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Cognitive inferences in fossil apes (Primates, Hominoidea): does encephalization reflect intelligence?

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Summary – *Paleobiological inferences on general cognitive abilities (intelligence) in fossil hominoids strongly rely on relative brain size or encephalization, computed by means of allometric residuals, quotients or constants. This has been criticized on the basis that it presumably fails to reflect the higher intelligence of great apes, and absolute brain size has been favored instead. Many problems of encephalization metrics stem from the decrease of allometric slopes towards lower taxonomic level, thus making it difficult to determine at what level encephalization metrics have biological meaning. Here, the hypothesis that encephalization can be used as a good neuroanatomical proxy for intelligence is tested at two different taxonomic levels. A significant correlation is found between intelligence and encephalization only at a lower taxonomic level, i.e. on the basis of a low allometric slope, irrespective of whether species data or independent contrasts are employed. This indicates that higher-level slopes, resulting from encephalization grade shifts between subgroups (including hylobatids vs. great apes), do not reflect functional equivalence, whereas lower-level metrics can be employed as a paleobiological proxy for intelligence. Thus, in accordance to intelligence rankings, lower-level metrics indicate that great apes are more encephalized than both monkeys and hylobatids. Regarding fossil taxa, encephalization increased during hominin evolution (particularly in* Homo*), but during the Miocene a significant shift towards higher encephalization (and inferred enhanced cognitive abilities) must have been also involved in the emergence of the great-ape-and-human clade (Hominidae). This is confirmed by the modern great-ape-like degree of encephalization displayed by the fossil great ape* Hispanopithecus*, which contrasts with the rather hylobatid-like degree of the stem hominoid* Proconsul*. The similarly low encephalization of* Oreopithecus *might result from secondary reduction under insularity conditions, but the australopith-like degree of encephalization of* Homo floresiensis *seems incompatible with the cognitive abilities inferred from the stone tools attributed to this taxon.*

Keywords – *Paleobiology, Cognition, Relative brain size, Hominidae, Great apes, Human evolution.*

> *"No one, I presume, doubts that the large size of the brain in man, relatively to his body, in comparison with that of the gorilla or orang, is closely connected with his higher mental powers"*
> *(Darwin, 1871, p. 145)*

Introduction

Encephalization and intelligence

The New Oxford American Dictionary defines 'intelligence' as "*the ability to acquire and apply knowledge*", and 'cognition' as *"the mental action* *or process of acquiring knowledge and understanding through thought, experience, and the senses*" (McKean, 2005). From a scientific viewpoint, the concept of intelligence (see review in Sternberg, 2000) is very slippery, especially when not applied exclusively to humans, but extended to other animal taxa. Given the sensory differences between different groups - the more distantly related, the worse -, intelligence is very difficult to quantify and compare across a wide spectrum of taxa (Radinsky, 1982; Deacon, 1992). This does not mean that intelligence is an unsubstantial psychological concept that cannot be measured at all, but rather that a specific theoretical framework is required in order to make possible meaningful measurements (Eysenck, 1981). Roth & Dicke (2005, p. 250) recently asserted "*There is no universally accepted definition of animal intelligence, or procedure to measure it*". However, within the framework of this paper, an operational definition of animal intelligence, applicable to different species of a particular group such as primates, is required. Stenhouse (1974, p. 61) defined intelligence as the built-in flexibility that allows individual organisms to adjust their behavior to relatively rapidly changing environments, while Jerison (1973) defined 'biological intelligence' as the information-processing capacity that enables to react to external and internal stimuli with proper responses. More recently, the latter author defined intelligence as "*the behavioral consequence of the total neural-information processing capacity in representative adults of a species, adjusted for the capacity to control routine bodily functions*" (Jerison, 2000, p. 216). Unfortunately, even if these definitions were agreed upon, no operational procedure for measuring intelligence is implicit on them, and critical authors might alternatively argue that different types of cognitive abilities (social, sensory...) are mixed with one another within the single label of 'biological intelligence'. This problem, however, has been partially overcome during the last decade, thanks to recent analyses that quantify intelligence (or domain-general cognitive abilities) across a broad sample of primate species (Johnson *et al.,* 2002; Deaner *et al.,* 2006, 2007; see later for further details).

The problem of intelligence becomes even worse when dealing with fossil remains, since the former cannot be directly measured but must be inferred on the basis of some neuroanatomical proxy. Humans are usually credited by our exceptional degree of intelligence, and information provided by the fossil record should be critical for deciphering the tempo of cognitive evolution. Yet behavior cannot be directly observed from fossil remains of past organisms, but must be inferred from morphology. Ever since Darwin (1871), the high degree of human intelligence has been related to its correspondingly large brain, which is about three times larger than that inferred for the last common ancestor of apes and hominins (Sherwood *et al.,* 2008). Due to the relatively large brains of humans, repeated efforts have been made to estimate and/or interpret the role of brain size during human evolution (Jerison, 1973; Pilbeam & Gould, 1974; McHenry, 1975, 1982, 1988; Hofman, 1983; Martin, 1994, 2000; Foley & Lee, 1991; Aiello & Wheeler, 1995; Kappelman, 1996; Wood & Collard, 1999; McHenry & Coffing, 2000; Falk *et al.,* 2000; Elton *et al.,* 2001; Schoenemann & Allen, 2006). However, comparatively little attention has been devoted to encephalization in extant and fossil apes (Martin, 2000; Begun, 2004; Begun & Kordos, 2004; Russon & Begun, 2004), even though these studies are critical for understanding the starting point of the great encephalization increase that took place during human evolution. Most psychobiological and ethological studies have concluded that great apes are more intelligent than other non-human primates, and it has been argued that most of the characters related to great ape intelligence were already present in the last common ancestor of great apes and humans (Begun, 2004). Nonetheless, inferring cognitive abilities in fossil apes requires being certain as to what neuroanatomical predictor best reflects intelligence among extant taxa.

As stated above, there seems to be a causal relationship between human intelligence and our expanded brain. The higher degree of intelligence associated to larger brains may be related to the larger number of total neurons available for data processing, as well as to the proliferation of functionally discrete modules associated to specialized functions following neocortical expansion (Sherwood *et al.,* 2008). In a broad mammalian context, however, absolute brain size cannot be employed for inferring intelligence, unless we accept that elephants and blue whales display greater cognitive abilities than modern humans. Brain size is highly correlated with body size, and it has been recognized since Dubois (1897) and Lapicque (1898) that their relationship is non-linear (allometric). Accordingly, simple ratios fail to adequately remove size-scaling effects from brain size (e.g. Gould, 1975; Shea, 2006); i.e., they fail to provide a reliable measure of relative brain size because they do not take into account the non-linear relationship between both variables. Although larger species tend to display larger brains on absolute terms, the brain size/body size ratio progressively decreases as body size increases within a given taxonomic sample, i.e. their relationship is negatively allometric. Accordingly, brain size–body size allometric regressions must be employed in order to adequately cope with body size scaling effects when computing encephalization, either as allometric residuals or quotients (see Materials and methods for further details). This approach, generalized by Jerison (1973) but dating back to Dubois (1897), assumes that brain size is determined simultaneously by body size and by intelligence. This so-called 'switchboard model' (Byrne, 1996; Byrne & Corp, 2004), or 'traffic maintenance hypothesis' (Deaner *et al.,* 2000, 2007), holds that "*at any given level of cognitive processing larger animals require larger nervous systems to coordinate their larger bodies*" (Deaner *et al.,* 2007, p. 115). Hence, removing scaling effects (the 'traffic portion' of the brain) would be necessary in order to compare the 'cognitive portion' (Deaner *et al.,* 2000). According to this assumption, during evolution brain size might increase passively - as a result of body size increase - or actively - due to selection for increasing intelligence (Aboitiz, 2001).

From an adaptive viewpoint, this seems a reasonable assumption: since large brains are metabolically very expensive (Armstrong, 1983; Aiello & Wheeler, 1995; Dunbar, 1998; Isler & van Schaik, 2009), increases in encephalization must necessarily involve strong selection pressures, likely related to enhanced information-processing capabilities and other cognitive abilities (Ward *et al.,* 2004). However, it is unclear how to control for 'neural traffic' in interspecific studies, so that according to Deaner *et al.* (2000, p. 49) "*there is no evidence that controlling for body mass yields measures that correspond with cognitive ability.*" The traffic maintenance hypothesis has been considered to be "*entirely unsuitable where cognition is concerned*", because cognitive capacity is "*a matter of neural computation*", which is more likely to depend upon the total amount of neural tissue (Byrne & Corp, 2004, p. 1694). As a result, it has been recently suggested that increases in absolute brain size by itself should be also considered from an adaptive viewpoint (Schoenemann, 2006). In fact, the relationship between intelligence and encephalization, even though appealing and intuitively obvious (Jerison, 1955, 1961, 1973, 1975, 1979), has been always problematic (Radinsky, 1975, 1982; Harvey & Krebs 1990; Deaner *et al.,* 2000; Schoenemann, 2006) and it remained largely untested until recently (Gibson *et al.,* 2001; Williams, 2002; Deaner *et al.,* 2007). Williams (2002) found a correspondence between intelligence and encephalization under some particular circumstances (see below), but most recently Deaner *et al.* (2007) tentatively concluded that no body-size correction of brain size is required to make cognitive inferences in primates. As a result, it is currently unclear whether absolute brain size or relative brain size (encephalization) should be used when trying to infer cognitive abilities in fossil taxa.

Recent investigations on encephalization and intelligence in great apes have explicitly recognized that the computation and interpretation of measures of relative brain size is not so straightforward as previously though (Williams, 2002; Begun, 2004; Ward *et al.,* 2004): "*Normalizing brain mass (controlling for overall body size) has proven to be a complex and vexing enterprise*" (Begun, 2004, p. 19), because different methods provide different results (Begun & Kordos, 2004). Moreover, interspecific allometric regressions rely on a particular sample of taxa (Harvey & Krebs, 1990), and accordingly the selection of the reference group remains critical (Schoenemann, 2006). The most serious problem associated to sample selection it is the so-called 'taxon-level effect' (Martin & Harvey, 1985; Pagel & Harvey, 1989), according to which allometric slopes tend to decrease at progressively lower taxonomic levels, and vice versa. As a result, the problem remains as to how determine the 'correct' taxonomic level at which biologically meaningful comparisons among closely related taxa should be made (Holloway & Post, 1982; Radinsky, 1982). Earlier researchers obtained exponents of 0.5-0.6 for interspecific regressions and exponents close to 0.28 for intraspecific regressions (Dubois, 1897; Lapicque, 1898, 1907; see review in Gayon, 2000). Similar values of 0.56-0.63 and 0.25 for inter- and intraspecific comparisons, respectively, were recently defended by Kruska (2005). Over the years, however, a multitude of different slopes have been determined, with those of 0.67 (von Bonin, 1937; Jerison, 1973; Gould, 1975) or 0.75 (e.g. Bauchot, 1978; Martin, 1981, 1990) being generally accepted by most workers.

Several hypotheses have been put forward to explain the taxon-level effect. Traditionally, allometric slopes at higher taxonomic levels have been interpreted on functional grounds (Jerison, 1955, 1973; Gould, 1975). Other authors, on the contrary, have suggested that these high slopes artefactually result from allometric grade shifts between included subgroups, with lower-level slopes reflecting true functional equivalence (Kruska, 1988). Departures from allometry can be employed to infer particular adaptations of individual taxa or groups of taxa. However, in order to do so it is essential that the allometric regression employed somewhat reflects functional equivalence at different body sizes. This is complicated by the existence of grade differences between subgroups within the whole sample (Isler *et al.,* 2008). If two subgroups do not differ in allometric slope, but display different intercepts, employing a single regression for the whole sample will inevitable distort the residual values for several taxa (Martin, 2000, 2003). Although there is no established method for detecting such allometric grade shifts a priori, they can be easily found empirically when grade differences are pronounced enough (Martin, 2000).

Interpreting encephalization residuals in terms of cognitive abilities is further complicated by the fact that there is no universally accepted operational definition of biological intelligence. Given the lack of an adequate metric of cognitive abilities, Williams (2002) ranked several primates by intelligence on the basis of learning ability evaluations, so that the correlation between intelligence and encephalization could not be tested because an adequate metric of cognitive abilities was lacking. As stated above, recent analyses have managed to quantify domain-general cognitive abilities across a broad sample of primate species (Johnson *et al.,* 2002; Deaner *et al.,* 2006, 2007). These studies permit one to test "*the assumptions of comparative neuroanatomical investigations*", which "*generally take for granted that a relative measure of the size of the brain or of a brain structure corresponds with some overall level of information processing capacity or 'intelligence'* " (Deaner *et al.,* 2006, p. 179). The research by Deane and co-authors, based on nine cognitive paradigms, supports the generalized belief that primates differ in some kind of general cognitive ability, confirming that apes are on average more intelligent than both monkeys and lesser apes (Johnson *et al.,* 2002; Deaner *et al.,* 2006, 2007). This agrees with traditional wisdom on primate cognition, but contrasts with the majority of previous studies on primate encephalization. Thus, although there are some exceptions (Williams, 2002; Shea, 2005), many recent studies showed that great apes largely overlap in encephalization with other anthropoids, including hylobatids (Martin, 1990, 2000; Begun & Kordos, 2004; Roth & Dicke, 2005; Rilling, 2006; Schoenemann, 2006). More recently, Isler *et al.* (2008) took into account allometric grade shifts between primates subgroups, and found that anthropoids are more encephalized than prosimians, while hominoids and cercopithecines are more encephalized than colobines and platyrrhines. This study, however, did not specifically test for allometric grade shifts between great apes and hylobatids, which might explain why great apes were not found to be particularly more encephalized than other non-human primates. The supposed lack of correspondence between encephalization and cognitive data would suggest that encephalization is inadequate for making cognitive inferences in fossil taxa (Gibson *et al.,* 2001; Roth & Dicke, 2005; Schoenemann, 2006; Deaner *et al.,* 2007). Deaner *et al.* (2007) confirmed the previous tentative results of Gibson *et al.* (2001), by noting that general cognitive ability is not strongly correlated with encephalization residuals, thus concluding that "*absolute brain size measures were the best predictors of primate cognitive ability.*"

The aim of this paper

The failure by Deaner *et al.* (2007) to find a significant correlation between intelligence and encephalization might reflect biological reality, or might be alternatively attributed to the problems associated with the computation of encephalization, such as the taxon-level effect. The latter interpretation would be consistent with the fact that a good correlation between encephalization and intelligence was found by the same authors when using a slope of 0.30 (Deaner *et al.,* 2007). In the past, some authors (Williams, 2002; Shea, 2005) have argued that lower allometric exponents, such as the 0.28 exponent proposed by Lapicque (1898) more than a century ago, provide a better fit to primate intelligence data than higher exponents. Shea (2006, p. 615) has explicitly warned that encephalization studies in fossil taxa should rely on the "*0.2-0.4 baseline criterion.*" Deciphering whether the results of Deaner *et al.* (2007) are dependent on the allometric exponent employed is absolutely essential for paleobiological studies on primate cognition. Accordingly, this paper tests the hypothesis that encephalization is a good proxy for intelligence in hominoids, at least when computed at some taxonomic level.

