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Brief Communication: Endocranial Volumes in an Ontogenetic Sample of Chimpanzees From the Taï Forest National Park, Ivory Coast

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ABSTRACT Ontogenetic samples of endocranial volumes (EVs) from great apes and humans are critical for understanding the evolution of the brain growth pattern in the hominin lineage. However, high quality ontogenetic data are scarce, especially for nonhuman primates. Here, we provide original data derived from an osteological collection of a wild population of *Pan troglodytes verus* from the Taï Forest National Park, Ivory Coast. This sample is unique, because age, sex, and pedigree information are available for many specimens from behavioral observations in the wild. We scanned crania of all 30 immature specimens and 13 adult individuals using high-resolution computed tomography. We then created virtual casts of the bony braincase (endocasts) to measure EVs. We also measured cranial length, width, and height and attempted to relate cranial distances to EV via regression analysis. Our data are consistent with previous studies. The only neonate in the sample has an EV of 127 cm^3 or 34% of the adult mean. EV increases rapidly during early ontogeny. The average adult EV in this sample is 378.7 ± 30.1 cm^3. We found sexual dimorphism in adults; males seem to be already larger than females before adult EV is attained. Regressions on cranial width and multiple regression provide better estimates for EV than regressions on cranial length or height. Increasing the sample size and compiling more high quality ontogenetic data of EV will help to reconcile ongoing discussions about the evolution of hominin brain growth. Am J Phys Anthropol 147:319–325, 2012.

Ontogenetic data of endocranial volumes (EVs) from chimpanzees are rare. Here, we present a small but well-documented ontogenetic sample of EVs of chimpanzees. The Taï chimpanzee osteological collection originates from a population of wild *Pan troglodytes verus* individuals living in the Parc national de Taï, Côte d'Ivoire. These chimpanzees have been observed systematically since the 1980s (Boesch and Boesch-Achermann, 2000). Therefore, dates of birth and death (and thereby calendar age), sex, behavioral data, and genetic relationships are known for many individuals (e.g., Boesch and Boesch-Achermann, 2000; Vigilant et al., 2001; Boesch et al., 2006; Smith et al., 2010; Smith and Boesch, 2011).

Ontogenetic samples of EVs of chimpanzees (as well as humans and other apes) are important because they serve as comparative data in evolutionary analyses of hominin brain growth. Understanding the pattern of brain growth is critical for a wide range of interrelated topics including the evolution of cognition and behavior (e.g., Smith and Tompkins, 1995; Fairbanks, 2000; Langer, 2000; Coqueugniot et al., 2004), life history (e.g., Martin, 1983; Harvey et al., 1987; Martin, 1996; Leigh, 2004; Leigh and Blomquist, 2007), diet and energy allocation (e.g., Aiello and Wheeler, 1995; Leonard and Robertson, 1997; Leonard et al., 2003), and childbirth (e.g., Trevathan, 1987, 1996; Rosenberg and Trevathan, 2001, 2002; Ponce de León et al., 2008; Weaver and Hublin, 2009). Despite decades of research on primate brain growth, the extent and biological significance of the differences in brain development between humans and chimpanzees are still controversially discussed. Although most researchers agree today that chimpanzee neonates have proportionally larger brains than human newborns, it is unresolved how much they differ (Schultz, 1940, 1941; Jordaan, 1976; Gould, 1977; Passingham, 1982; Martin, 1983; Dienske, 1986; Smith and Tompkins, 1995; Coqueugniot et al., 2004; Leigh, 2004; DeSilva and Lesnik, 2006, 2008; Hublin and Coqueugniot, 2006; but see also Fragaszy et al., 2004; Kennedy, 2005; Vinicius, 2005). Moreover, there is long-standing debate as to the importance of possible species differences in the duration of brain growth (Vrba, 1998; Rice, 2002; Coqueugniot et al., 2004; Leigh, 2004, 2006; Hublin and Coqueugniot, 2006; Robson and Wood, 2008). These controversies are partly rooted in the scarcity of high quality ontogenetic data. For chimpanzees, many studies rely on brain weight data collected at the Yerkes National Primate Research Center (e.g., Herndon et al., 1999; DeSilva and Lesnik, 2006, 2008; Robson and Wood, 2008). Brain weight, however, cannot be measured for fossil hominins as brains are not preserved in the fossil record. The variable that can be also obtained for fos-

