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Estimating the Statistical Significance of Hominin Encephalization

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Abstract

Encephalization, the increase in endocranial volume through the Pleistocene, is examined from a creationist perspective. By correcting for body size using a linear regression model based on extant primates, the residual can be used to estimate the significance of the encephalization of fossil taxa. Using this method, significant encephalization is seen only in *Homo* and two australopiths, *A. africanus* and *A. sediba*. Since Wood (2010, 2016b) classifies all of *Homo* and *A. sediba* as human, these results indicate that all humans except *H. naledi* and only one nonhuman (*A. africanus*) are significantly encephalized. Based on these results, creationist neuroscientists ought to consider the possible causes of the encephalization trend in humans.

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Introduction

Thanks to a 2006 blog post by Nicholas Matzke (http://www.pandasthumb.org/archives/2006/09/fun_with_homini.html), a simple diagram of hominin endocranial volume (ECV) as a function of radiometric date (Figure 1) has become a recurring feature of anticreationist literature. The diagram gives a striking visual impression of expanding hominin brain size over time, although researchers have long understood that the diagram is oversimplified (e.g., Tobias 1971). To begin, the trend plays on the misconception that evolution is a linear progression from simple to complex by ignoring the potential influence of the putative hominin phylogeny. Indeed, Bruner et al. (2003) found that the ontogenetic pattern of brain expansion in Neandertals differed from that of modern humans, thus indicating that the trend in ECV is not purely anagenetic but should be considered phylogenetically. The diagram also ignores the fact that ECV is known to scale with body mass (e.g., Martin 1981), and thus should be corrected or normalized before comparisons between taxa can be made. Nevertheless, the diagram does strikingly illustrate a lack of discontinuity between what we creationists would recognize as human and nonhuman. As such, it still has value and warrants a response.

Previous creationist treatments of hominin ECV have disputed the relationship between intelligence and brain size (Jue 1990) or focused on the accuracy of ECV estimates for fossil hominins (Young 2006). Rana and Ross (2005) attempted to produce their own diagram of normalized cranial capacity averaged over individual hominin taxa. They concluded that there was a noticeable gap separating humans (in their view *Homo sapiens sapiens*) from non-humans. They later admitted that they omitted important taxa from the diagram (namely Neandertals), but they did not produce a new diagram despite continuing to affirm a difference between the ECV of *Homo sapiens sapiens* and all other hominins (Rana and Ross 2015; see also Wood 2016a).

An important question remains: Why do we creationists expect a discontinuity between humans and nonhumans in this one variable, ECV (normalized or not)? It is not clear that creationists should expect *a priori* that every feature of true humans would significantly differ from non-humans. Defending the existence of this discontinuity distracts us from pertinent questions: What is the source of the striking trend of increasing hominin ECV over radiometric time? Is the trend merely an allometry of increasing body size? How significant is the increase in ECV?

Here, the latest primate and hominin ECV and body mass data sets are used to re-evaluate the trend of increasing ECV. Typically, ECV is corrected by a procedure introduced by Jerison (1974), in which the raw ECV is normalized by an expected ECV calculated from body mass. The resulting metric is called an encephalization quotient. Here, a similar procedure will be used, and the results

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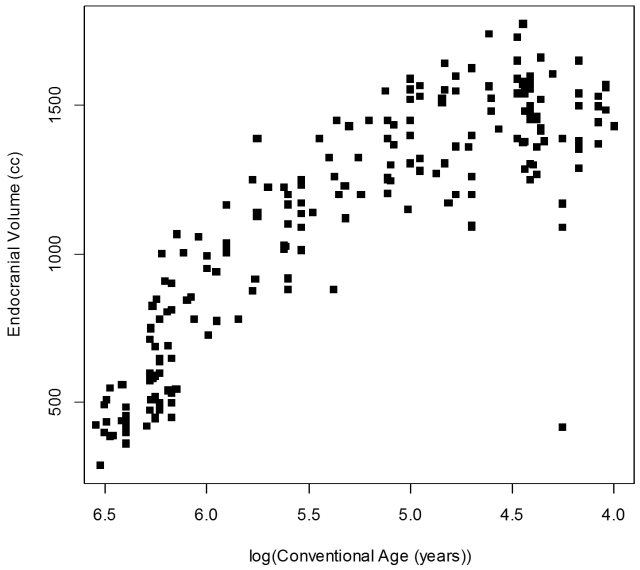

Figure 1. Radiometric age (in Ma) and endocranial volume (in cubic centimeters) for 173 fossil hominin and primate specimens in the present study.