This hypothesis is compatible with the significant correlation between absolute brain (and body) size and intelligence reported by Deaner *et al.* (2007) within a broad taxonomic context. The hypothesis predicts, however, that at least some metric of encephalization will be also correlated with intelligence, further reflecting the reported cognitive differences between hylobatids and great apes. The hypothesis also predicts that, if brain size and body size are correlated with intelligence within a broad taxonomic context, when computed at the correct level encephalization (in its turn, computed from brain size and body size measurements) must be also broadly correlated with brain size and body size. These predictions of the null hypothesis are tested by investigating the relationship between encephalization and intelligence in extant haplorrhine primates, with particular emphasis in lesser and great apes. Encephalization was computed by means of allometric residuals empirically-derived at two different taxonomic levels (haplorrhines and great apes), in order to control for the taxon-level effect. Following Williams (2002), encephalization quotients based on different allometric exponents were also employed (see Materials and Methods for further details). The hypothesis being tested does not require that their predictions are fulfilled at all taxonomic levels. However, given the taxon-level effect, it is expected that lower-level and higher-level residuals should provide similar results to lower and higher allometric exponents, respectively. If the above-mentioned predictions are only fulfilled at one of the two taxonomic levels, this must be taken as an indication that biologically meaningful comparisons of encephalization must be restricted to this level. The reliability of encephalization metrics for predicting intelligence is further evaluated by comparing them with other potential predictors, such as absolute brain size and body size.

Materials and Methods

Variables and measurements

Cranial capacity (CC), also referred to as endocranial volume, can be defined as the internal volume of the neurocranium. It was selected as the variable measuring brain size because it can be determined directly from fossils and museum collections of skeletal material (Martin, 1990; Smith *et al.,* 1995). Two other measurements of brain size (Smith *et al.,* 1995), brain mass and brain volume, tend to be somewhat smaller because they exclude other tissues such as blood vessels, nerves, meninges and cerebrospinal fluid (Armstrong, 1985; Falk, 2007). In fact, CC and brain mass display an isometric relationship (Isler *et al.,* 2008), but despite some pitfalls associated to the measurement of CC (Hemmer, 2007), the alternative use of brain mass is not advisable here because it cannot be directly measured from fossils. Indeed, it has been argued that, given the influence of preservational techniques upon brain mass, CC might be even a more reliable estimator of brain size (Isler *et al.,* 2008). With regard to body size, body mass (BM) was selected following the generalized view that it is the best and most meaningful overall size variable to be employed in allometric studies (e.g. Jungers, 1984, 1985; Jungers & Susman, 1984). It should be taken into account that encephalization measurements rely simultaneously on both CC and BM (see 'Statistical techniques' below). In extant taxa, average CC and BM values, usually derived from relatively large samples, are employed. In the case of fossil taxa, however, samples are much more restricted (even sometimes relying on a single individual). Moreover, at least BM cannot be directly measured but must be inferred from anatomical estimators. As such, encephalization values for fossil taxa should remain very tentative and must be interpreted with great care.

Finally, regarding cognitive abilities, an intelligence ranking derived for several non-human primate genera by means of a meta-analysis of historical psychological data using Bayesian methods was taken from the literature (Johnson *et al.,* 2002; Deaner *et al.,* 2006, 2007). This analysis was based in 9 cognitive paradigms (i.e. experimental settings designed to investigate different aspects of cognition or intelligence) and 30 procedures within these paradigms. The authors found that some genera performed consistently better than others, thus supporting the view that primate taxa somewhat differ in general cognitive ability. Thus, following Deaner *et al.* (2007), differences in global cognition between the several haplorrhine genera were taken from the "reduced model" column in Deaner *et al.* (2006, Fig. 1b; means reported in their Fig. 2), with the sign reversed in order to facilitate interpretation (see also Supplementary Tab. 2).

The taxonomic framework

There is some controversy regarding the definition of the family Hominidae, so that it is necessary to clarify that it is used here in a broad sense. Thus, as employed in this paper, the Hominidae refer to the group containing Ponginae (*Pongo*) and Homininae (*Gorilla*, *Pan* and *Homo*), plus all extinct forms more closely related to them than to the Hylobatidae (lesser apes). While this broad concept of Hominidae is currently employed by many paleoprimatologists (e.g. Begun, 2002, 2007; Kelley, 2002; Moyà-Solà *et al.,* 2009b), the traditional, more restrictive usage of Hominidae s.s. that includes modern humans plus all the taxa more closely related to them than to *Pan* (i.e., postdating the divergence between humans and chimpanzees), here classified into the tribe Hominini, is still employed by other authors (e.g., White *et al.,* 2009, footnote 2).

The primate sample

Sex-specific mean data (i.e., separate male and female means) for both CC and BM in extant haplorrhine species were mainly taken from Isler *et al.* (2008: Supplementary Table 3), further supplemented by other sources (Ricklan & Tobias, 1986; Kappelman, 1996; Smith & Jungers, 1997). Separate male and female means where employed, in order to take body size sexual dimorphism into account. Mean data for hominoid fossil species, used for computing encephalization residuals but not for deriving allometric equations, were also taken from the literature (Szalay & Berzi, 1973; Walker *et al.,* 1983; Jungers, 1987; Wood & Collard, 1999; McHenry & Coffing, 2000; Begun & Kordos, 2004; Falk *et al.,* 2005a; Schoenemann & Allen, 2006; Lovejoy *et al.,* 2009; Suwa *et al.,* 2009). All the CC and BM means employed in this paper are reported in Supplementary Table 1. In the case of fossil apes, a range of ±20% of uncertainty in BM and CC was considered, since BM and, especially, CC estimates are very tentative; in the case of *H. floresiensis*, the BM range published by Brown *et al.* (2004) was taken into account.

Statistical techniques

CC and BM do not maintain a linear relationship across different taxa, so that the allometric equation $y = b \cdot x^k$ (Gould, 1966; Martin, 1989; Martin & Barbour, 1989; Klingenberg, 1998; Gayon, 2000) was employed in order to control for size-scaling effects. Incidentally, it should be noted that this power equation was originally devised, many years before the term 'allometry' was formally proposed by Huxley & Teissier (1936), for describing brain size–body size relationships (see Snell, 1892; Dubois, 1897; Lapicque, 1898). ln-transformed data were used in order to linearize the relationship between the two variables, so that best-fit lines could be derived by means of bivariate line-fitting ($\ln y = \ln b + k \cdot \ln x$), where k is the allometric slope and $\ln b$ the intercept. There are three main methods of least-squares line-fitting (see review in Warton *et al.,* 2006): linear regression (usually referred to as ordinary least-squares regression, OLS), major axis (MA) and standardized major axis (or reduced major axis, RMA). These line-fitting methods estimate the line by minimizing the sum of squares of residuals from the best-fit line, differing in the direction in which errors from the line are measured (Warton *et al.,* 2006). OLS linear regression would not be appropriate when the primary interest of an allometric study is the slope of the best-fit line (Martin & Barbour, 1989; Smith, 1994; Warton *et al.,* 2006), such as for example when making biomechanical inferences. In the past, the use of linear regression in interspecific allometric studies has been discouraged for predictive purposes by some authors (e.g., Martin & Barbour, 1989). However, most researchers do favor the use of this method for making predictions (Smith, 1994). In fact, linear regression is the appropriate method of line-fitting in most practical instances, because most biological problems can be conceptualized as the prediction of one variable Y from a second variable X (Warton *et al.,* 2006). In other words, residuals are usually conceptualized as vertical (parallel to the y-axis) departures from the best-fit line, and this is the direction along which squared deviations are minimized by OLS linear regression, but not by MA and RMA (Smith, 1994). Accordingly, following the commonest practice in this field (e.g. Barton, 2006), in this paper linear regression was employed in most instances because regressions were mainly devised to compute allometric residuals, rather than making functional interpretations from the particular values of the allometric slopes. MA and RMA slopes were provided for comparison in the case of regressions based on independent contrasts (see later), but only OLS allometric regressions, with ln CC as the dependent variable and ln BM as the independent variable, were employed as a criterion of subtraction (Gould, 1975; Smith, 1984; Shea, 1984) for removing size-scaling effects from brain size. Allometric residuals of encephalization (ER), computed as ER = ln CC (observed) – ln CC (predicted) from the allometric regressions, were employed as size-independent variables of encephalization. These residuals measure the vertical departure of each particular point from the allometric regression line, thus reflecting positive and negative deviations as symmetrical values around zero. Traditionally, encephalization has been computed by means of several indices, such as the index of progression (IP; Bauchot & Stephan, 1966, 1969), the encephalization quotient (EQ; Jerison, 1973), or the index of cranial capacity (ICC; Martin, 1990). These indices are ratios between observed and expected brain size, and can be thus interchangeably expressed as residuals by applying logarithms (Smith, 1984).

Residuals (or indices) computed from an interspecific allometric regression are not an inherent trait (or character) of particular taxa in a strict sense (e.g. Shea, 1983), but depend on the particular reference sample employed to derive the regression. Hemmer (1971, 2007) took a somewhat different approach by computing a constant of cephalization - here labeled 'encephalization constant' (EC) to avoid confusion with cranial capacity - on the basis of a common intraspecific allometric exponent of 0.23: EC = observed brain mass / body mass$^{0.23}$. This approach, which has been employed by several workers in the past (Leutenegger, 1973, 1984; McHenry, 1975, 1976), provides an encephalization metric more directly comparable because it does not incorporate the intercept empirically-derived from the reference sample. This procedure should not distort the results, as long as different subgroups differ in intercept but not in slope. However, it is as dependent on the validity of the allometric exponent as ER or EQ. Williams (2002), in fact, followed this approach in order to test the reliability of different exponents - k = 0.28 (Lapicque, 1898), k = 0.67 (von Bonin, 1937; Jerison, 1973) and k = 0.75 (Martin, 1990) - , although he labeled this metric as an EQ. Given the taxon-level effect, testing if lower-level residuals reflect intelligence better than higher-level ones remains essentially equivalent to testing whether lower exponents perform better than higher ones.

When allometric regressions derived from mean specific data are employed, diverging functional adaptations can be inferred for particular taxa (outliers) that significantly depart from the regression line. Similarly, when separate regressions are computed for several groups, allometric grade shifts can be further inferred for those groups that display a similar scaling relationship (no significant differences in allometric slope) but significantly different intercepts (Martin, 1980, 1989; Martin & MacLarnon, 1988; Isler *et al.,* 2008). Allometric grade shifts between different groups were tested by means of analysis of covariance (ANCOVA), which is a particular case of the general linear model that tests homogeneity among group means for a dependent variable (in this case, brain size) by taking into account the group's differences in the independent variable (in this case, body size), which is termed the covariate (Sokal & Rohlf, 1995). This adjustment is performed by means of linear regression, and the main significance test in ANCOVA is a test of homogeneity of intercepts, although it is a necessary prerequisite that the regression lines for the several groups are parallel (Sokal & Rohlf, 1995). Accordingly, equality of slopes between different regression lines was tested by means of the general linear model, by taking ln CC as response and ln BM, group and the interaction between BM and group as factors. When the interaction term was non-significant ($p > 0.05$), equality of slopes could not be discarded, so that the model was recalculated with the factors BM and group only, in order to carry out the ANCOVA and test for equality of intercepts. Several different groupings of taxa were tested by means of ANCOVA performed on average-sex mean data. Also, on the basis of the compiled haplorrhine database (Supplementary Tab. 1), the following linear regressions were computed: non-human haplorrhines (tarsiers and simians), monkeys (ceboids and cercopithecoids), Old World monkeys (cercopithecoids), apes (non-human hominoids), lesser apes (hylobatids), and great apes (non-human hominids). Humans were excluded from all the regressions because they are clear outliers. Regressions were computed on the basis of sex-specific species means, and also on the basis of average-sex species means. ER were computed at two distinct taxonomic levels on the basis of the haplorrhine (ER_H) and great-ape (ER_{GA}) allometric regressions with sex-specific data, while EC were also computed on the basis of the 0.67 ($EC_{0.67}$) and 0.28 ($EC_{0.28}$) exponents.