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sils is EV. Ontogenetic samples (rather than single values) of EV, however, are rarely available for extant species. Sometimes, brain weights are converted to EVs using conversion factors based on the specific gravity of brain tissue (e.g., Hofman, 1983). However, this adds a source of possible error (see Hublin and Coqueugniot, 2006). Moreover, there is evidence that the relation between brain volume and EV changes with age (at least in old age, see Wanifuchi et al., 2002).

The aim of this article is to make data of EV and standard cranial distances derived from the cross-sectional growth series of *Pan troglodytes verus* from the Taï chimpanzee collection available to other researchers. We briefly discuss the brain growth pattern and sexual dimorphism of chimpanzees based on this sample. Finally, we provide and discuss regression formulas for predicting EV from standard cranial distances.

MATERIAL AND METHODS

When chimpanzees of the Taï National Park populations die, their cadavers are recovered, identified, and buried to facilitate decay. The skeletal material is then transported to the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany (formerly to the University of Zürich, Switzerland) after CITES approval. The osteological collection currently comprises 75 specimens; for 70 individuals, cranial remains have been recovered (Tab. 1). Forty of those are adults (individuals with fully erupted maxillary M3s, age group A in Table 1). Defining adulthood in this way, we make our data comparable to fossil and museum specimens, but it is worth noting that this dental definition of adulthood does not necessarily conform to adulthood as seen from a behavioral perspective. The calendar ages of 16 of the 30 immature individuals (maxillary M3s not erupted) are known because dates of birth and death were recorded (at least the month and year), and the ages of six additional immature individuals can be approximated using estimates of the year of birth (Boesch and Boesch-Achermann, 2000). For detailed information on identities and ages of individuals, please see Boesch and Boesch-Achermann (2000) and Smith et al. (2010).

We scanned 43 crania of this collection using a BIR ACTIS 225/300 micro computed tomography (CT) scanner at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. CT data were reconstructed with a resolution between 0.065 and 0.125 mm (isovoxels) and resampled to yield a voxel size between 0.2 and 0.25 mm. The CT sample includes all 30 immature individuals and 13 adults of the collection.

CT images were used to generate virtual endocasts by a combination of two- and three-dimensional semiautomated segmentation in Avizo (Visualization Sciences Group) following the protocol described in our previous work (Neubauer et al., 2009, 2010; Gunz et al., 2010): 1) segmentation of bone by setting a gray value range based on the half maximum height method (Spoor et al., 1993), 2) generation of an area within the endocranial cavity that is completely enclosed by artificially expanding segmented bone via adding a predefined number of voxel layers and thereby closing small foramina and sutures, as well as manual segmentation to close the foramen magnum, 3) defining this enclosed area as endocast and expansion of this endocast by the same amount as bone was expanded in step 2 so that the boundary of the segmented endocast matches the boundary between bone and air-filled endocranial cavity. The volume of these endocasts (endocranial volume; EV) was measured with the built-in volume measurement tool of Avizo. A virtual endocast of one individual is illustrated in Figure 1. Using calipers, we measured three cranial distances on all original crania of the collection ($n = 70$): maximum cranial length (the distance between glabella and opisthocranion; *L*), maximum cranial width (the distance between the most projecting points on the parietal bones in occipital view; *W*) and basion-bregma height (*H*). For the CT sample ($n = 43$), we measured these distances also on the electronic representations of the crania using the distance measurement tool of Avizo. Individuals are listed in Table 1, including sex, age, age group (dental stage), and obtained measurements. An online version of this table (http://www.eva.mpg.de/evolution/files/downloads.htm) will be continuously updated as new specimens become available.

We used linear regression to predict EV based on cranial length, width, and height. The EV of all specimens that have not been CT scanned yet ($n = 27$) was estimated using the obtained regression functions. To examine endocranial growth trends, we plotted EV against age. We also computed proportional endocranial volume (PEV), i.e., EV as a percentage of the adult mean EV.

