment would have better standing (Bermúdez de Castro et al., 2014). If this was the case, the argument can actually be countered with the same evidence that suggests that the Skull 5 individual used its teeth heavily in

activities such as gripping, and that the individual would already have been an older adult in its 50's (Lordkipanidze et al., 2013). Skull 5 would have undergone the significant morphing of its "original" architecture that it did in that time, which would understandably not be seen in the relatively younger individuals (or the edentulous Skull 4). These "adaptations", then, would arguably be seen in the younger individuals had they lived longer. This also begs the question: would developmental adaptation to different ecological niches *as individuals grow* be grounds for their treatment as a separate species when they are older?

Indeed, in this light, there is a noticeable trend that single-species proponents, in addition to their heavy usage of inter-species comparison, use Dmanisi as a diagnostic tool for understanding the fossil record instead of the other way around. This is compelling; it implies that traditional methods of examining the fossil record, such as comparisons with extant hominoids (apes, for instance) are not sufficient to understand the wealth of variability in hominids, especially those from the Late Pleistocene.

So how about comparisons with other human species in relatively the same time period, such as *H. erectus*?

Comparisons with *H. erectus* may not support the view that the Dmanisi paleodeme is taxonomically *H. e. e. georgicus*, but morphological evidence does show similarities between Dmanisi and *H. erectus*, as well as *H. habilis*. For instance, Rightmire et al. (2017) cites that some traits that describe *H. erectus* as a species are seen in Dmanisi, such as prominent supraorbital tori and relatively great breadth across supramastoid crests, among other features. These affinities with *H. erectus* are

arguably emphasized in D4500. *H. habilis* comparisons with the Dmanisi specimens also show that, between the two groups, there are derived similarities that can be found, such as crown outlines (also seen in D4500).

Thus, comparisons of variations within and between these seemingly closely related demes are appropriate. That is, the variation within populations of *H. erectus* and *H. habilis* can justifiably be used to assess the variation within Dmanisi. Indeed, variability in traits such as endocranial volume is similar in Dmanisi and *H. erectus* populations (Rightmire et al., 2017). Principal components analyses, especially PC1, also show that Dmanisi clusters to about the same extent as the Zhoukoudian fossils (Rightmire et al., 2017). Even on PC4, accounting for 5.6% of variation, Dmanisi's clustering is comparable to six Ngandong individuals (Rightmire et al., 2017). To this extent, Dmanisi represents a single species.

But even when variation in Dmanisi seems to “fall off the charts of comparison” with *H. erectus* and *H. habilis*, the argument that Dmanisi still shows within-species variation—not taxon diversity—seems to hold. After all, paleoanthropologists still do not have a completely conclusive understanding of variations within early hominids, especially early *Homo (habilis)* as Rightmire & Lordkipanidze (2009) argue. Skull 5, whose existence is at the center of the multi/single specie argument, could also just potentially show an outlier within the (very small) group. Thus, Dmanisi could demonstrate that substantial morphological variation is present within early *Homo* paleodemes, until *compelling* evidence to the contrary is presented (Rightmire & Lordkipanidze, 2009).

Furthermore, as far as inter-species comparisons are concerned, the articles proposing the multiple-species hypothesis seem to overlook this idea. They instead focus on the differences within Dmanisi with the relatively unsubstantiated assumption that great differences within these early species “should not be seen”. It is true that Bermúdez de Castro et al.’s (2014) comparison with the Atapuerca-SH sample seems to touch on this, but the Atapuerca-SH sample is shown to be generally young at 400,000 years, whereas Dmanisi is at 1.77 my (Lordkipanidze et al., 2013).

Arguments against this view of Dmanisi, however, can still be raised. For instance, the taxonomic importance of molar sizes, which in D2600 shows a primitive/derived trait rather than sexual dimorphism, is one such matter that challenges single-species opinions. Furthermore, Bermúdez de Castro et al.’s (2014) article still proposes stratigraphic evidence against the single-species hypothesis that could potentially damage, but not entirely preclude, this position. If the paper Rightmire et al. (2017) published is proven to be false in its Dmanisi-*erectus-habilis* variability comparisons, this, too, would challenge Dmanisi as a “diagnostic for variation” series of fossils. Finally, if new, relatively contemporaneous fossil evidence is found that shows little variation within the sample, as opposed to Dmanisi, my position will be retracted.

In conclusion, on the grounds that the Dmanisi fossils show variation similar to closely related species, the idea that the fossils at Dmanisi represent a single, dimorphic species in between an evolving *habilis-erectus* lineage can be established (Rightmire et al., 2017). This claim is also supported the view that some arguments for the multiple-species hypothesis, are effectively counter-argued by supporting evidence for the single-species hypothesis, such as the discussion of mandibular height (Rightmire et al.,

2008 vs Bermúdez de Castro et al., 2014). Whether this means that the Dmanisi hominids should be contained within one distinct species is still up for examination.

Finally, a case can be made in which Dmanisi justifiably challenges the traditional approach to examining taxonomic variation, where morphological features are not fully substantiated by comparative evidence with intra and inter-species variations of both extinct and extant populations. The Dmanisi sample, with its admittedly huge differences between specimens, can be used to explain similar variations in other situations, such as the Sangiran 1 and Sangiran 6 (Indonesian *H. erectus*) mandibles.

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