Differences in ER and EC between several taxa were tested by means of analysis of variance (ANOVA) and post-hoc multiple comparisons (Bonferroni method), by dividing haplorrhines into tarsiers, New World monkeys, Old World monkeys, hylobatids, great apes, australopiths (*Australopithecus* spp. + *Paranthropus* spp.) and humans (living and extinct *Homo* spp., except *H. floresiensis*). *H. floresiensis*, like *Proconsul*, *Oreopithecus*, *Hispanopithecus* (formerly considered a junior subjective synonym of *Dryopithecus*, but recently resurrected by Moyà-Solà *et al.,* 2009a) and *Ardipithecus*, were evaluated individually. The reliability of ER and EC at different taxonomic levels as intelligence predictors was evaluated on the basis of their correlation with CC and BM in both haplorrhines and great apes by using linear regression. In the case of haplorrhines, in order to ensure that spurious correlations did not emerge between encephalization metrics and brain/body size due to the phylogenetic non-independence of taxa, independent contrasts (Felsestein, 1985; Nunn & Barton, 2000; Nunn & Barton, 2001) were employed. These contrasts were calculated as differences between pairs of taxa, between a taxon value and an ancestral node, or between higher nodes, beginning at the tips of the tree. Contrasts for the independent variable were forced to be positive, regressions were forced through the origin, and contrasts were standardized on the basis of branch lengths. These independent contrasts were computed and evaluated by means of the PDAP module of Mesquite 2.71 (Midford *et al.,* 2003; Maddison & Maddison, 2009), while phylogenetic information was taken from the primate supertree with branch lengths reported by Purvis (1995). Sex-averaged species-mean values were employed when possible as raw data for computing the independent contrasts; however, given the lack of topology and/or branch lengths for several taxa, in some instances mean values were averaged for groups of species or genera. Finally, the reliability of encephalization metrics at different levels was also evalutated on the basis of their correlation with intelligence; the correlation of intelligence vs. CC and BM was also computed in order to evaluate the correlations between encephalization and size. To compute these correlations, given the fact that intelligence data were only available at the genus level, average ER, EC, CC and BM were computed for the several genera included in the ranking (see Supplementary Tab. 2). These data were also evaluated by means of independent contrasts, as explained above.

All statistical computations except independent contrasts were made by means of SPSS 16.0 statistical package.

Results

Allometric grade shifts

The brain size–body size allometric regressions derived in this paper on the basis of OLS linear regression, including those employed for computing ER_H and ER_{GA}, are reported in Table 1 (see also Fig. 1); all the reported regressions were found to be significant at $p < 0.001$. The regressions for sex-specific means and average-sex species mean are very similar. The haplorrhine regression displays a slope close to the theoritical value of 0.75, which is higher than the slopes for the several included subgroups (see Tab. 1), as expected from the taxon-level effect; great apes, however, differ from other investigated groups by displaying a remarkably lower slope. Independent contrasts for haplorrhines as a whole (67 contrasts) confirm that the correlation between CC and BM is high and very significant ($r = 0.927$, $p < 0.001$), with a somewhat lower OLS slope of 0.629 (0.660 the MA slope, and 0.679 the RMA slope). In the case of great apes, independent contrasts show a high and significant correlation ($r = 0.982$, $p < 0.05$) with a low slope of 0.313 (OLS; MA slope of 0.314, and RMA slope of 0.318), which is very similar to the slope obtained on the basis of sex-specific mean species data.

ANCOVA comparisons were carried out by using the following groupings of taxa: (1) ceboids, cercopithecoids and hominoids; (2) following Isler *et al.* (2008), callithricines, other ceboids, cercopithecines, colobines and hominoids; (3) callithricines, other ceboids, cercopithecines, colobines, hylobatids and great apes; (4) cercopithecoids and hylobatids only; and (4) hylobatids and great apes only. In the first instance, equality of slopes could be rejected at $p < 0.001$, which precludes testing for equality of intercepts. With the second grouping of taxa, equality of slopes could not be rejected ($p = 0.354$), while equality of intercepts was rejected with $p < 0.001$, thus confirming the allometric grade shifts found by Isler *et al.* (2008). Nevertheless, when hylobatids and great apes are considered separately, as in (3), the same results are found (equality of slopes cannot be rejected with $p = 0.191$, while equality of intercepts can be rejected at $p < 0.001$). The existence of allometric grade shifts between cercopithecoids and hylobatids, and hylobatids and great apes, is confirmed by ANCOVA results: in (4), equality of slopes cannot be rejected at $p = 0.917$, while differences in intercept are significant at $p < 0.001$; in (5), equality of slopes can be

Tab. 1 - Interspecific brain size–body size allometric equations[1].

			SEX-SPECIFIC INTERSPECIFIC MEAN DATA					
TAXON	**N**	**R**	**SLOPE**	**95% CI**		**INTERCEPT**	**95% CI**	
Haplorrhines	313	0.96	0.720	0.698	0.742	3.011	2.968	3.053
Tarsiers	6	0.58	0.614	-0.600	1.827	2.466	-0.101	5.033
Monkeys	278	0.95	0.701	0.674	0.728	3.030	2.982	3.077
Apes	29	0.98	0.580	0.538	0.621	3.542	3.416	3.669
Old World monkeys	166	0.84	0.578	0.430	0.525	3.457	3.362	3.553
Callithricines	33	0.95	0.610	0.533	0.686	2.726	2.654	2.799
Other ceboids	79	0.89	0.670	0.590	0.750	3.160	3.051	3.269
Cercopithecines	102	0.93	0.522	0.480	0.563	3.464	3.384	3.544
Colobines	64	0.84	0.566	0.472	0.661	3.132	2.931	3.333
Lesser apes	17	0.81	0.497	0.301	0.693	3.669	3.299	4.040
Great apes	12	0.97	0.291	0.239	0.342	4.787	4.570	5.004

			AVERAGE-SEX INTERSPECIFIC MEAN DATA					
TAXON	**N**	**R**	**SLOPE**	**95% CI**		**INTERCEPT**	**95% CI**	
Haplorrhines	147	0.97	0.738	0.706	0.771	2.984	2.921	3.048
Monkeys	129	0.96	0.710	0.673	0.748	3.010	2.944	3.076
Apes	14	0.99	0.578	0.523	0.633	3.535	3.364	3.707
Old World monkeys	78	0.88	0.522	0.457	0.586	3.366	3.236	3.496
Callithricines	16	0.96	0.613	0.504	0.722	2.731	2.628	2.833
Other ceboids	35	0.87	0.670	0.538	0.802	3.169	2.986	3.351
Cercopithecines	49	0.96	0.563	0.512	0.613	3.371	3.273	3.469
Colobines	29	0.88	0.616	0.487	0.745	3.029	2.754	3.304
Lesser apes	8	0.82	0.497	0.149	0.845	3.668	3.010	4.327
Great apes	6	0.99	0.305	0.248	0.361	4.719	4.478	4.960

Abbreviations: N = sample size; r = correlation coefficient; CI = confidence interval.

[1] Independent variable: ln BM; dependent variable: ln CC. Sex-specific mean data (i.e., separate male and female means) employed to derive the equations are reported in Supplementary Table 1. Average-sex mean data were computed as the average between male and female means. Humans were excluded from all regression equations. The tarsier regression with average-sex values is not reported because, due to small sample size, it was not significant.

neither rejected at $p = 0.168$, but the differences in intercepts are also significant at $p < 0.01$. The existence of grade shifts between several groups is reflected in the different values of the intercepts for the several regressions reported in Table 1, although in most instances allometric grade shifts are somewhat obscured by differences in allometric proportionality. Differences in allometric slopes and/or intercepts between several haplorrhine subgroups can potentially distort the biological meaning of allometric residuals when computed at high taxonomic levels. Thus, in order to evaluate the reliability of encephalization metrics at different taxonomic levels (i.e., on the basis of different allometric slopes), differences in encephalization residuals between haplorrhine subgroups were further investigated on the basis of the haplorrhine and the great ape regressions (see below).

Higher- and lower-level encephalization metrics

Descriptive statistics of encephalization for several haplorrhine groups and fossil Hominini are reported in Table 2, while separate, sex-specific values are reported in Table 3 (extant great apes and fossil hominoids) and Supplementary Table 1 (all extant taxa). Hominins overlap in BM with great apes (Fig. 2A) but display larger CC (Fig. 2B). As such, the former are expected to display higher encephalization values than great apes, no matter how encephalization is computed. ANOVA results indicate that, for the four encephalization metrics employed, there are significant differences at $p < 0.001$ (see Table 4 for post-hoc multiple comparisons). For most groups, haplorrhine encephalization residuals (Fig. 2C) yield similar results to higher-exponent encephalization constants (Fig. 2E), whereas great-ape residuals (Fig. 2D) give similar results to lower-exponent constants (Fig. 2F). Thus, irrespective of the encephalization metrics employed, both modern and fossil humans clearly diverge from non-hominin haplorrhines by their disproportionately huge degree of encephalization ($p < 0.001$). On the basis of lower-level metrics (Tabs. 2,4; Figs. 2D,F), encephalization would increase from tarsiers to ceboids, from ceboids to cercopithecoids and hylobatids, from cercopithecoids and hylobatids to great apes, and from great apes to hominins (with australopiths being somewhat intermediate between great apes and humans); hylobatids would be on average more encephalized than cercopithecoids, although post-hoc comparisons indicate that differences are not significant. The results for higher-level metrics (Tabs. 2,4; Figs. 2C,E) are similar to those derived by lower-level metrics in most instances. However, the former show some inconsistencies regarding hominoids: in particular, great apes would not be more encephalized than monkeys and hylobatids, and the latter would be significantly more encephalized than monkeys, even tending to be more encephalized than great apes (although the latter differences are not significant). To sum up, higher-level metrics fail to recover the higher encephalization of great apes as compared to hylobatids that would be expected on the basis of the null hypothesis, whereas, on the contrary, lower-level metrics fulfill the predictions of the hypothesis being tested.

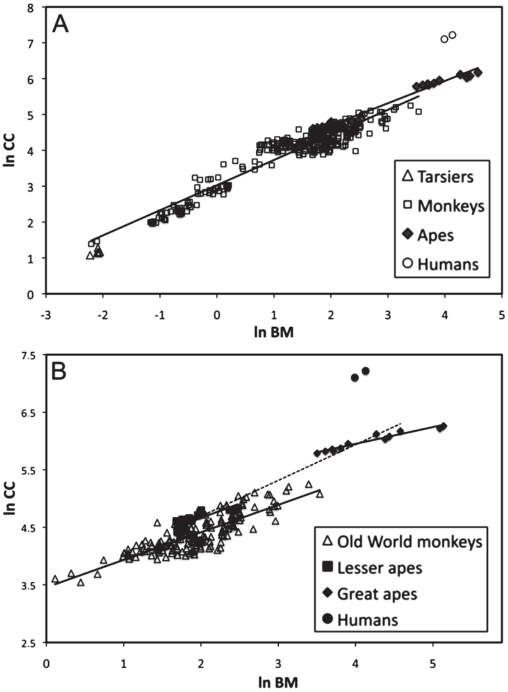

Fig. 1 – Brain size–body size allometric relationships in haplorrhines (A) and catarrhines (B). Solid lines represent the monkey and ape regression lines in (A), and the cercopithecoid, hylobatid and great ape regression lines in (B); the discontinuous line in (B) represents the ape regression line. Only humans are clear outliers, but note in (B) that there is a grade shift between great apes and lesser apes (the latter being more similar to monkeys), which is obscured when all apes are combined into a single regression.

Encephalization and absolute size

The correlations between several encephalization metrics and absolute measures of brain size and body size are reported in Table 5 (see

Tab. 2a - Descriptive statistics for encephalization residuals (ER¹) in several taxonomic groups.

HAPLORRHINE ENCEPHALIZATION RESIDUALS (ER_H)							
Taxonomic group	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Tarsiers	6	-0.32	0.05	-0.38	-0.26	-0.37	-0.23
New World monkeys	112	0.01	0.29	-0.04	0.07	-0.78	0.63
Old World monkeys	166	-0.02	0.22	-0.05	0.01	-0.53	0.54
Lesser apes	17	0.24	0.10	0.19	0.29	0.03	0.39
Great apes	12	-0.02	0.24	-0.17	0.14	-0.46	0.26
Modern humans	2	1.23	0.01	1.14	1.32	1.22	1.24
Fossil humans²	6	0.95	0.18	0.75	1.14	0.72	1.19
Australopiths	4	0.56	0.09	0.42	0.70	0.47	0.68

GREAT-APE ENCEPHALIZATION RESIDUALS (ER_{GA})							
Taxonomic group	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Tarsiers	6	-3.00	0.06	-3.06	-2.94	-3.06	-2.90
New World monkeys	112	-1.55	0.64	-1.67	-1.43	-2.75	-0.59
Old World monkeys	166	-0.97	0.20	-1.00	-0.94	-1.37	-0.46
Lesser apes	17	-0.73	0.09	-0.78	-0.68	-0.87	-0.57
Great apes	12	0.00	0.04	-0.03	0.03	-0.05	0.09
Modern humans	2	1.19	0.05	0.72	1.67	1.16	1.23
Fossil humans²	6	0.90	0.26	0.62	1.17	0.60	1.27
Australopiths	4	0.34	0.09	0.20	0.48	0.24	0.44

Abbreviations: N = sample size; SD = standard deviation; CI = confidence interval.

¹Allometric regressions employed to derive ER have been reported in Table 1.