RESULTS

Measured cranial distances (*L*, *W*, and *H*) and EV as well as estimated EV for every individual are summarized in Table 1 and illustrated in Figure 3. The average adult EV of this sample is 378.7 cm^3 (S.D.= 30.1, $n = 13$), ranging from 328 to 434 cm^3 (87 to 115% of the adult mean). For female and male adults, the mean is 367.5 ± 28.5 cm^3 ($n = 6$) and 395.5 ± 25.4 cm^3 ($n = 6$), respectively. The difference between sexes does not reach statistical significance at $\alpha = 0.05$ but shows a tendency of a mean difference (permutation test with replacement and original group sizes, 10,000 permutations, $P = 0.09$). The two youngest individuals of the sample have an EV of 127 cm^3 (specimen 11787, a few days old) and 221 cm^3 (specimen 15015, 66 days old). PEV (i.e., EV related to the average adult EV) of these two individuals is 34% and 58%, respectively. The sample includes only a few very young individuals. However, they indicate a rapid increase of EV early in life (see Fig. 3). The oldest immature individual that has an EV below the adult range of 328 to 434 cm^3 is 5.19 years old (specimen 11783, 315 cm^3).

Differences between cranial distances measured with calipers on the original crania and on CT scans are equal to or less than 1 mm (with two exceptions, see Table 1). Mean differences are 0.4, 0.6, and 0.4 mm for *L*, *W*, and *H*, respectively. These small differences indicate a low measurement error. To compute the regressions, we used measurements obtained with calipers, as they are available for the entire sample, not only the CT sample. Relationships between cranial distances and EV are illustrated in Figure 2. Pearson's correlation coefficients (*r*) between cranial distances and EV (all variables transformed to natural logarithms - [ln]) are 0.89 (*L*), 0.96 (*W*), and 0.92 (*H*). The two youngest individuals of the sample (specimens 11787 and 15015) have far smaller *L*, *W*, *H*, and EV than the rest of the sample and greatly influence correlation coefficients and regressions (dashed line in Fig. 2). The solid regression line in Figure 2 was computed without these two specimens; the corresponding correlation coefficients are 0.59 (*L*),