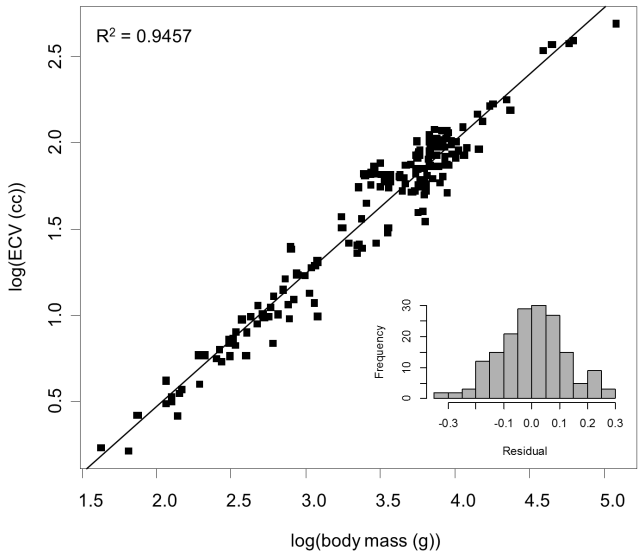

Figure 2. Body mass (in grams) and endocranial volumes (in cubic centimeters) for 227 extant primate species, averaged by species. The linear regression line is also shown with a histogram of the normally distributed residuals (inset).

will be evaluated in light of radiometric dates of specimens, Dembo et al.'s hominin phylogeny (2015), and Wood's (2010, 2016b) hominin baraminology results.

Methods

Endocranial and body mass measurements and estimates were derived from two primary sources. For extant primates, the comprehensive dataset of Isler et al. (2008) was used, and for fossil hominins, Schoenemann's (2013) dataset was used. The fossil dataset was supplemented with estimates for *Homo floresiensis* (Falk et al. 2005), *Australopithecus sediba* (Berger et al. 2010; Grabowski et al. 2015), and additional hominin specimens from De Miguel and Henneberg (2001). A body mass estimate for A.L. 288.1 was also obtained from Jungers (1988), and body mass and cranial capacity estimates for *Homo naledi* were obtained from Berger et al. (2015). All statistical calculations were made using R v. 3.2.0.

Results

To create a linear model to predict expected ECV for hominins, body mass and ECV of extant primates, averaged by species, were obtained from Isler et al. (2008). A log-log plot reveals a strong linear trend, as expected (Figure 2), with an R^2 of 0.9457. The predicted ECV ($ECV_{predicted}$) can be obtained by standard linear regression (the lm function in R) and is given by the formula

$$(1) \quad \log(ECV_{predicted}) = 0.77438 \times \log(\text{body mass}) - 1.07775$$

The residuals are normally distributed (Figure 2), from which a statistical significance can be calculated. Here, the residual will be referred to as an "encephalization residual" (ER), after Jerison's encephalization quotient. ER is calculated as

$$(2) \quad ER = \log(ECV_{obs}) - \log(ECV_{predicted})$$

where ECV_{obs} is the calculated or measured endocranial volume and $ECV_{predicted}$ is the endocranial volume predicted from the body mass and equation (1).

It can be shown that ER is equal to the common logarithm of encephalization quotient (EQ), given by

$$(3) \quad EQ = ECV_{obs}/ECV_{predicted}$$

According to equation (2), the ER can be expressed as

$$(4) \quad ER = \log(ECV_{obs}) - \log(ECV_{predicted})$$

$$= \log(ECV_{obs}/ECV_{predicted})$$

By substitution with equation (3):

$$(5) \quad ER = \log(EQ)$$

The ER distribution shown in figure 2 has a mean of -8.3×10^{-18} and a standard deviation of 0.1194. Given that 95% of a normal distribution lies within ±1.96 standard deviations from the mean, we can assign statistical significance of $p < 0.025$ for ER values greater than 0.234 and less than -0.234.