²The group 'fossil humans' does not include *Homo floresiensis*.

also Fig. 3). In haplorrhines as a whole, there is a significant and high positive correlation between encephalization and both CC (Fig. 3A) and BM (Fig. 3B) when lower-level metrics are employed, whereas the correlation is much lower and in some cases even unsignificant when higher-level metrics are used (Figs. 3A,B). Independent contrasts analysis (on the basis of 67 contrasts) confirm that the correlation is very significant and high (particularly in the case of CC) for lower-level residuals, while high-level residuals are indeed uncorrelated or even negatively correlated with body size and brain size measurements. The lack of correlation between encephalization and brain/body size shown by high-level residuals is not to be expected within haplorrhines as a whole, given the correlation between intelligence and brain/body size (Deaner *et al.,* 2007; see also next subsection), which more closely agrees with the results of lower-level residuals. On the contrary, in great apes there is no significant correlation when lower-metrics are employed (Figs. 3C,D), which is to be expected in a group of closely-related taxa with similar cognitive abilities irrespective of body size, whereas a very significant and high *negative* correlation if found when higher-level metrics of encephalization are used; these results are partially confirmed on the basis of independent contrasts, although admittedly they are based on a very small number of contrasts (only three, due to the use of average-sex mean-genus data).

Tab. 2b - Descriptive statistics for encephalization constants (EC) in several taxonomic groups.

0.67 ENCEPHALIZATION CONSTANTS ($EC_{0.67}$)							
Taxonomic group	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Tarsiers	6	13.28	0.73	12.51	14.05	12.63	14.56
New World monkeys	112	22.15	7.29	20.79	23.52	10.48	39.71
Old World monkeys	166	21.14	6.97	20.08	22.21	0.15	37.46
Lesser apes	17	28.47	2.55	27.16	29.78	23.73	32.54
Great apes	12	25.11	5.00	21.94	28.29	16.59	31.22
Modern humans	2	84.97	1.25	73.73	96.21	84.09	85.86
Fossil humans[1]	6	64.95	12.59	51.73	78.16	51.00	83.06
Australopiths	4	42.82	3.84	36.72	48.93	38.97	48.03

0.28 ENCEPHALIZATION CONSTANTS ($EC_{0.28}$)							
Taxonomic group	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Tarsiers	6	5.82	0.35	5.46	6.18	5.47	6.45
New World monkeys	112	31.12	18.49	27.66	34.59	7.45	68.12
Old World monkeys	166	45.11	14.15	42.94	47.27	5.25	77.86
Lesser apes	17	59.26	5.64	56.36	62.16	51.34	69.35
Great apes	12	125.62	5.34	122.23	129.02	120.50	137.93
Modern humans	2	414.23	22.13	215.36	613.10	398.58	429.88
Fossil humans[1]	6	316.88	85.38	227.27	406.48	227.07	449.70
Australopiths	4	175.90	15.94	150.54	201.27	159.36	194.32

Abbreviations: N = sample size; SD = standard deviation; CI = confidence interval.

[1] The group 'fossil humans' does not include *Homo floresiensis*.

The results reported above must be interpreted in the following way. According to the null hypothesis (i.e., that encephalization reflects intelligence), higher-level metrics would suggest that, within haplorrhines as a whole, higher cognitive abilities would be only loosely related to increased brain size and body size (if at all), whereas in great apes the larger-bodied species would be less intelligent than smaller-bodied ones (including male gorillas as compared to female ones). On the contrary, following the null hypothesis, lower-level metrics would indicate that, within a broad taxonomic context, higher cognitive abilities would be simultaneously related to increased brain size and body size, whereas the several great ape taxa would not display considerable differences in cognitive abilities between each other. In order to decide between these competing and mutually excluding alternatives, i.e. in order to test which metrics are biologically meaningful from a cognitive viewpoint, it is necessary to investigate the correlation between size and encephalization relative to intelligence.

Encephalization and intelligence

When intelligence rankings for several primate species are taken into account (Johnson *et al.,* 2002; Deaner *et al.,* 2006), some simplification is required, because these data are available only for a reduced number of genera. Even though genus-averaged encephalization metrics must be employed, several interesting results

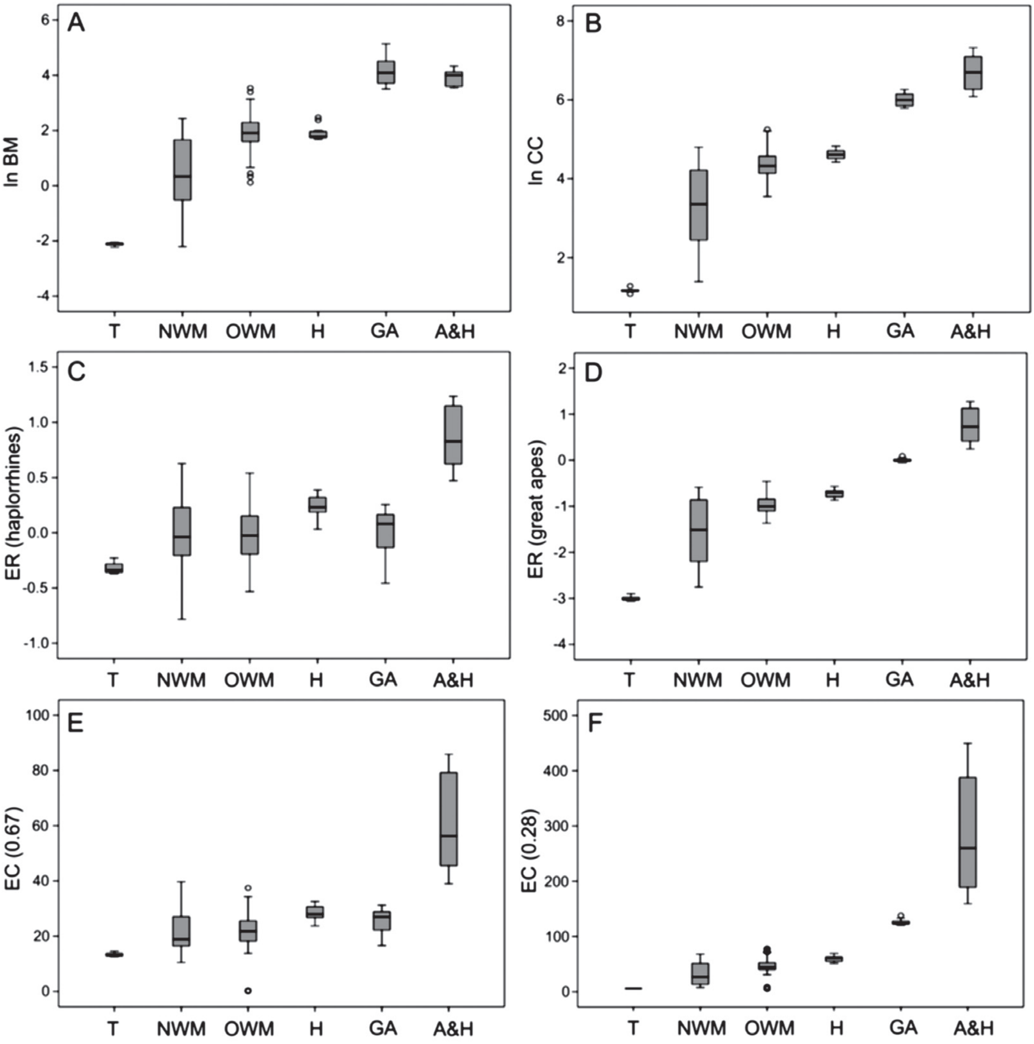

Fig. 2 – Boxplots of size and encephalization in extant haplorrhines and fossil hominins. (A) Body size (ln BM); (B) Brain size (ln CC); (C) Haplorrhine residuals (ER_H); (D) Great-ape residuals (ER_{GA}); (E) 0.67 constant ($EC_{0.67}$); (F) 0.28 constant ($EC_{0.28}$). Abbreviations: T = tarsiers; NWM = New World monkeys; OWM = Old World monkeys; H = hylobatids; GA = great apes; A&H = australopiths and humans.

emerge. Linear regressions between intelligence and several of its potential predictors (Fig. 4) are reported in Table 6. Intelligence does not show a significant correlation with higher-level metrics, whereas the correlation with lower-level metrics is high and very significant ($p < 0.001$; Figs. 4A,B), even when independent contrasts are taken into account ($p < 0.05$). The correlation between intelligence and absolute size measures (BM and CC, logarithmically-transformed following Deaner *et al.*, 2007, Fig. 4C) is similarly high and very significant ($p < 0.001$), also

Tab. 3 - Body mass (BM[1]), cranial capacity (CC[1]), encephalization residuals (ER[2]) and encephalization constants (EC) in extant great apes and the fossil hominoids included in the study.

TAXON	BM	CC	ER_H	ER_{GA}	$EC_{0.67}$	$EC_{0.28}$
Pongo abelii (male)	84.5	437.78	-0.12	0.00	22.40	126.40
Pongo abelii (female)	41.1	341.21	0.15	-0.04	28.28	120.50
Pongo pygmaeus (male)	80.1	417.03	-0.13	-0.03	22.11	122.21
Pongo pygmaeus (female)	36.9	337.72	0.21	-0.01	30.08	122.92
Gorilla beringei (male)	162.5	502.40	-0.46	-0.05	16.59	120.78
Gorilla beringei (female)	97.5	480.15	-0.13	0.05	22.32	133.19
Gorilla gorilla (male)	170.4	524.92	-0.45	-0.02	16.79	124.53
Gorilla gorilla (female)	71.5	455.89	0.04	0.09	26.09	137.93
Pan paniscus (male)	45.0	356.33	0.12	-0.02	27.81	122.73
Pan paniscus (female)	33.2	326.25	0.26	-0.02	31.22	122.36
Pan troglodytes (male)	49.6	386.16	0.14	0.03	28.25	129.45
Pan troglodytes (female)	40.4	350.54	0.19	0.00	29.42	124.47
Proconsul heseloni	15.0	167.00	0.16	-0.46	27.21	78.24
Hispanopithecus hungaricus	31.0	329.46	0.31	0.01	33.01	125.96
Oreopithecus bambolii	32.0	200.00	-0.21	-0.50	19.61	75.79
Ardipithecus ramidus	51.0	300.00	-0.14	-0.23	21.53	99.77
Australopithecus afarensis	37.0	438.00	0.47	0.24	38.97	159.36
Australopithecus africanus	35.5	452.00	0.53	0.29	41.35	166.37
Paranthropus boisei	41.5	521.00	0.56	0.39	42.93	183.56
Paranthropus robustus	36.0	530.00	0.68	0.44	48.03	194.32
Homo habilis	34.5	612.00	0.86	0.60	57.07	227.07
Homo rudolfensis	55.5	752.00	0.72	0.67	51.00	244.24
Homo ergaster	61.0	871.00	0.80	0.79	55.44	275.50
Homo erectus	57.0	1016.00	1.00	0.96	67.68	327.53
Homo heidelbergensis	62.0	1198.00	1.11	1.10	75.43	377.21
Homo neanderthalensis	76.0	1512.00	1.19	1.27	83.06	449.70
Homo floresiensis	27.4	417.00	0.64	0.28	45.38	165.03

Abbreviations: N = sample size; SD = standard deviation; CI = confidence interval.

[1] Mean BM (in kg) and CC (in cm^3) taken from the literature (see references and figures for extant taxa in Supplementary Tab. 1).

[2] Allometric regressions employed to derive ER have been reported in Tab. 1.

when independent contrasts are employed ($p < 0.01$). Correlation coefficients (Tab. 6) indicate that brain size ($r = 0.804$) and body size ($r = 0.818$) are good predictors of intelligence (Deaner *et al.,* 2007), but further suggest that lower-level metrics of encephalization are almost as good predictors (contra Deaner *et al.,* 2007). To sum up, within the context of haplorrhines, both absolute body size and brain size are good predictors of intelligence. This, however, does not invalidate the use of encephalization, but merely warns us that only lower-level metrics (those that display a good correlation with intelligence rankings) should be employed.

Tab. 4 - Post-hoc multiple comparisons[1] (Bonferroni method) of different encephalization metrics[2] between several haplorrhine subgroups.

		TARSIERS	NW MONKEYS	OW MONKEYS	LESSER APES	GREAT APES	MODERN HUMANS	FOSSIL HUMANS
ER_H	NW monkeys	0.035						
	OW monkeys	0.091	1.000					
	Lesser apes	0.000	0.010	0.001				
	Great apes	0.369	1.000	1.000	0.150			
	Mod. humans	0.000	0.000	0.000	0.000	0.000		
	Foss. humans	0.000	0.000	0.000	0.000	0.000	1.000	
	Australopiths	0.000	0.000	0.000	0.497	0.001	0.048	0.419

		TARSIERS	NW MONKEYS	OW MONKEYS	LESSER APES	GREAT APES	MODERN HUMANS	FOSSIL HUMANS
ER_{GA}	NW monkeys	0.000						
	OW monkeys	0.000	0.000					
	Lesser apes	0.000	0.000	0.586				
	Great apes	0.000	0.000	0.000	0.000			
	Mod. humans	0.000	0.000	0.000	0.000	0.004		
	Foss. humans	0.000	0.000	0.000	0.000	0.000	1.000	
	Australopiths	0.000	0.000	0.000	0.000	1.000	0.444	0.962

		TARSIERS	NW MONKEYS	OW MONKEYS	LESSER APES	GREAT APES	MODERN HUMANS	FOSSIL HUMANS
$EC_{0.67}$	NW monkeys	0.067						
	OW monkeys	0.183	1.000					
	Lesser apes	0.000	0.014	0.001				
	Great apes	0.020	1.000	1.000	1.000			
	Mod. humans	0.000	0.000	0.000	0.000	0.000		
	Foss. humans	0.000	0.000	0.000	0.000	0.000	0.013	
	Australopiths	0.000	0.000	0.000	0.006	0.000	0.000	0.000

		TARSIERS	NW MONKEYS	OW MONKEYS	LESSER APES	GREAT APES	MODERN HUMANS	FOSSIL HUMANS
$EC_{0.28}$	NW monkeys	0.036						
	OW monkeys	0.000	0.000					
	Lesser apes	0.000	0.000	0.084				
	Great apes	0.000	0.000	0.000	0.000			
	Mod. humans	0.000	0.000	0.000	0.000	0.000		
	Foss. humans	0.000	0.000	0.000	0.000	0.000	0.000	
	Australopiths	0.000	0.000	0.000	0.000	0.000	0.000	0.000

[1] Differences between mean values of different subgroups are taken to be significant at $p < 0.05$.