TABLE 1. Taï chimpanzee sample of EVs

No	ID	sex	Age (years)	Age group	Length (mm)		Width (mm)		Height (mm)		Cranial capacity (cm^3)		
											Measured[a]	Estimated[b]	Estimated[c]
11775	Agathe	f	15.39	A	131	(131)	101	(102)	89	(89)	410	410.1	410.0
11776	Ariane	f	12.38	J3	122	(123)	97	(98)	88	(88)	364	378.3	374.2
11777	Bambou	m	2.13	J1	115	(115)	93	(94)	82	(80)	340	340.7	340.3
11778	Bijou	f	18.93	A	130	(130)	97	(97)	88	(87)	358	376.0	374.2
11779	Clyde	m	12.57	J3	130	(130)	99	(99)	85	(85)	391	387.9	391.9
11780	Fanny	f	25.39	A	127	(126)	94	(95)	84	(85)	328	347.7	348.6
11781	Kendo	m	25.39	A	129	(128)	98	(98)	88	(88)	381	384.4	383.0
11782	?	m	?	J3	118	(118)	95	(95)	89	(89)	350	364.8	357.0
11783	Manon	f	5.19	J2	113	(113)	92	(92)	82	(82)	315	333.7	332.1
11784	?	?	?	A	125	(125)	94	(94)	87	(87)	345	352.3	348.6
11786	Ondine	f	38.41	A	124		94		90			356.4	348.6
11787	Ovide	m	0.01	N	75	(75)	67	(66)	54	(55)	127	156.8	162.4
11788	Piment	f	3.76	J1	114	(114)	99	(100)	85	(86)	389	392.8	391.9
11789	Gipsy?	?	?	A	128		100		88			401.2	400.8
11790	Tina	f	9.61	J3	124	(125)	94	(94)	82	(82)	333	345.8	348.6
11791	Goshu	f	6.45	J2	121	(121)	98	(99)	81	(81)	364	376.5	383.0
11792	Zerlina	f	12.3	J3	126	(125)	100	(101)	82	(82)	360	392.7	400.8
11794	?	f	?	A	130		99		86			389.4	391.9
11795	?	m	?	A	136		101		94			416.0	410.0
11796	?	m	?	J3	125	(125)	97	(97)	87	(87)	355	376.0	374.2
11797	?	?	?	J3	120	(120)	94	(95)	83	(82)	352	348.3	348.6
11798	?	?	?	J2	114	(115)	89	(90)	77	(77)	311	304.9	308.2
11800	Kiri	f	22.62	A	128	(129)	97	(96)	87	(88)	373	375.2	374.2
11903	Fitz	m	19.47	A	135	(135)	101	(101)	91	(91)	434	411.9	410.0
12175	Hector	m	5.69	J2	122	(122)	98	(99)	85	(86)	388	382.1	383.0
12176	?	m	?	A	131		101		90			411.6	410.0
13430	?	m	?	A	131	(131)	99	(99)	88	(88)	382	392.0	391.9
13432	Léonardo	m	1.77	J1	110	(111)	94	(95)	83	(83)	372	351.2	348.6
13433	Lefkas	m	7.61	J2	124	(125)	99	(100)	86	(87)	402	391.2	391.9
13434	Loukoum	f	26.87	A	132		100		86			397.0	400.8
13435	Mkubwa	m	40.16	A	137		102		90			418.3	419.2
13436	?	f	?	A	132		100		91			404.4	400.8
13437	Kana	f	11.39	J3	123	(124)	100	(100)	90	(90)	401	405.7	400.8
13438	?	f	?	A	130		95		91			364.0	357.0
13439	Castor	f	22.88	A	129	(129)	99	(98)	87	(86)	351	391.1	391.9
14991	Endora	f	7.96	J2	126	(126)	97	(97)	88	(87)	362	377.1	374.2
14992	?	m	?	J2	117	(118)	93	(94)	82	(82)	345	340.1	340.3
14993	Ophélia	f	0.74	NJ1	106	(106)	88	(88)	75	(75)	296	297.4	300.4
14994	?	f	?	A	134		97		90			377.6	374.2
14995	Oreste	m	5.24	J2	124	(123)	97	(98)	86	(87)	423	374.9	374.2
14996	?	f	?	A	126		90		88			322.8	316.0
14997	?	f	?	A	132		99		92			397.4	391.9
14999	Haraka?	f	?	A	134		102		87			414.7	419.2
15000	?	?	?	NJ1	111	(111)	90	(91)	77	(77)	332	312.9	316.0
15001	Vénus	f	26.92	A	136		98		89			383.8	383.0
15002	?	f	?	A	128		92		86			334.8	332.1
15003*	?	?	?	NJ1			82	(81)					256.1
15004	Goma	f	28.39	A	132		100		87			398.5	400.8
15005	Max	m	6.44	J2	121	(121)	96	(97)	84	(84)	376	365.0	365.6
15006	?	?	?	A	132		99		86			388.8	391.9
15007	Janine	f	6.42	J2	125	(125)	96	(97)	85	(86)	391	365.2	365.6
15008	Nérone	m	?	A	137	(137)	98	(99)	90	(90)	420	385.0	383.0
15009	?	?	?	A	128		94		85			348.8	348.6
15010	?	?	?	?	126	(126)	103	(103)	85	(85)	457	422.5	428.5
15011	Noah	m	6.63	J2	122	(123)	99	(99)	85	(85)	406	390.3	391.9
15012	Léo	m	18.64	A	135	(135)	96	(96)	89	(88)	386	368.0	365.6
15013	Candy	f	?	A	130	(130)	98	(97)	87	(88)	385	382.7	383.0
15014	Vasco	m	?	A	128		96		98			381.6	365.6
15015	Isha's baby	?	0.18	N	94	(96)	78	(79)	63	(63)	221	221.3	228.8
15016	?	?	?	adult	137		100		94			407.2	400.8
15017	?	?	?	adult	130		99		86			389.4	391.9
15018	?	?	?	A	130		96		87			366.6	365.6
15019	Aramis	m	?	A	132	(132)	96	(95)	88	(88)	370	367.4	365.6
15020	Dorry	f	9.98	J3	124	(124)	98	(97)	84	(85)	360	380.1	383.0
15021	Gargantua	m	10.16	J3	120	(120)	94	(94)	85	(85)	353	351.0	348.6
15022	?	?	?	adult	121		91		86			329.1	324.0
15023	Rubra?	f	37.9	A	134		100		93			406.6	400.8
15024	?	?	?	A	138		101		95			416.8	410.0
15025	?	?	?	adult	134		101		90			410.7	410.0
15026	?	?	?	A	132		99		91			396.0	391.9