Body mass and ECV for 173 fossil hominins and primates are shown in Figure 3. The solid line represents the linear model of expected ECV calculated from extant primates, given by equation (1). The dashed lines mark the ER with $p < 0.05$, calculated by adding ±1.96 standard deviations of the ER (0.1194) to the

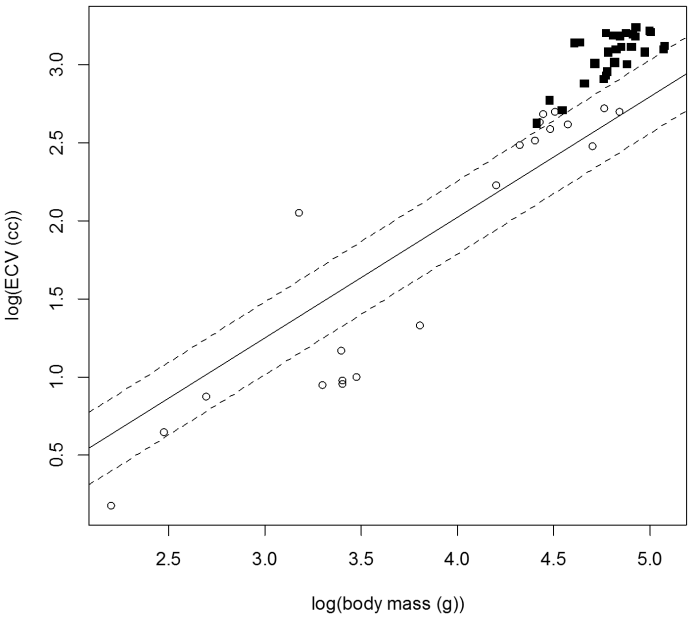

Figure 3. Body mass (in grams) and endocranial volumes (in cubic centimeters) for 50 hominins and fossil primates. The regression line calculated from 227 extant primate species is shown as a solid line. The dashed lines represent the boundaries of statistically significant encephalization residuals, according to the linear model of extant primates. Taxa classified as human by Wood (2010, 2016b) are shown as filled squares, and nonhuman taxa are shown as open circles.

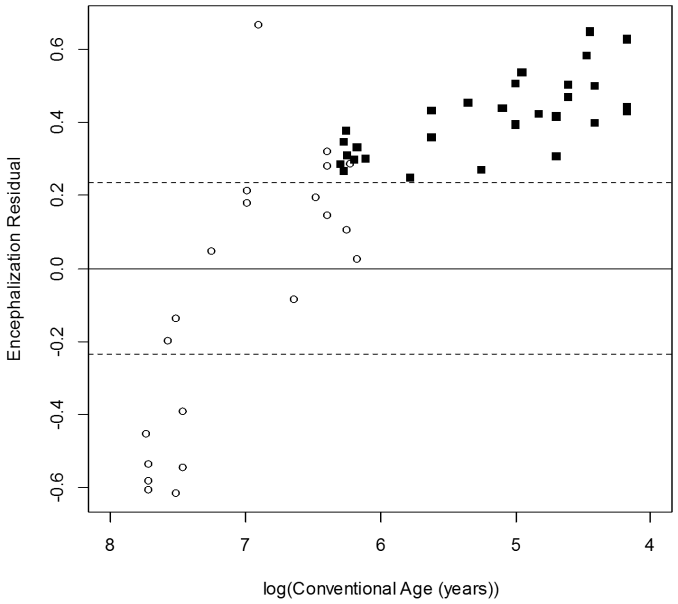

Figure 4. Radiometric date and encephalization residual for 50 hominins and fossil primates. The solid line represents the average residual, and the dashed lines represent the boundaries of statistically significant encephalization residuals, according to the linear model of extant primates. Taxa classified as human by Wood (2010, 2016b) are shown as filled squares, and nonhuman taxa are shown as open circles.