[2] Descriptive statistics for these variables have been reported in Table 2.

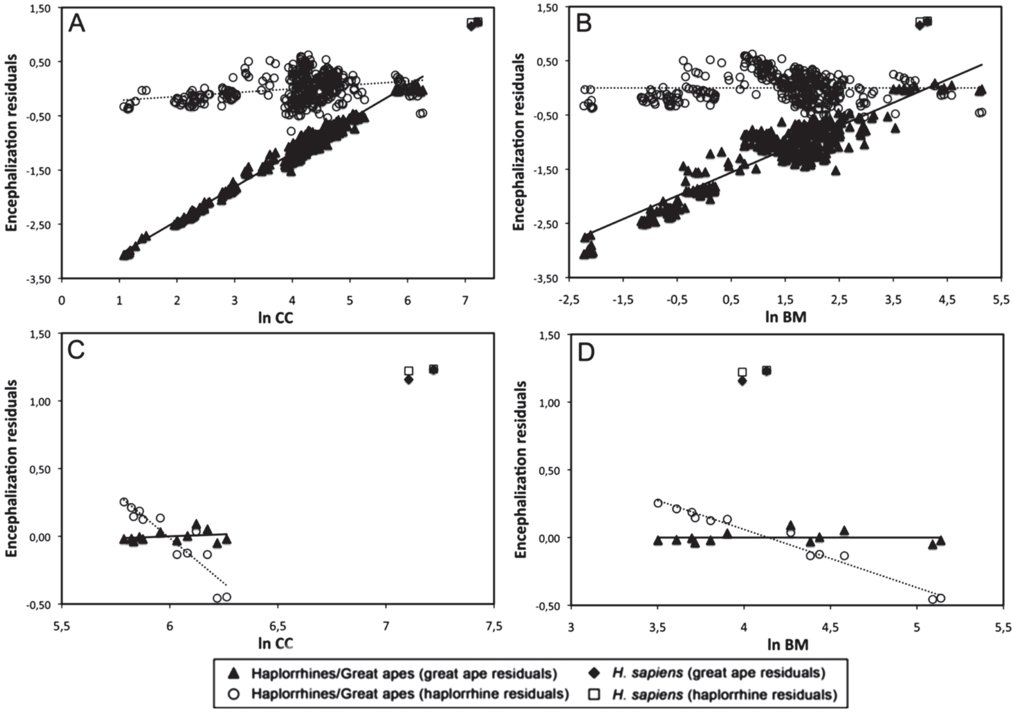

Fig. 3 – Relationships between encephalization and brain size (A, C), and between encephalization and body size (B, D), in haplorrhines (A, B) and great apes (C, D). Note that when encephalization is measured by means of haplorrhine residuals (discontinuous line), there is an inverse relationship between encephalization and body mass; on the contrary, this relationship disappears when great-ape residuals are employed (solid line). Humans are much more encephalized than great apes irrespective of how encephalization is measured.

Discussion

Encephalization, intelligence and functional equivalence

Different definitions of intelligence are possible, but following Jerison (1955, 1961, 1973, 1975, 1979), biological intelligence may be understood as the information-processing capability of a particular species. As such, differences in intelligence among different taxa must be somewhat reflected in concomitant differences in the brain and associated sensory-motor structures. Such definition, however, leads to a somewhat circular reasoning, and requires further testing in order to assess what neuroanatomical differences among taxa best reflect underlying differences in intelligence. In other words, the reliability of encephalization estimates of intelligence strongly rely on whether there is a good correlation between encephalization and intelligence, especially given previous reports that no significant correlation can be found (Deaner *et al.,* 2007). Moreover, different metrics of encephalization must be evaluated (Williams, 2002), given the controversy regarding the particular level at which cognitive functional equivalence is reflected on encephalization.

The refined statistical methodology employed by Johnson *et al.* (2002; see also Deaner *et al.,* 2006) enables to test the correlation between intelligence and encephalization. These authors employ the term 'intelligence' as a theoretical construct, implying that some cognitive abilities are domain-general, or at least applicable to many

Tab. 5 – Correlation[1] between several encephalization metrics and absolute size[2] in non-human haplorrhines and great apes, on the basis of sex-specific species means as well as independent contrasts computed on the basis of average-sex genus means.

SEX-SPECIFIC MEAN SPECIES DATA								
	Brain size (ln CC)				Body size (ln BM)			
	Haplorrhines		Great apes		Haplorrhines		Great apes	
	r	p	r	p	r	p	r	p
ER_H	0.266	< 0.001	-0.915	< 0.001	0.000	1.000	-0.986	< 0.001
$EC_{0.67}$	0.341	< 0.001	-0.922	< 0.001	0.123	< 0.05	-0.987	< 0.001
ER_{GA}	0.987	< 0.001	0.244	0.445	0.908	< 0.001	0.000	1.000
$EC_{0.28}$	0.843	< 0.001	0.384	0.217	0.780	< 0.001	0.148	0.647

INDEPENDENT CONTRASTS								
	Brain size (ln CC)				Body size (ln BM)			
	Haplorrhines		Great apes		Haplorrhines		Great apes	
	r	p	r	p	r	p	r	p
ER_H	0.025	0.839	-0.948	0.052	-0.352	<0.01	-0.990	< 0.01
$EC_{0.67}$	0.185	0.130	-0.941	0.059	-0.194	0.112	-0.987	< 0.05
ER_{GA}	0.962	< 0.001	0.320	0.680	0.788	< 0.001	0.140	0.860
$EC_{0.28}$	0.864	< 0.001	0.642	0.358	0.742	< 0.001	0.489	0.510

Abbreviations: r = correlation coefficient; p = significance.

[1] Correlation was taken to be significant at $p < 0.05$.

[2] Descriptive statistics for the several encephalization metrics have been reported in Tab. 2.

Tab. 6 – Correlation and significance for intergeneric linear regressions between intelligence and several of its potential predictors[1], on the basis of both original variables and independent contrasts.

	ORIGINAL VARIABLES[2]				INDEPENDENT CONTRASTS[3]			
Predictor	**N**	**r**	**Significance**		**N**	**r**	**Significance**	
ER_H	17	0.223	F = 0.786	p = 0.389	16	-0.141	F = 0.303	p = 0.590
ER_{GA}	17	0.781	F = 23.507	p < 0.001	16	0.569	F = 7.175	p < 0.05
$EC_{0.67}$	17	0.073	F = 0.080	p = 0.781	16	-0.012	F = 0.002	p = 0.963
$EQ_{0.28}$	17	0.775	F = 22.551	p < 0.001	16	0.536	F = 6.038	p < 0.05
ln CC	17	0.804	F = 27.504	p < 0.001	16	0.613	F = 9.029	p < 0.01
ln BM	17	0.818	F = 30.276	p < 0.001	16	0.632	F = 9.966	p < 0.01

Abbreviations: N = sample size; r = correlation coefficient.

[1] Intelligence rankings taken from Deaner *et al.* (2006: Fig. 2), with the sign reversed, were taken as the independent variable. Mean genus encephalization residuals and constants, as well as ln-transformed BM and CC (computed from data reported in Supplementary Table 1), were taken as the dependent variables.

[2] Mean genus values reported in Supplementary Tab. 2.

[3] Phylogeny and branch lengths (ln-transformed) for the several primate genera were taken from Purvis (1995). Regressions were taken to be significant at $p < 0.05$.

different situations. Their results indicate that domain-general cognitive abilities (intelligence in a broad sense) can be estimated adequately by a unidimensional global variable, further confirming that great apes display on average greater cognitive abilities than other non-human primates (see also discussion in van Schaik & van Duijnhoven, 2004, pp. 128-131; Sherwood *et al.,* 2008). Interestingly, lesser apes do not cluster with great apes, but are rather intermixed with a wide array of monkeys. These differences in intelligence between great and lesser apes are in accordance with other tests of cognitive abilities, which show that great apes excel in several aspects, including tool-using and even tool-making (Whiten *et al.,* 1999; van Schaik *et al.,* 1999, 2003), high rates of deception (Byrne & Whiten, 1992), increased representational understanding (Byrne, 1995) and mirror self-recognition (Inoue-Nakamura, 1997; de Veer & van den Bos, 1999; Heschl & Burkart, 2006). These cognitive abilities of great apes exceed those reported for hylobatids, which for example do not pass the standard mirror self-recognition test that is regularly passed by great apes (Lethmate & Dücker, 1973; Inoue-Nakamura, 1997; Hyatt & Hopkins, 1995).

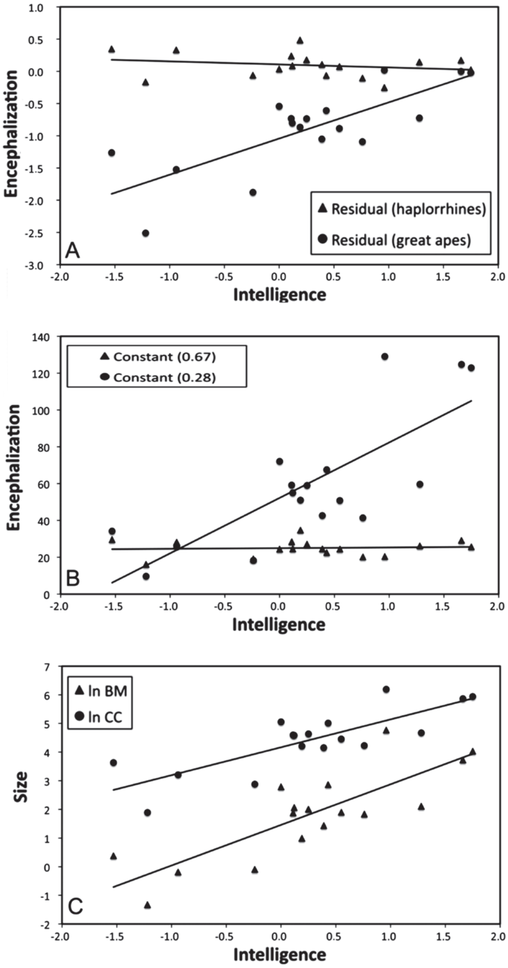

Fig. 4 – Relationships between intelligence, encephalization and size in haplorrhine genera. (A) Encephalization residuals relative to intelligence, separately for haplorrhine and great ape encephalization metrics; (B) Encephalization constants relative to intelligence, separately for higher exponent and lower exponent metrics; (C) Absolute size relative to intelligence, separately for body mass and cranial capacity. Note that intelligence is correlated with encephalization only when lower-lever residuals or constants are employed. Note also that both body and brain size are significantly correlated to intelligence.

The results of this study show that encephalization can reflect differences in cognitive abilities between haplorrhine subgroups (contra Deaner *et al.,* 2007), including great apes and hylobatids, but only under some particular circumstances. Although Hemmer (2007) found a significant correlation between different encephalization metrics, this study shows that some of them are to be preferred, because a significant correlation between encephalization and intelligence is only found when lower-level metrics are employed. Accordingly, when making cognitive inferences, lower allometric exponents derived at low taxonomic levels should be preferred. Higher-level metrics tend to increase due to underlying allometric grade shifts, thus precluding a meaningful interpretation of encephalization in terms of cognition. The recognition that cognitive functional equivalence is reflected in lower-level encephalization metrics confirms the results of some previous authors (Hemmer, 1971; Williams, 2002; Shea, 2005, 2006) and it is very promising for paleobiological studies trying to infer the cognitive abilities of extinct species on the basis of relative brain size computed from fossils. At the same time, it warns against the indiscriminate use of a single primate or haplorrhine regression (e.g. Martin, 1990; Begun & Kordos, 2004) for all groups.

Encephalization and the taxon-level effect

The brain size–body size allometric regressions derived in this paper for haplorrhine primates at several taxonomic levels confirm the taxon-level effect, i.e. that different scaling relationships (lower allometric slopes) can be found at increasingly lower taxonomic levels. The confidence interval for the slope of the haplorrhine regression excludes the value of 0.75 computed for placental mammals as a whole (Bauchot, 1978; Martin, 1981, 1982, 1983; Armstrong, 1983), thus contrasting with a previous study by Martin (1990, 2000), based on a considerably smaller sample of sex-averaged values. The slope for haplorrhines as a whole is nonetheless very high, intermediate between the traditional slopes of 0.67 and 0.75 (albeit closer to the latter one), and in any case higher than the figure of 0.56-0.63 proposed by Kruska (2005) for interspecific comparisons; the MA and RMA slopes computed on the basis of independent contrasts, however, are much more similar to the theoretical value of 0.67. On the other hand, the 0.29 OLS slope empirically derived in this paper for sex-specific mean data in great apes closely resembles the slope of 0.28 favored by Williams (2002), following Lapicque (1898), and further resembles the 0.23 slope employed by other authors (Hemmer, 1971; Leutenegger, 1973, 1984; McHenry, 1975, 1976). Both average-sex species means regression and independent contrasts yield a great ape slope only slightly higher, around 0.31. These 0.29-0.31 slopes are intermediate between the slopes of 0.18 (Clutton-Brock & Harvey, 1980) and 0.34 (Pilbeam & Gould, 1974; Shea, 1983), previously derived by other workers on the basis of mean specific data.