For cranial distances (length, width, and height), measurements from original crania are listed with measurements from CT scans in brackets. Age groups: N, no teeth erupted; NJ1, incomplete deciduous dentition; J1, complete deciduous dentition; J2, M1 erupted; J3, M2 erupted; A, M3 erupted (adults).

[a] measured from virtual endocast.

[b] estimated from multiple regression.

[c] estimated from regression on width.

* Specimen 15003 is preserved only by frontal, parietal and occipital bones so that EV could be estimated only based on the regression on width.

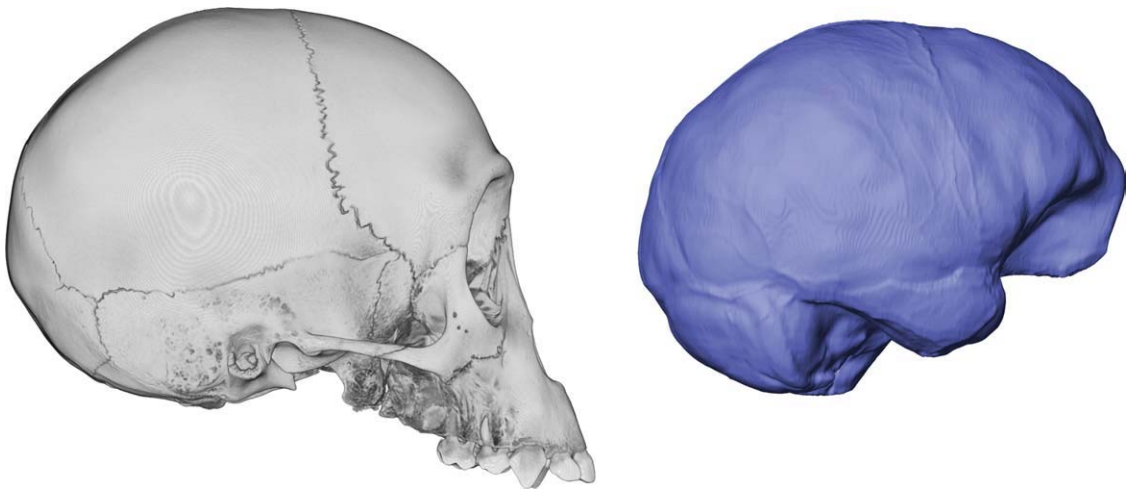

Fig. 1. An immature Taï chimpanzee: three-dimensional representation based on CT scans (left) and its virtual endocast (right). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