intercept value of the model line. All taxa designated as human by Wood (2010, 2016b) are significantly over-encephalized, while smaller-bodied taxa are significantly under-encephalized. Only four non-human specimens are significantly over-encephalized: BAC-208 (*Oreopithecus*, ER = 0.667, p = 1.13 × 10-8), KNM-ER 732 (*Paranthropus boisei*, ER = 0.288, p = 0.00788), Sts 5 (*Australopithecus africanus*, ER = 0.322, p = 0.00354), and Sts 71 (*Australopithecus africanus*, ER = 0.282, p = 0.00905). The seven significantly under-encephalized specimens are AMNH 4194 (*Tetonius*, ER = -0.453, $p = 7.40 \times 10^{-5}$), YPM 12152 (*Smilodectes*, ER = -0.581, $p = 5.63 \times 10^{-7}$), BM 20192 (*Adapis parisiensis*, ER = -0.605, $p = 2.04 \times 10^{-7}$), Cambridge M.538 (*Adapis parisiensis*, ER = -0.534, $p = 3.85 \times 10^{-6}$), CGM 40237 (*Aegyptopithecus*, ER = -0.544, $p = 2.65 \times 10^{-6}$), CGM 85785 (*Aegyptopithecus*, ER = -0.391, $p = 5.31 \times 10^{-4}$), and DPC 18651 (*Parapithecus*, ER = -0.614, $p = 1.33 \times 10^{-7}$).

Plotted against radiometric date, encephalization gradually increases among humans as designated by Wood (2010, 2016b) ($R^2 = 0.4865$, F-statistic 27.52, $p = 1.57 \times 10^{-5}$) (Figure 4). Among nonhuman taxa, there is also a significant trend ($R^2 = 0.5605$, F-statistic 25.23, $p = 8.84 \times 10^{-5}$), but the trend is dominated by "older" taxa, which are significantly under-encephalized. Significantly over-encephalized, non-human taxa span a conventional age range of 9.85 Ma (*Dryopithecus*) to 1.7 Ma (*Paranthropus boisei*).

The ECV and body masses of fourteen fossil hominin taxa can be averaged by taxon, from which a taxon ER can be calculated (Table 1). Of the fourteen, nine are human according to Wood (2010, 2016b). Nine of the taxa, including eight of the human taxa, have statistically significant ER. Only the nonhuman *Australopithecus africanus* has a statistically significant ER (0.288, p = 0.0079). The newly discovered *Homo naledi* has a nonsignificant ER (0.201, p = 0.046), reflecting the unusual combination of a moderate body mass and surprisingly small cranium.

Considered from a phylogenetic perspective, taxon average ECV changes relatively smoothly from *Ardipithecus* to *Homo sapiens*, based on the phylogeny of Dembo et al. (2015) (Figure 5); however, ER changes much more irregularly. On the clade that begins with the most recent common ancestor of *Homo sapiens* and *A. africanus* (Figure 5, clade 1), all taxa have significant ER, suggesting that significant encephalization had only one evolutionary origin. Subsequent clades do not see a drastic increase in ER until the clade of *H. sapiens*, *H. neanderthalensis*, and *H. heidelbergensis* (Figure 5, clade 2). For example, both *H. habilis* and *H. rudolfensis* have slightly larger ER values than *H. erectus* (0.37, 0.37, 0.34 respectively). Thus, the phylogenetic "trend" of increasing ER seems to be limited to an initial ER increase at the *A. africanus* + *Homo* clade and a subsequent increase at the *sapiens*/*neanderthalensis*/*heidelbergensis* clade.

Table 1. ECV, Body Mass, and ER averaged by taxon.

Taxon	Mean ECV (cc)	ECV Measurements	Mean Body Mass (g)	Body Mass Measurements	ER	P value
Aridipithecus ramidus	300	1	50,000	1	-0.084	0.759
Australopithecus afarensis	419.5	6	30,400	1	0.229	0.0275
Paranthropus aethipicus	410	1	37,666	1	0.147	0.109
Paranthropus boisei	503.3	8	53,141.7	3	0.120	0.157
Australopithecus africanus	441.7	13	27,244	2	0.288	0.00788
Australopithecus sediba	420	1	25,800	1	0.285	0.00854
Homo habilis	609.3	6	32,584.5	2	0.368	0.00103
Homo rudolfensis	788.5	2	45,597	1	0.367	0.00106
Homo ergaster	800.7	3	58,329	2	0.291	0.00746
Homo erectus	960.1	40	63,361.5	4	0.342	0.00211
Homo naledi	513	2	42,800	16	0.201	0.0458
Homo neanderthalensis	1391.4	34	84,508.4	8	0.406	0.000337
Homo heidelbergensis	1231.6	16	98,879.7	3	0.300	0.00597
Homo sapiens	1463.8	68	64,686.1	8	0.518	7.2×10^{-6}