A marked decrease of the allometric slope at increasingly lower taxonomic levels is not surprising, since the taxon-level effect has been widely reported in the literature (Gould, 1975; Clutton-Brock & Harvey, 1980; Holloway & Post, 1982; Riska & Atchley, 1985; Martin & Harvey, 1985; Pagel & Harvey, 1989; Martin 1990). This has been attributed to differential selection on brain size and body size, so that differences among closely related species would mainly result from body size selection, with brain size merely evolving as a correlated response that cannot keep pace (Jerison, 1973; Gould, 1975; Lande, 1979; Riska & Atchley, 1985; but see Deaner & Nunn, 1999). This explanation has led to the widely-held belief that slopes at higher levels reflect true functional equivalence, with the 0.75 slope being interpreted on energy availability grounds (Martin, 1981; Armstrong, 1983), given its correspondence to Kleiber's law. According to this interpretation, decreased allometric slopes at lower taxonomic levels would be merely a statistical artifact (Martin, 2000). Such lower-level slopes, however, do closely resemble the 0.2-0.4 slopes that are customarily derived for intraspecific adult regressions (Hemmer, 1971; Pilbeam & Gould, 1974; Gould, 1975; Radinsky, 1982; Shea, 1983, 2006; Kruska, 2005). Accordingly, other authors have suggested that the 0.75 slope artefactually results from combining different degrees of encephalization among different groups into a single regression line (Kruska, 1988; Barton, 2006). This is usually termed a problem of 'grade confusion' (e.g., Martin, 2003). As noted by the latter author, in allometric analyses it is common to observe that the data are subdivided into two or more subsets with a similar scaling trend (with the same allometric slope) but vertically separated along the Y-axis (i.e., displaying different intercepts); such subsets are referred to as 'grades' and the vertical separation between them as 'grade shifts'. Individual best-fit lines should be computed for each grade separately, and the interpretation of the single best-fit line for the whole sample can led to erroneous conclusions due to this so-called problem of 'grade confusion' (Martin, 2003; Martin *et al.,* 2005). Kruska (1988) contended that brain size-body size allometric regressions at lower levels would reflect true functional equivalence, whereas higher-level allometric slopes would tend to artefactually increase due to allometric grade shifts between subgroups that differ in body size. The results of this paper regarding cognitive functional equivalence support the latter interpretation.

Several allometric grade shifts had been previously identified between several mammalian orders, not only primates as compared to other mammals (Shea, 1987, 2006), but also carnivores, artiodactyls and perissodactyls as compared to rodents and lagomorphs, and the latter as compared to insectivores (Kruska, 2005). Similar grade shifts, such as between strepsirrhines and haplorrhines (or prosimians and anthropoids) have also been identified (Gould, 1975; Martin, 1990; Barton, 2006; Isler *et al.,* 2008). ANCOVA results of the present study further confirm that allometric grade shifts do exist within haplorrhine primates, even when great apes are compared to hylobatids. This is confirmed by ANOVA comparisons of several encephalization metrics. Irrespective of the methodology employed, humans emerge as the most encephalized, whereas australopiths appear as somewhat intermediate between humans and great apes. Given the correlation between intelligence and encephalization only when lower-level metrics are employed, it is concluded that higher-level metrics of encephalization result from the combination of increased encephalization degrees with larger body masses. As such, only lower-level metrics of encephalization are able to recover the higher encephalization great apes as compared to hylobatids that is expected on the basis of the higher cognitive abilities of the former, and which is confirmed by ANCOVA comparisons. In other words, the results of this study confirm that only lower-level brain size-body size allometric slopes do reflect cognitive functional equivalence, thus favoring the interpretation of the taxon-level effect as a problem of grade confusion.

Encephalization, body size and the traffic maintenance hypothesis

The greater reliability of lower-level encephalization metrics is further reflected on their relationship with body size. This study shows that these metrics completely remove size-scaling (i.e. allometric) effects among great apes, while at the same time displaying a positive correlation with body size and brain size within a broader taxonomic context. This is to be expected, given the previously reported positive correlation between intelligence and brain size/body size (Deaner *et al.,* 2007). Several workers had previously noted a negative correlation between encephalization and body size (Jerison, 1973; Kappelman, 1996; Begun & Kordos, 2004), with larger-bodied taxa tending to be less encephalized than smaller ones. This study shows that such a negative correlation, which runs against the predictions of the hypothesis being tested, can be only found in great apes when higher-level metrics are employed. On the contrary, no correlation (either positive or negative) is found for great apes when lower-level metrics are employed, indicating that only the latter do adequately reflect cognitive functional equivalence.

Deaner *et al.* (2007) argue that their failure to find a significant correlation between encephalization and intelligence (using both the traditional 0.67 slope and a >0.75 empirically-derived slope) is a strong challenge to the 'traffic maintenance hypothesis', according to which the brain can be divided (at least statistically) into a somatic and a cognitive portion. These authors recognize that, in a broad taxonomic framework, some relationship between brain size and body size must be taken into account, but suggest that within primates absolute brain size is enough for making reliable cognitive inferences. However, it must be stressed that Deaner *et al.* (2007) found a significant correlation between encephalization and intelligence when using a 0.3 slope. The coincidence of the 0.29-0.31 slopes empirically derived in this paper for great apes with the traditional 0.28 slope employed by Williams (2002), following Lapicque (1898), is very remarkable, especially in the light of empirical evidence in mice that selection for increased body size leads to a brain size increase with slopes around 0.2-0.4 (Lande, 1979; Riska & Atchley, 1985). Taken together, available evidence support the validity of the traffic maintenance hypothesis, with 0.2-0.4 slopes merely reflecting the brain size increase required by changes in body size among closely-related taxa, and higher slopes reflecting selection on brain size independent of body size. From a neurophysiological perspective, the relationship between brain size and body size may be at least partially explained by the need to conserve the speed and efficiency of information processing through increasing cell size and white matter volume (Barton, 2006). From an ontogenetic viewpoint, it has been suggested that lower-level slopes may result from the fact that body size diversification occurs preferentially by differential selection of postnatal growth rates (Shea, 1983, 1992, 2006), which disproportionately affect the body as compared to the brain (Riska & Atchley, 1985).

Once it is recognized that lower-level slopes do reflect cognitive functional equivalence, the question arises as to how higher-level slopes must be interpreted. The reflection of intelligence by lower-level encephalization metrics does not necessarily mean that allometric slopes at higher levels are statistical artefacts entirely devoid of any biological meaning. Allometric grade shifts would not result in higher allometric slopes if the several subgroups did not display different body size ranges. It is the combination of encephalization grade shifts and different body size ranges that causes increased allometric slopes (towards 0.67-0.75) at higher levels such as haplorrhines or primates as a whole. Major shifts towards higher encephalization during haplorrhine evolution, although with some exceptions (most notably hominins), are closely matched by concomitant increases not only in brain size, but also in body size: ceboids as compared to tarsiers, cercopithecoids as compared to ceboids (although with substantial overlap), and great apes as compared to cercopithecoids and hylobatids. This explains the correlation between encephalization (and intelligence) with regard to body size, and suggests that, during haplorrhine evolution, encephalization has increased in a stepwise fashion, so that important increases in the degree of encephalization have been accompanied by significant increases in body size. As a result, higher-level slopes might ultimately reflect some underlying structural constraint, with body size precluding, either directly or indirectly, the attainment of higher levels of encephalization until a particular threshold is surpassed.

There are different hypotheses that might explain the relationship between encephalization and body size. Testing all the possible alternative possibilities is outside the scope of this paper, but two main alternatives deserve consideration. Given the high energy requirements of the brain, metabolic considerations should be taken into account (Martin, 1981; Armstrong, 1983; Aiello & Wheeler, 1995; Isler & van Schaik, 2009). It has been previously suggested that body size enlargement during evolution might be an adaptive response per se: this is because it would enable to take pace with environmentally-driven selection pressures that require enhanced cognitive abilities, by releasing developmental and metabolic constraints on neocortical volume (Byrne & Corp, 2004). Alternatively, one might consider the strong relationship between brain size and life history (Shea, 1987, 2006; Smith, 1989; Smith *et al.,* 1995; Godfrey *et al.,* 2001; Hemmer, 2007), at least in some mammalian lineages (see Isler & van Schaik, 2009). Hylobatids and humans do not follow the relationship between encephalization and body size: the former tend to be somewhat more encephalized than monkeys, whereas humans are much more encephalized than great apes, in spite of considerable body size overlap. In both cases, there is a delay in maturation (Kelley, 1997, 2002a; Kelley & Smith, 2003), suggesting that the relationship between encephalization and body size may be merely attributable to the general correlation between extended maturation and larger size.

Paleobiological inferences

Extant hominoids

Although some previous studies on encephalization show that great apes are more encephalized than monkeys (Hemmer, 1971; Leutenegger, 1973, 1984; Pilbeam & Gould, 1974; Shea, 2005), many other papers conclude that living and fossil great apes largely overlap with monkeys and are not particularly encephalized (Walker *et al.,* 1983; Martin, 1990, 2000; Begun & Kordos, 2004; Tartarelli & Bisconti, 2006; Schoenemann, 2006; Rilling, 2006). The reliance of such results on the allometric slope selected for computing encephalization was explicitly noted by Radinsky (1982, p. 32), who argued that "*the lower slopes are substituted in an ad hoc way that may reflect the investigators' preconceived beliefs rather than objective analysis. Most workers have a preconceived belief that apes are ... at least smarter ... and because of that expect to find relatively larger brains in apes than monkeys*." In the light of current psychobiological research, however, lower slopes must be clearly favored, because an overlap in encephalization between monkeys and great apes would stand in clear contradiction with the reported higher cognitive abilities of the latter. Regrettably, with the remarkable exception of Williams (2002), the problems associated with the computation of encephalization have not been generally investigated. Instead, several investigators have criticized the utility of encephalization measurements (e.g. Schoenemann, 2006), even suggesting that they should be abandoned in favor of absolute brain size (Deaner *et al.,* 2007). The results of this paper, on the contrary, validate the previous results by Williams (2002), according to which lower-level encephalization metrics adequately reflect functional equivalence. On this basis, it is shown that great apes (mean ER_{GA} = 0.00) are markedly more encephalized than other non-human haplorrhines, including hylobatids (mean ER_{GA} = -0.73), in accordance to the greater cognitive abilities of the former. The failure by other previous studies to show such a correspondence between intelligence and encephalization is due to a problem of grade confusion and the attribution of cognitive functional equivalence to higher-level allometric regressions.

According to the intelligence ranking employed in this paper (Johnson *et al.,* 2002; Deaner *et al.,* 2006), orangutans and chimpanzees are the most intelligent non-human primates, whereas hylobatids are intermixed with monkeys. This agrees with lower-level encephalization results, according to which *Hylobates* s.l. (mean ER_{GA} = -0.73) is much less encephalized than both *Pongo* (mean ER_{GA} = -0.02) and *Pan* (mean ER_{GA} = 0.00). An allometric grade shift between great apes and hylobatids in this regard is further confirmed by ANCOVA comparisons. According to higher-level metrics, on the contrary, hylobatids would be more encephalized than great apes, chimpanzees much more encephalized than orangutans and gorillas, and *Miopithecus* more encephalized than them all (whereas just the opposite pattern is obtained by the intelligence ranking, where *Miopithecus* is the least intelligent haplorrhine genus). The high encephalization traditionally attributed to *Miopithecus*, which is the smallest extant catarrhine monkey, has been explained as a result of phyletic dwarfism (Bauchot & Stephan, 1969; Gould, 1975), and particularly to ontogenetic scaling with size truncation during the postnatal period (Shea, 1983, 1992). Similarly, the traditionally low encephalization of *Gorilla* has been attributed to phyletic giantism (Pilbeam & Gould, 1974; Gould, 1975) by through changes in postnatal ontogeny (Shea, 1983), although other authors have associated it with dietary differences (Clutton-Brock & Harvey, 1980). The fact that gorillas and chimpanzees display similar brain size–body size intraspecific allometric relationships (Holloway, 1980) further suggests that brain size differences between the two African ape genera are basically attributable to differences in body size, in the same way that differences between the talapoin monkey and other cercopithecids have been attributed to decreased rates of growth in size with no dissociation of allometric trajectories (Shea, 1992).