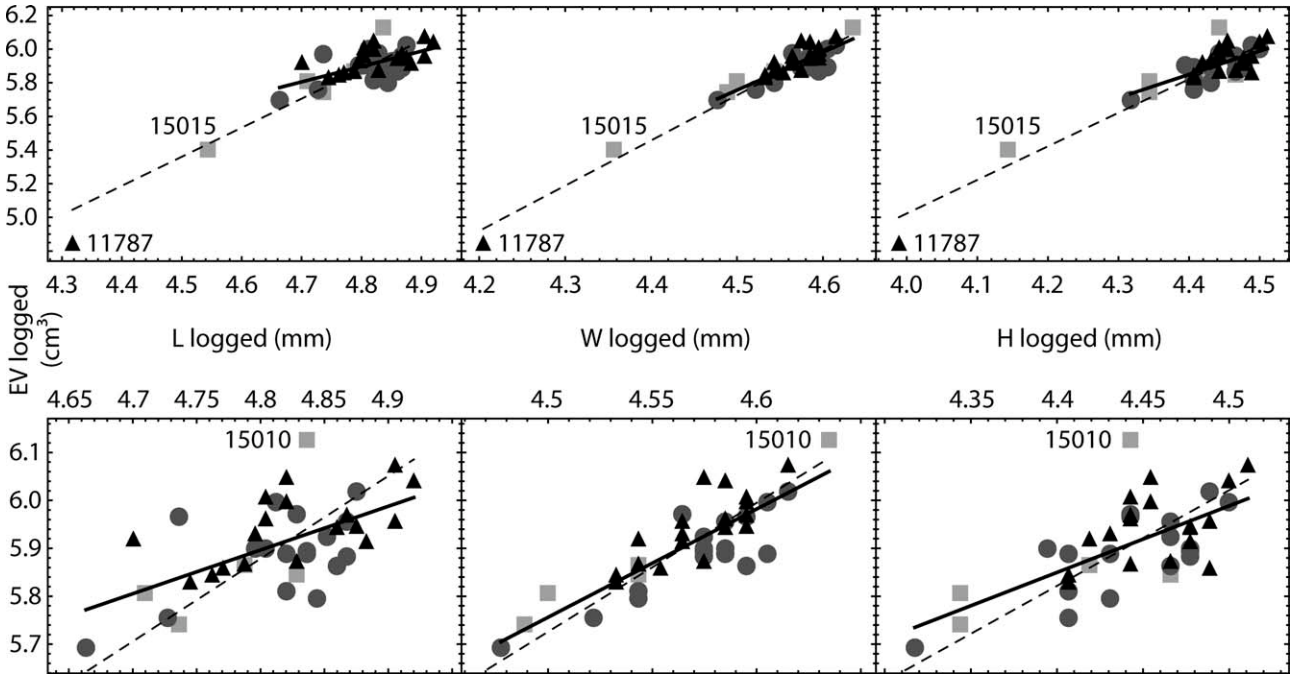

Fig. 2. Relationships between cranial distances and endocranial volume. top row from left to right: ln(L) vs. ln(EV), ln(W) vs. ln(EV), ln(H) vs. ln(EV), bottom row: close-ups without the two smallest individuals (specimens 11787 and 15015). Females (dark gray circles), males (black triangles), indeterminate sex (light gray squares). Least squares regression line based on entire sample (dashed) and the sample excluding the two smallest individuals (solid). Specimens that the text refers to are labeled with their catalogue number.

0.84 (W), and 0.66 (H). Regression equations fitted to the data (excluding specimens 11787 and 15015) are:

$$\ln(\mathrm{EV}) = 1.51789 + 0.912207\ \ln(L) \quad (R^2 = 0.34)$$
$$\ln(\mathrm{EV}) = -4.39926 + 2.25678\ \ln(W) \quad (R^2 = 0.71)$$
$$\ln(\mathrm{EV}) = -0.264154 + 1.38951\ \ln(H) \quad (R^2 = 0.43)$$
$$\ln(\mathrm{EV}) = -4.56253 - 0.0963455\ \ln(L) + 2.07865\ \ln(W) + 0.324265\ \ln(H)\ (\text{adjusted } R^2 = 0.69)$$

Because coefficients of determination (R^2) for the regression based on L and H are low, we only used the linear regression of EV on W and the multiple regression for estimating EVs of the 27 specimens for which CT data were not available. The average estimated EV of these 27 adult individuals is 383.6 ± 29.2 cm^3 (estimated based on W) and 386.3 ± 27.8 cm^3 (estimated based on L, W, and H). Estimations of EVs of these not yet scanned individuals did not change considerably when regressions were based on cranial distances obtained digitally, with calipers, or the mean of both. When we increased the sample sizes by including the estimated EVs in the adult sample (n = 19 females and 10 males), male adult chimpanzees had significantly higher