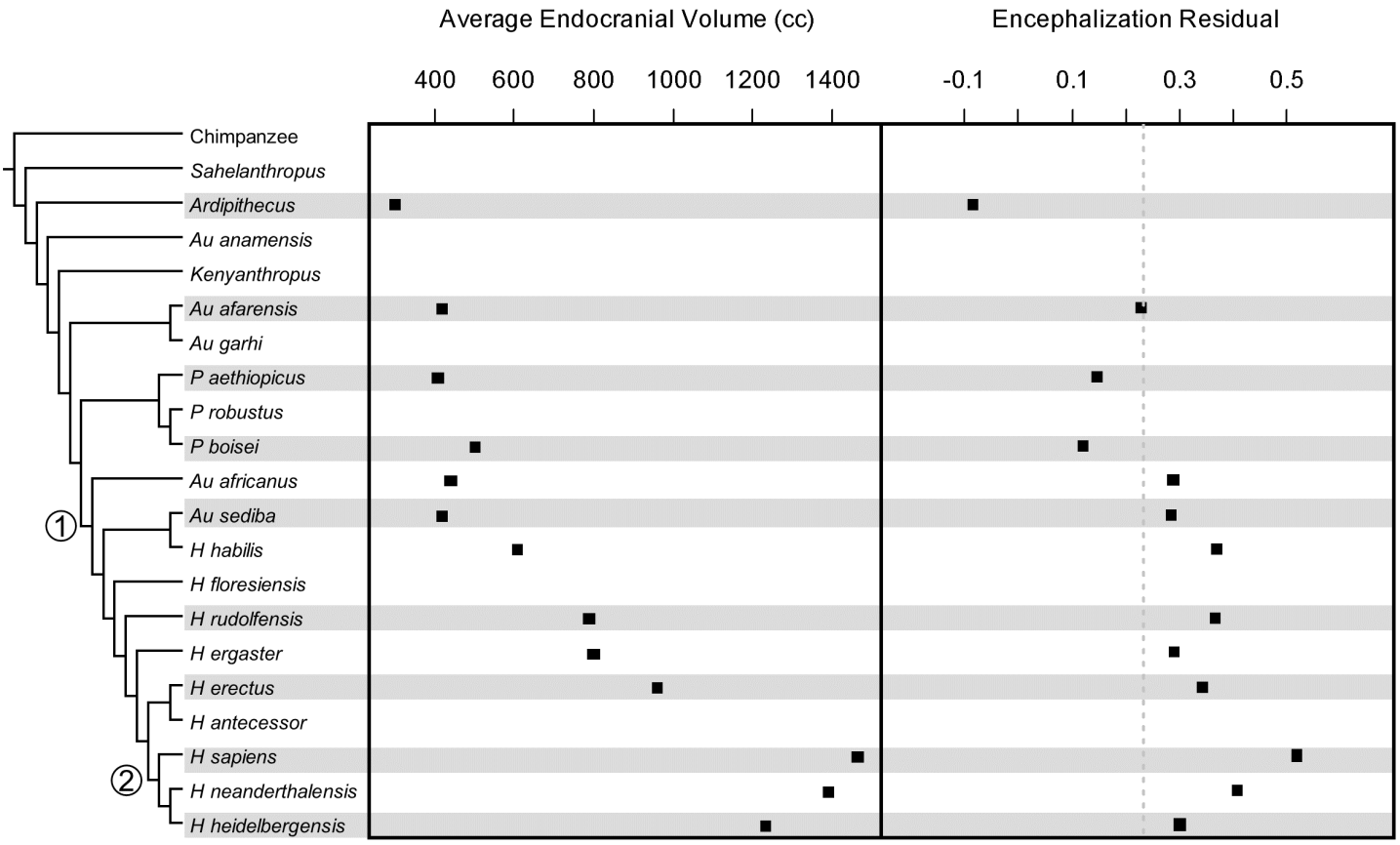

Figure 5. Taxon average endocranial volume and encephalization residual according to the phylogeny of Dembo et al. (2015). The dashed line represents the boundaries of statistically significant encephalization residuals, according to the linear model of extant primates.