The two examples above, in any case, highlight an interesting issue that cannot be much explored here: being simultaneously dependant on both CC and BM, encephalization cannot merely evolve by through changes in brain size (potentially related to cognition), but also to changes in body mass (potentially unrelated to it). There is a progressive decrease in brain size-body size allometric slopes during ontogeny: they are nearly isometric during fetal growth, negatively allometric during most of postnatal growth, and nearly inexistent after sexual maturation (Gould, 1975; Martin 1983, 1990; Martin & Harvey 1985). This is due to the fact that the central nervous system develops rapidly in comparison to other organs (Martin & Harvey, 1985), with the brain attaining its definitive size earlier than other parts of the body, which still grow for a great amount of time once brain growth has been considerably slowed down. It is therefore expected that, if changes in body size are selected, some correlated response in brain size would follow. This is because both traits share a common developmental basis, particularly during fetal and early postnatal development (Lande, 1979; Atchley *et al.,* 1984; Riska & Atchley 1985). This explanation, which has been empirically corroborated in giant transgenic mice (Shea *et al.,* 1987), was proposed for chimpanzees and gorillas by Shea (1983). According to him, the low interspecific allometric slopes among African apes could be explained if the same ontogenetic shifts that produce differences between small and large adults of the same species also had produced the evolutionary differences between adults of different species, which progressively emerge during ontogeny as a result of changes in later developmental stages. The same explanation proposed for gorillas has been invoked, in a reverse direction, for talapoin monkeys. These small cercopithecids display a paedomorphic morphology that has been interpreted as a correlated allometric consequence of a decrease in overall growth rates and terminal body mass, probably related to adaptation to leaping and/or insectivory but unrelated to cognition (Shea, 1992). Nevertheless, the purported higher encephalization in dwarfed taxa such as *Miopithecus*, or lower encephalization in larged-bodied taxa such as gorillas, only hold when higher-level metrics are employed. Bauchot & Stephan (1969) cautioned against interpreting higher-level encephalization metrics on cognitive grounds in taxa such as *Miopithecus* that have been likely miniaturized along the intraspecific scaling curve. The results reported by this paper on the correlation between lower-level metrics of encephalization and intelligence rankings suggest that gorillas and talapoins should not be considered exceptions, but rather extreme cases indicating that higher-level residuals are not reliable for making cognitive inferences. The use of lower-level residuals, however, does not completely resolve the case of gorillas by placing them at the same encephalization level than other great apes. This is because gorillas display a relatively low intelligence ranking (Johnson *et al.,* 2002; Deaner *et al.,* 2006), even when compared with some monkeys such as *Ateles*. Although Shea (1983, p. 46) noted that "*many studies do not support the claim (and widespread belief) that gorillas are less "intelligent" than chimpanzees*", the recent study by Deaner *et al.* (2006) do paradoxically confirm a lower degree of intelligence. This disagrees with lower-level encephalization metrics, according to which gorillas are not less encephalized than other great apes. This gorilla paradox is neither resolved by employing absolute brain size, since gorillas possess absolutely larger brains than other great apes. The intelligence score of gorillas, lower than expected on the basis of encephalization, brain size and body size, therefore remains unexplained and its interpretation must await future behavioral studies.

The present study further suggests on the basis of encephalization metrics that hylobatids tend to be somewhat more encephalized than average monkeys, which is confirmed by ANCOVA comparisons. On the basis of higher-level regressions, it had been previously noted that, in spite of their cognitive abilities intermediate between great apes and monkeys, hylobatids were more encephalized than some great apes, which was attributed to the (hypothetically) secondarily reduced body mass of the former (Begun, 2004; Begun & Kordos, 2004). This study, on the contrary, shows that there is no need to hypothesize that hylobatids are a dwarfed lineage, since their previously reported high degrees of encephalization merely resulted from a problem of grade confusion. Several authors have favored the hypothesis that hylobatids experienced a body size reduction during evolution, having evolved from larger-bodied, more great-ape-like ancestors (Pilbeam, 1996; Pilbeam & Young, 2004; Young & MacLatchy, 2004). It is certainly

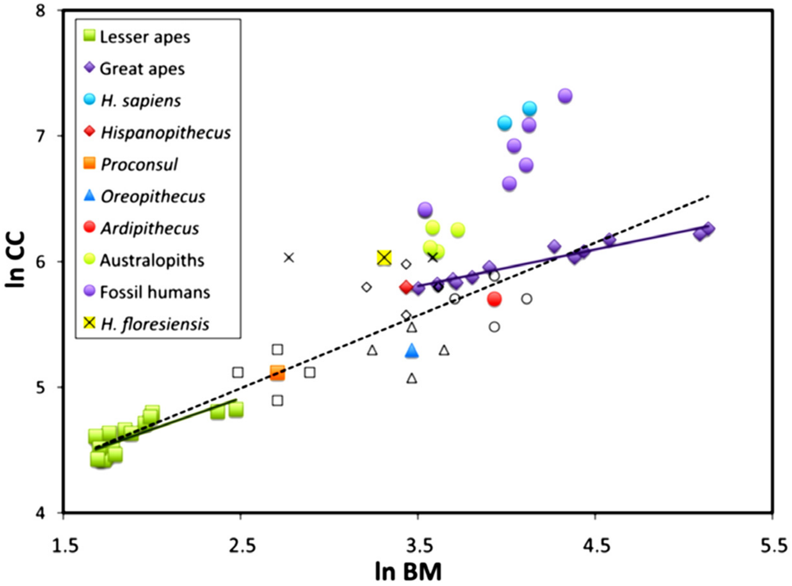

Fig. 5 – Brain size–body size allometric relationships in living and fossil apes and humans. Discontinuous line: living apes; solid lines: lesser apes and great apes separately. Note that all hominins are more encephalized than living great apes, with the exception of Ardipithecus. Among fossil apes, Dryopithecus displays a great-ape degree of encephalization, while both Proconsul and Oreopithecus are less encephalized, thus more closely resembling the hylobatid condition. The open symbols around each fossil ape taxon correspond to a 20% of uncertainty in BM and CC estimates, except in the case of H. floresiensis, where the box of uncertainty takes into account the maximum-minimum BM estimates published for this taxon.

conceivable that size reduction in hylobatids might have accompanied the adaptation to their acrobatic locomotor behaviors (ricochetal brachiation) that enable them to perform agile and rapid movements throught the canopy. If so, the lower encephalization (and associated cognitive abilities) of hylobatids as compared to great apes, instead of representing the primitive hominoid condition, might also be a reversal related to a secondarily-derived reduced body size. It has been hypothesized in the preceding subsection that, due to metabolical constraints, allometric grade shifts towards increased encephalization might be untenable until a certain body size threshold is crossed by whatever reason. That would predict that lineages that have experienced a phyletic size reduction (such as hylobatids according to some authors) would concomitantly experience an evolutionary decrease in both absolute and relative brain size, in spite of the associated cognitive disadvantages. Unfortunately, given the virtual lack of hylobatid fossil record, all these considerations must remain, for the time being, highly speculative.

Overall, although lower-level metrics fail to recover the exact pattern indicated by intelligence rankings, at least great apes clearly stand as more encephalized than other taxa (including hylobatids), hylobatids are no more encephalized than *Ateles*, and *Miopithecus* is one of the least encephalized haplorrhines. According to the evidence provided by extant taxa, therefore, there seems to be no doubt that the most significant enlargement of relative brain size in hominoid evolution, before the emergence of the bipedal hominins, must have taken place after the splitting between lesser and great apes. Hence, a major significant increase in encephalization and associated cognitive abilities can be inferred to have been involved in the origins of the great ape and human clade (Hominidae s.l.), but not of apes (Hominoidea) as a whole.

Encephalization in fossil hominoids

The correlation between encephalization and intelligence, when lower-level encephalization metrics are employed, provides a sound basis for paleobiological inferences of intelligence in fossil Miocene great apes and Plio-Pleistocene hominins (Fig. 5; see also Tab. 3). Of course, brain evolution in fossil apes and hominins cannot be entirely conceptualized as the evolution of relative brain size and concomitant allometric consequences. The lineage leading to *H. sapiens* has undergone a substantial change in both brain size and brain organization (Sherwood *et al.,* 2008), as shown for example by the widening of the frontal lobes in the genus *Homo* (Bruner & Holloway, 2010), which might be potentially associated to particular cognitive functions. Nevertheless, encephalization provides a first approximation to the inference of cognitive capabilities in fossil taxa. Of course, as previously noted by other authors (Radinsky, 1982; Rightmire, 2004; Falk, 2007), these inferences should be taken with great care, given uncertainties regarding brain size and/or body size estimates in fossil taxa. Nevertheless, interesting results emerge even when a degree of uncertainty in these estimates is taken into account (Fig. 5).

The fossil great ape *Hispanopithecus*, with estimates of 329 cm^3 and 31 kg, perfectly fits a modern great-ape degree of encephalization (ER_{GA} = 0.01), thus supporting the notion that increased cognitive capabilities were already present in the last common ancestor of the great ape and human clade (Begun, 2004). A great-ape degree of encephalization for this taxon was previously suggested by Kordos & Begun (1998) and Begun & Kordos (2004). However, the EQ ranges derived by Begun & Kordos (2004) for several haplorrhine groups largely overlap (cebids 1.38 – 4.79; cercopithecids 1.05 – 2.76; hylobatids 1.93 – 2.74; hominids 1.53 – 2.48). Thus, although Begun & Kordos (2004) suggested a great-ape level of encephalization for *Hispanopithecus*, the 2.35 EQ that they reported for this taxon is equivocal, since it might be equally considered to display a monkey-like or hylobatid-like degree of encephalization. On the contrary, the ER_{GA} derived in this paper for *Hispanopithecus* falls well within the great-ape range (-0.05 – 0.09), but does not overlap with either hylobatids (-0.87 – -0.57) or Old World monkeys (-1.37 – -0.46). As such, this is the first time that modern great-ape cognitive abilities can be inferred on a sound basis for a fossil great ape.

The results for *Hispanopithecus* contrast with those obtained for *Proconsul* (ER_{GA} = -0.46) on the basis of estimates of 167 cm^3 (Walker *et al.,* 1983) and 15 kg (Begun & Kordos, 2004), which are intermediate between extant lesser and great apes. There has been controversy around the encephalization of *Proconsul*, resulting not only from different estimates (compare Walker *et al.,* 1983 and Manser & Harrison, 1999 with Martin, 2000), but also from the uncertainty regarding whether higher (Walker *et al.,* 1983, 1984) or lower (Leutenegger, 1984) encephalization metrics should be employed. Walker *et al.* (1983), on the basis of an 11 kg estimate, suggested that *Proconsul* was more encephalized than modern monkeys of comparable size. These authors, however, employed a high exponent of 0.76, and accordingly they were unable to find significant differences in encephalization between apes and monkeys (Walker *et al.,* 1983, p. 526). This approach was criticized by Leutenegger (1984), who on the basis of the same estimates, but employing a 0.23 exponent, showed that *Proconsul* was situated on the upper end of the monkey range and below the “ape” level (in fact, “great ape”, because hylobatids were not taken into account). Later on, and on the basis of a high exponent, Martin (1990) concluded that the estimates published for *Proconsul* would yield an encephalization higher than in extant great apes, although he later suggested (Martin, 2000), on the basis of revised estimates of 200 cm^3 and 20 kg, that this taxon was on the encephalization range of modern chimpanzees and gorillas. More recently, Begun & Kordos (2004, p. 266), on the basis of 166 cm^3 and 15 kg estimates, concluded that the 1.94 EQ for *Proconsul* "is not especially hominoid-like", given the fact that this figure is below the great ape range.

In contrast to previously published papers, this study shows that *Proconsul* (ER_{GA} = -0.46) does not display either a monkey-like/hylobatid degree of encephalization - contra Leutenegger (1984) and Begun & Kordos (2004) - or a great-ape degree - contra Walker *et al.* (1983) and Martin (2000). Instead, *Proconsul* is intermediate between them, although closer to the hylobatid than to the great ape condition. This intermediate condition for *Proconsul* stands also when the estimates of Walker *et al.* (1983) or Martin (2000) are employed, which respectively yield ER_{GA} of -0.37 and -0.36, even more intermediate between hylobatids and great apes. This suggests that evolution towards an increased, great-ape-like encephalization might have been already under way during the Early Miocene (Smith & Walker, 1984), although it remains to be ascertained how the monkey-like encephalization degree of hylobatids, lower than that of *Proconsul*, should be interpreted. It is worth noting that while *Hispanopithecus* is on the lower end of the modern great-ape body size range, the body size of *Proconsul* is intermediate between hylobatids and extant great apes. Moreover, the reported results are coincident also with the few available life-history data for fossil apes (Kelley, 1997, 2002a; Kelley & Smith, 2003), according to which the putative pongine *Sivapithecus* already possessed and essentially modern, delayed life-history profile, whereas the stem hominoid *Afropithecus* from the Early Miocene would be somewhat intermediate in this regard. Overall, this suggests that the major encephalization shift concomitant with great ape origins was related to a body size increase and a slow-down of the life-history profile, although the direction of causality remains, for the time being, obscure.

The results for *Proconsul*, *Hispanopithecus* and extant great apes indicate that encephalization, after a significant increase associated to the origins of the great ape and human clade, could have remained quite stable amongst different great ape lineages, only to progressively accelerate during the evolution of the human lineage (Leutenegger, 1973; Pilbeam & Gould, 1974; Kappelman, 1996; Martin, 2000; Williams, 2002). The putative early hominin *Ardipithecus*, on the basis of the published estimates of 51 kg (Lovejoy *et al.,* 2009) and 300 cm^3 (Suwa *et al.,* 2009), displays a relatively low value of encephalization (ER_{GA} = -0.23). Absolute brain size in *Ardipithecus* roughly agrees with the lower value hypothesized by the last common ancestor of African apes and hominins (ca. 300-400 g; Sherwood *et al.,* 2008). Relative brain size would suggest that this taxon was somewhat less encephalized than extant great apes, although when the uncertainty in CC estimation is taken into account (i.e., a 20% increase in CC, close to the upper range of uncertainty of 300-350 cm^3 favored by Suwa *et al.,* 2009), it emerges that *Ardipithecus* might have merely displayed a great-ape degree of encephalization. In any case, these results clearly indicate that *Ardipithecus* would not have been more encephalized than extant great apes. To the latter regard, *Ardipithecus* differs from australopiths (*Australopithecus* and *Paranthropus*), which on the basis of their ER_{GA} range of 0.24-0.44 would have already displayed enhanced cognitive abilities as compared to great apes (Leutenegger, 1973; Pilbeam & Gould, 1974; McHenry, 1976, 1988; Kappelman, 1996; Williams, 2002). Thus, contrary to some recent reports (Falk, 2007), australopith brains where already larger than expected for great apes of their body mass. The results of this paper further confirm an encephalization increase concomitant with the origin of the genus *Homo* (McHenry, 1976; Kappelman, 1996), as well as an evolutionary trend towards increased encephalization within this genus (Pilbeam & Gould, 1974; contra Kappelman, 1996). Except for *H. floresiensis* (see later), all fossil human species are more encephalized (ER_{GA} range of 0.60-1.27) than australopiths, further displaying an evolutionary increase from *H. habilis* to *H. rudolfensis*, to *H. ergaster*, to *H. erectus*, to *H. heidelbergensis*, to *H. sapiens* and *H. neanderthalensis* (see Table 3). The results of this paper therefore contradict the notion (Ruff *et al.,* 1997), based on a 0.76 slope, that encephalization remained static between 1.8 and 0.6 Ma (see also Rightmire, 2004, for a detailed account of the encephalization increase between *H. erectus* and *H. heidelbergensis* and its likely relationship to increased technological skills). During the evolution of the genus *Homo*, the increase in encephalization is roughly accompained by a body size enlargement. However, in contrast to the great-ape encephalization shift, the human encephalization increase is not associated initially with a larger body size, thus requiring a proportionally greater amount of energy devoted to the brain, possibly thanks to dietary (Aiello & Wheeler, 1995) and/or locomotor (Isler & van Schaik, 2006) changes.