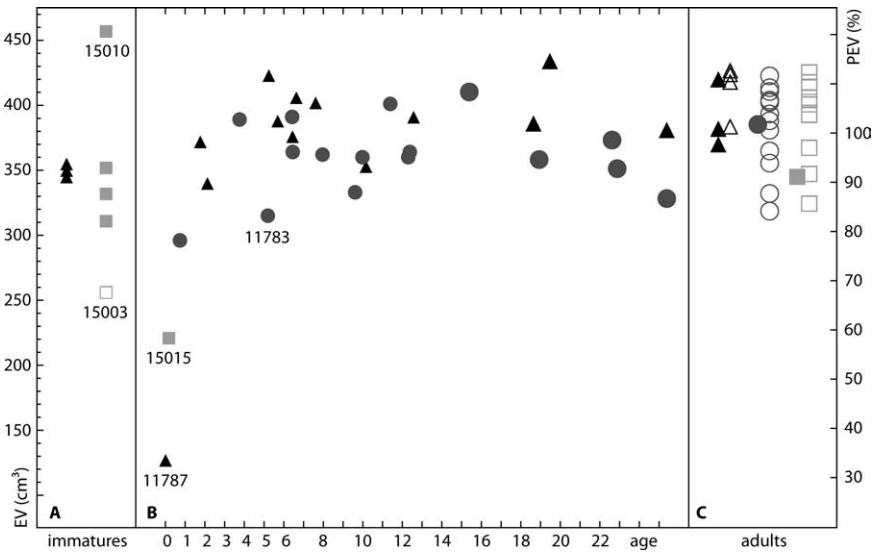

Fig. 3. Relationship of endocranial volume and age. (**A**) EV of immature individuals, unknown age. (**B**) EV of individuals with known age. (**C**) EV of adult individuals, unknown age. Females (dark gray circles), males (black triangles), indeterminate sex (light gray squares). Immature individuals, i.e., M3 not erupted (small symbols), adult individuals (large symbols). EVs estimated via multiple regression (open symbols). Specimens that the text refers to are labeled with their catalogue number. EV estimate of specimen 15003 based on regression of EV on *W*.

TABLE 2. EVs according to age groups in comparison to Zuckerman's (1928) data

	This study			Zuckerman 1928		
Age group	Mean	S.D.	*n*	Mean	S.D.	*n*
N	174	66.5	2			0
NJ1	314	25.5	3	340	0	2
J1	367	24.9	3	307.8	33.2	9
J2	371.2	36.3	11	350.5	27.2	11
J3	361.9	20	10	375.7	46	7
A	378.7	30.1	36	384.5	41	61

Age groups: N, no teeth erupted; NJ1, incomplete deciduous dentition; J1, complete deciduous dentition; J2, M1 erupted; J3, M2 erupted; A, M3 erupted (adults).

EVs than female adults (400.1 ± 22.1 cm^3 vs. 376.4 ± 28.3 cm^3, permutation test with replacement and original group sizes, 10,000 permutations, $P = 0.03$).

DISCUSSION

We presented original data of EV obtained from the cross-sectional sample of the Taï Forest chimpanzees; a sample unique because additional information (most importantly age) has been recorded for many individuals while they were observed in the wild during life.

The only neonate of this sample (specimen 11787) has an EV of 127 cm^3, corresponding to 34% of the adult EV in this sample. Previous literature reported a similar EV of 128 cm^3 for one neonate (Schultz, 1941). Another value of 171 cm^3 (Schultz, 1940) often quoted as a neonatal EV was based on an individual that was already 74 days old (Vinicius, 2005; DeSilva and Lesnik, 2006; Hublin and Coqueugniot, 2006). PEV of the Taï neonate (34%) is smaller than 42% computed based on EVs of three chimpanzees up to 19 days of age (Hublin and Coqueugniot, 2006). It is also at the lower range of neonatal proportional brain size of 40.1 ± 5.7% computed based on brain weights (based on 22 chimpanzees up to 11 days old; DeSilva and Lesnik, 2006). This individual died the same day its mother died. It is, therefore, unlikely that its health condition caused a relatively small brain size, assuming that the mother's course of disease did not influence prenatal brain growth. However, using the average adult value to assess the PEV of dead immature individuals in cross-sectional studies results in an exaggerated variation of this ratio when extreme values of the EV are considered (see comment in Hublin and Coqueugniot, 2006). Therefore, PEV of one single neonate (specimen 11787) should not be overinterpreted: this individual could have grown to be an adult with a relatively small EV that is well below the adult average and, therefore, has a relatively low PEV.