Discussion

Estimating trends of ECV or ER is hindered by paucity and uncertainty of data. Identifying body mass and ECV for the same individual is difficult with the fragmentary fossil record of extinct hominins, and even when we have good fossil material, body mass estimates can vary significantly. The present study includes only six specimens of *A. afarensis* and nine specimens of *A. africanus*. Of those, only one and two respectively include body mass estimates. Even when body mass estimates are available, they may not be accurate. Grabowski et al.'s (2015) multivariate method of estimating body mass still had substantial confidence intervals of at least 12 kg for most fossil hominin taxa. Since none of their taxon body mass estimates exceeded 51.4 kg, the uncertainty comprises about 25% of their estimate. There is also uncertainty associated with the conventional dating of the fossils and, if considering taxon averages, with the classification. Finally, the statistical significance of the encephalization residual will depend on the model being used, which would be different if different taxa (such as great apes only) were chosen. Taking all of these drawbacks into consideration, the conclusions of the present study should be considered tentative at best.

Even with the drawbacks, there is definitely a trend in encephalization over radiometric time and according to Dembo et al.'s (2015) phylogeny. Phylogenetically, the trend in uncorrected ECV does not appear to begin until the clade of hominins that includes *A. africanus*, *A. sediba*, and all of *Homo* (Figure 5, clade 1), but the ER suggests only two changes in encephalization rather than a gradual increase.

In Wood's (2010, 2016b) baraminology studies, the category "human" (descendant of Adam and Eve) includes all *Homo* species and *Australopithecus sediba*. In the present study, every human taxon except *Homo naledi* has statistically significant ER. In most cases, then, the human taxa appear to be different from the nonhuman taxa, which mostly lack significant ER. As noted in the results, there are exceptions, namely *Australopithecus africanus*, which has a slightly higher ER than *Australopithecus sediba* and *Homo naledi*. This significant ER is unsurprising, since *A. africanus* was exceptionally similar to humans in the first hominin baraminology study (Wood 2010).

Other than *A. africanus*, no non-human taxon had a statistically significant, positive ER. Instead, extinct taxa from Eocene and Oligocene sediments have statistically significant, negative ER, indicating that the ECV is substantially smaller than would be predicted based on the body mass of extant primates. These nonhuman taxa together give the impression of an increasing encephalization trend, from the under-encephalized Oligocene and Eocene taxa to the slightly encephalized *A. africanus* in the Pliocene and Pleistocene.

Should creationists be concerned about these trends? For young-age creationists, the fact that almost every human representative in the present study is significantly encephalized would seem to fit well with the creationist notion of humans with unique properties that set them apart from nonhuman creatures. The existence of one non-human taxa with significant, positive ER is more unsettling; however, if we adopt a more restrictive circumscriptions of the human holobaramin than Wood (2010, 2016b), we would have several additional non-human taxa with significant ER. For example, following the traditional Lubenow human classification, which recognizes only *H. erectus*, *H. ergaster*, Neandertals, *H. sapiens*, and possibly *H. rudolfensis*, leaves six non-human hominins with significant encephalization. Following Rana and Ross's (2016) classification of only *Homo sapiens sapiens* as human, there are ten non-human hominins with significant encephalization. Thus, Wood's (2010, 2016b) classification (derived from more characters than just ECV) seems to have the least trouble accommodating the encephalization trend in hominins.

Even if we accept Wood's classification, however, there remains the question of why the encephalization trend occurs in humans at all. There has been much written about this subject in the evolutionary literature (e.g., Tobias 1971, Begun 2004, de Sousa and Cunha 2012, Shultz et al. 2012, Zollikofer and Ponce de León 2013, among many others), and it will need to be carefully re-evaluated from a creationist perspective, preferably by one trained in neuroscience. At present, though, we can see that encephalization is no more an insurmountable problem for creationists than for evolutionists.

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