This paper also confirms previous studies (Harrison, 1989; Martin, 2000; Begun & Kordos, 2004), according to which the Late Miocene great ape *Oreopithecus* displays a low degree of encephalization as compared to living great apes. On the basis of 200 cm^3 and 32 kg estimates for a male specimen, the low encephalization of *Oreopithecus* (ER_{GA} = -0.50) is very similar to that of *Proconsul*. However, a reliable evolutionary interpretation of these results is hampered by the uncertain phylogenetic relationships of this fossil hominoid. If *Oreopithecus* is considered a relatively primitive taxon within the great-ape and human clade (e.g. Begun, 2002), its low encephalization could be interpreted as a primitive retention, just like in the stem hominoid *Proconsul*. The postcranial remains of *Oreopithecus*, however, rather suggest that this taxon must be interpreted as a hominoid of modern aspect (Pilbeam, 1996, 1997), perhaps descended from a *Hispanopithecus*-like ancestor (Moyà-Solà & Köhler, 1997; Harrison & Rook, 1997). If the latter hypothesis is correct, then the low encephalization of *Oreopithecus* must be interpreted as a secondary reduction, which is even favored by authors supporting the primitive status of this taxon (Begun & Kordos, 2004). This reduction of relative brain size in *Oreopithecus* has been attributed to relaxed cognitive selection pressures in an insular environment (Moyà-Solà & Köhler, 1997; Alba *et al.,* 2001). Surprising as it might seem from an anthropocentric perspective, this phenomenon has been repeatedly documented in domestic mammals (Kruska, 2005), as well as in extinct insular endemic taxa such as the bovid *Myotragus* (Köhler & Moyà-Solà, 2004; Palombo *et al.,* 2008). Although there is a general trend towards greater encephalization in primates and other mammals throughout the Cenozoic (Kruska, 2005; Shea, 2006), this does not rule out the possibility that encephalization may be reduced under particular ecological situations. Brain size reduction may be selectively advantageous under insularity conditions, given the energetic constraints and the lack of eutherian predators that characterize insular ecosystems (Köhler & Moyà-Solà, 2004; Niven, 2005, 2007; Köhler *et al.,* 2008). Given "*the costs of producing and maintaining a brain ... brain size should be secondarily reduced by natural selection whenever the costs outweigh the benefits*" (Safi *et al.,* 2005: p. 283), i.e. when energy and resources are limiting and/or when demands on neural processing are reduced (Niven, 2005). A relationship between smaller brain size and a poor quality diet has been found in orangutans (Taylor & van Schaik, 2007), thus giving more plausibility to a brain size reduction in an endemic, insular hominoid such as *Oreopithecus*.

The case of *Oreopithecus*, at a first approximation, gives some plausibility to the putative fossil human species *H. floresiensis*, which displays a remarkably small CC of about 400 cm^3 (Brown *et al.,* 2004; Falk *et al.,* 2005a). This plausibility, however, does not pass a close scrutiny (see also Köhler *et al.,* 2008). The original describers of *H. floresiensis* attributed the small body size and brain size of this taxon to insular dwarfing (Brown *et al.,* 2004; Morwood *et al.,* 2004), albeit recognizing that brain size reduction might have taken place beyond the mere scaling effects resulting from body size reduction alone (Brown *et al.,* 2004). The status of *H. floresiensis* as a distinct species from *H. sapiens* has been criticized by several authors, usually on the basis that the type specimen belongs to a pathologically microcephalic individual (Weber *et al.,* 2005; Martin *et al.,* 2006; Jacob *et al.,* 2006; Richards, 2006; Hemmer, 2007; Köhler *et al.,* 2008); several explanations, such as primary growth hormone insensitivity (Hershkovitz *et al.,*

2007) or cretinism (Obendorf *et al.,* 2008) have been proposed. Other authors, on the contrary, maintain the validity of the species (Morwood *et al.,* 2005; Falk *et al.,* 2005a,b, 2006, 2009a,b; Argue *et al.,* 2006; Niven, 2007; Groves, 2007; Gordon *et al.,* 2008), usually by arguing that it was an insular dwarf and/or closely related to an early *Homo* species. While Brown *et al.* (2004) argued that encephalization in *H. floresiensis* could overlap with some fossil human species (other than *H. sapiens*), Falk *et al.* (2006) favored a great ape/australopithecine degree of encephalization. Niven (2007), on the basis of an allometric regression for placental mammals as a whole, and several body mass estimates for the specimen, further reiterated that *H. floresiensis* displays a large relative brain size, perhaps even closer to *H. erectus* and *H. sapiens* than to australopiths.

The latter view is contradicted by the results of this paper, which indicate that *H. floresiensis* was only slightly more encephalized ($ER_{GA} = 0.28$) than extant great apes, close to the lower range of australopiths, and clearly less encephalized than early *Homo* species. In particular, *H. floresiensis* displays a degree of encephalization fully comparable to that of early australopiths, and hence lower than the least encephalized *Homo* species (even when the minimum and maximum body mass estimates are taken into account). As shown by *Miotragus* and other insular mammals, such a reduction of encephalization would be conceivable under insularity conditions (Niven, 2005, 2007; Weston & Lister, 2009). However, on the basis of intraspecific brain-body size scaling relationships within fossil and living humans, it is incompatible with mere body size dwarfism (Shoenemann & Allen, 2006). The latter would imply a higher (instead of lower) relative brain size, so that a hypothetically reduced encephalization in *H. floresiensis* would require, as implicitly recognized by Brown *et al.* (2004), specific selection for brain size reduction, as in *Myotragus* and *Oreopithecus*. It is unclear why a behaviorally plastic and omnivorous human species would have suffered from the same energetic and dietary constraints that are execerted upon larger herbivores under insularity conditions (Harrison, 2006). More dramatically, given the correlation found in this paper between intelligence and encephalization among haplorrhine primates, the low degree of encephalization of *H. floresiensis* would indicate a relatively low (australopith-like) degree of intelligence. A drastic reduction of relative brain size at the expense of some cognitive abilities is conceivable for an insular ape such as *Oreopithecus*, but as noted by Köhler *et al.* (2008) it is completely at odds with the advanced lithic technology that has been attributed to *H. floresiensis* (Morwood *et al.,* 2004) - and the hunter-gatherer lifestyle that can be inferred from it. Overall, the low encephalization of this putative extinct human relative, together with cranial and postcranial abnormalities that would have severely compromised survival (Jacob *et al.,* 2006; Köhler *et al.,* 2008), and the weak evidence supporting insular conditions (Köhler *et al.,* 2008), strongly favor the hypothesis that *H. floresiensis* is not a valid species (Jacob *et al.,* 2006; Hemmer, 2007; Köhler *et al.,* 2008).

Conclusions

Different aspects of great ape biology and ecology have been discussed in relation to cognitive abilities and/or encephalization (see reviews in Ward *et al.,* 2004; Russon & Begun, 2004; Potts, 2004; Shea, 2006): positional repertoire, diet and foraging strategies, sociality, predation risk, metabolism, and life history. This paper, however, does not intend to explore the selective causes underlying evolutionary changes in intelligence and/or encephalization. Rather, this paper focuses on the relationship between encephalization and intelligence amongst extant great apes and other haplorrhine primates. The aim is to test the reliability of paleobiological inferences of cognition made on the basis of relative brain size. The fact that intelligence (as a measure of domain-general cognitive abilities) can be explained on the basis of a single factor (Johnson *et al.,* 2002; Deaner *et al.,* 2006, 2007) suggests that the primate brain functions in a highly coordinated and integrated way, i.e. a largely non-modular nature of the brain. That would imply that, even if selection for increased intelligence is restricted to a particular type of cognitive ability, a generalized brain size increase would follow as a result of structural and/or developmental constraints (Finlay *et al.,* 2001). Eventually, this might result in the enhancement of other cognitive abilities not directly under selection. From an epistemological perspective, this would complicate or perhaps even preclude the determination of the original target(s) of selection underlying relative brain size increase in a particular lineage. At the same time, however, this circumstance provides a plausible theoretical basis for making meaningful paleobiological inferences on cognitive abilities from neuroanatomical variables such as relative brain size.

The results of this paper permit to refute the hypothesis being tested - that encephalization can be employed as a good proxy for intelligence - only when higher-level encephalization metrics are employed. The correlation between intelligence and lower-level metrics indicates that low interspecific allometric exponents (close to those found in intraspecific comparisons) do reflect functional equivalence in cognition among closely-related taxa differing in body size, thus providing support to the neural traffic hypothesis. According to this, the higher allometric slopes derived at increasingly higher taxonomic levels would result from a problem of grade confusion, i.e. allometric grade shifts in encephalization coupled with size differences among several subgroups. Higher slopes around 0.67-0.75, hence, do not reflect functional cognitive equivalence, although they may stem from an underlying structural constraint related to energy-availability and/or life history. This is supported by the correlation of encephalization and intelligence with respect to body size, suggesting that major shifts towards higher encephalization required crossing a body size threshold. Overall, the results of this paper therefore vindicate a long tradition in paleobiological investigation, which has mostly relied on encephalization for making cognitive inferences in fossil taxa. At the same time, however, these results urge caution against employing encephalization metrics indiscriminately, since only when computed at lower-taxonomic levels (or on the basis of low allometric exponents) encephalization enables to make biologically meaningful inferences of intelligence. This provides a sound basis for reviewing hominoid cognitive evolution on the basis of encephalization estimates in extant and selected fossil taxa.

Lower-level residuals do not recover the exact intelligence ranking reported for ape genera, but they clearly indicate that great apes are significantly more encephalized than hylobatids, as confirmed by ANCOVA comparisons. This is in agreement with behavioral and psychobiological studies, which indicate that great apes, uniquely among non-human primates, show causal and logical reasoning, planning, imitation, intentional deception, self-awareness and rudimentary comprehension of others' mental states (Russon, 1998; Potts, 2004; Subiaul, 2007). With some exceptions (Williams, 2002; Shea, 2005), these cognitive differences between great apes and hylobatids had not been previously found to be reflected in corresponding differences in encephalization (e.g. Deaner *et al.,* 2007; Isler *et al.,* 2008), mainly because these studies did not consider the allometric grade shift between the two groups. Overall, the results obtained in this paper for fossil and living apes suggest that cognitive abilities significantly improved during two distinct phases in hominoid evolution: during the Miocene, being associated with the origins of the great ape and human clade; and second, by the Plio-Pleistocene, being associated with the emergence of habitual terrestrial bipeds (australopiths) and later being further accelerated from the emergence of the genus *Homo* onwards. Whereas the major shift in encephalization during the origins of the great-ape and human clade can be associated with an increase in body size and/or an extended life-history profile, the hominin shift in encephalization is more clearly related to delayed maturation.

Although the slow life-history profile of great apes and humans may be related to their higher encephalization, it is currently unclear whether the former should be considered a direct consequence of selection acting on cognition, or rather a necessary prerequisite that originally evolved for a different reason and was later co-opted. High levels of encephalization require an extended life-history profile, especially a long gestation period (necessary for such a large brain to grow) and extended infantile and juvenile periods (given the high learning requirements). As noted by Shea (2006), this is likely to be related to evolution in stable tropical environments, with predictable resource distribution, competition levels and mortality schedules. This applies to primates in general, and to great apes in particular; but even in this context, the selective reasons underlying the evolutionary increase of great ape cognitive abilities, as compared to hylobatids and other primates, are currently unclear. Russon (1998) suggested that selection pressures related to arboreal foraging for difficult foods had played a preponderant role, and Potts (2004) further suggested that a persisting frugivory-forest bias in this clade had placed great apes in a sort of 'cognitive trap'. According to the latter hypothesis, great apes would "*have evolved an exceptional degree of intelligence that enables them to maintain their reliance on wooded habitats in the face of strong environmental variability*", which nevertheless makes them to be "*highly susceptible to extinction as these habitats have declined and continue to be eliminated*" (Potts 2004, p. 225). This hypothesis is supported by encephalization in *Hispanopithecus*, which suggests that, from the early Late Miocene onwards, cognitive abilities in great apes might have remained constant in spite of increasing environmental deterioration. Ultimately, the high behavioral plasticity of great ape populations might have finally resulted in a low evolvability in front of drastic environmental changes, with most lineages simply becoming extinct or being restricted to a few refuges where their preferred habitats still remain. Only hominins, and especially the genus *Homo*, would have ultimately managed to escape from the great-ape cognitive trap, by progressively becoming more and more encephalized. This, together with innovative locomotor behaviors (terrestrial bipedalism), would have allowed fossil humans to survive and diversify into new habitats, at a time when the environmental conditions to which their great ape ancestors had been so well adapted were dramatically changing.

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