Although only a few young individuals are available, it is evident that EV increases very rapidly directly after birth. This is consistent with analyses of brain weights (e.g., Vrba, 1998; Herndon et al., 1999; Leigh, 2004). Specimen 11783, aged 5.19 years, still has an EV well below the average adult EV. However, this value is close to the lower limit observed in the adults, and it is, therefore, possible that the brain of this chimpanzee would have increased in size only insignificantly by adulthood. Table 2 lists mean cranial capacities of dental age groups and compares the Taï sample to a sample published by Zuckerman (1928). Mean values for adults and the age group including individuals with an erupted M2 but not M3 (J3) are remarkably similar between these two samples. Mean values for age group J2 (erupted M1) are also similar when taking the standard deviations around the means into account. For younger age groups, the means are more different, but sample sizes are small. Furthermore, our sample comprises only *Pan troglodytes verus*, whereas Zuckerman (1928) included different groups of chimpanzees because he lacked data on the origin of the chimpanzees.

The average EV of adult Taï chimpanzees (378.7 ± 30.1 cm^3) is similar to group means reported previously

(*Pan troglodytes verus:* n = 18, 367.7 ± 36.7 cm^3, EV data compiled by Isler et al., 2008; chimpanzees comprising different subspecies or subspecies not specified: n = 363, 383.4 cm^3, EV data compiled by Tobias, 1971; 367.6 ± 40.7 cm^3, n = 115, EV data compiled by Isler et al., 2008). Specimen 15010 has the highest EV of the sample (457 cm^3), although it is immature. Unfortunately, the identity of this individual is unknown, and therefore, information on age and sex is missing. Estimation of this individual's age is difficult because only the neurocranium is preserved, but the unfused sphenobasilar synchondrosis and its completely open sutures clearly demonstrate that it is subadult. It is also an outlier in the correlation between cranial length and height with EV (see Fig. 2).

Furthermore, we found sexual dimorphism of adult EV in accordance with differences between sexes in previously reported samples (350.5 ± 30.0 cm^3, n = 60 females and 386.2 ± 42.9 cm^3, n = 55 males, respectively, Isler et al., 2008; 371.1 cm^3, n = 200 females and 398.5 cm^3, n = 163 males, respectively, Tobias, 1971) as well as studies based on brain weights (Herndon et al., 1999; Leigh, 2004). Leigh (2004) found sexual differences in brain weights after about 4 years of age. In this study, EV in males also seems to be already larger than in females before adult EV is attained (see Fig. 3).

The multiple regression (cranial length, width, and height) and the regression on cranial width have moderate to high coefficients of determination (R^2 = 0.69 and 0.71, respectively). The equations should be used with caution, however, especially when estimating single individuals, because residuals can be quite high (see the extreme of specimen 15010, for example). Cranial length or height alone is not appropriate and should not be used to estimate EV (low coefficients of determination, R^2 = 0.34 and 0.43, respectively). The low correlation between cranial length and height with EV seems to be related to ectocranial superstructures like, for example, supraorbital tori that are variably pronounced independent of EV. In contrast, measurements of cranial width do not capture cranial superstructures (or do so less) and, therefore, have a higher correlation with EV.

Making EVs as well as age and sex information from the cross-sectional ontogenetic sample of the wild *Pan troglodytes verus* population from the Taï Forest available to other researchers; we attempted to enhance high quality ontogenetic data of EV, the variable that can also be measured for fossils, and thereby to stimulate the discussion on differences in brain growth patterns among extant primates and extinct hominins.

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