

Supplementary Information for “Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*”.

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Supplementary Table 1. Comparisons of slope and y-intercepts of ‘late ontogenetic’ and ‘ontogenetic’ dwarfing models

Species	n	slope	Confidence intervals	y-intercept	r	ANCOVA	
						slope	y-intercept
<i>H. amphibius</i> (2- 40 yrs)	33	0.35 (MA) 0.34 (LS)	0.28 – 0.41	1.30 (MA) 1.34 (LS)	0.89	Comparisons with <i>H. amphibius</i> (late ontogenetic)	
<i>H. lemerlei</i>	12	0.37 (MA) 0.34 (LS)	0.15 – 0.63	1.05 (MA) 1.18 (LS)	0.74	N	S
<i>H. madagascariensis</i>	12	0.46 (MA) 0.41 (LS)	0.20 – 0.79	0.72 (MA) 0.93 (LS)	0.75	N	S
Dwarf species pooled	24	0.45 (MA) 0.40 (LS)	0.27 – 0.67	0.72 (MA) 0.97 (LS)	0.71	N	S
<i>H. amphibius</i> (static adult)	18	0.40 (MA) 0.35 (LS)	0.19 – 0.64	1.07 (MA) 1.29 (LS)	0.69	N	N
<i>C. liberiensis</i> (static adult)	6	0.57 (MA) 0.42 (LS)	-0.49 – 13.1	0.36 (MA) 0.95 (LS)	0.59 [†]	S	0.001*
<i>H. amphibius</i> (0 – 40 yrs)	37	0.47 (MA) 0.47 (LS)	0.44 – 0.50	0.74 (MA) 0.75 (LS)	0.99	Comparisons with <i>H. amphibius</i> (ontogenetic)	
Dwarf species pooled	24	0.45 (MA) 0.40 (LS)	0.27 – 0.67	0.72 (MA) 0.97 (LS)	0.71	N	S
<i>H. amphibius</i> (2- 40 yrs)	33	0.35 (MA) 0.34 (LS)	0.28 – 0.41	1.30 (MA) 1.34 (LS)	0.89	S	0.002*

Major Axis Regression (MA), Least Squares Regression (LS), not significant (N), significant (S), * $p \leq 0.01$, ** $p \leq 0.001$, † weakly correlated, exponents spurious.

The appropriate line-fitting method used to define biological relationships has been much debated in the literature and is reviewed in ref. 31. Model II regression (Major Axis and Reduced Major axis, RMA) is generally favoured when both variables are subject to measurement error and when the primary objective is to determine the slope and describe how size variables are related. In contrast least squares regression is considered suitable when the aim of the investigator is one of prediction but the independent variable x is assumed to be measured without error. Data from MA and LS regression analyses are given above and the RMA slopes can be derived by dividing the LS exponents by the correlation coefficients provided in Supplementary Table 1. In this analysis not all relationships are highly correlated (i. e., $r > 0.9$) so discrepancies between slope values exist (see Supplementary Table 1). However, overall there is a fairly good agreement between the MA and LS exponent values relative to the unrealistically high exponent values derived from the RMA regression in cases of weak correlation, thus the MA values are reported in the main article. The major axis confidence limits were determined using a computer macro based on the computation given in ref. 32. In terms of the scaling models discussed in the main text the choice of exponent (LS MA or RMA) does not influence the results. In the case of *C. liberiensis*, though values are reported above, the data are weakly correlated and the exponent values spurious (see 95% confidence intervals).

Supplementary Table 2. List of Malagasy hippo cranial specimens (*H. lemerlei* and *H. madagascariensis*).

Accession No.	Species	Malagasy Locality	Endo-cranial capacity	Estimation cranial volume	Dental Group ³³
NHM M82187 (VA-5)	<i>H. lemerlei</i>	Lamboharana	370	MD	VII
MNHN MAD 308a	<i>H. lemerlei</i>	Ambolisatra	390	MD	VIII
NHM M82188 (VA-7)	<i>H. lemerlei</i>		345	10496	XII
PMU M3975	<i>H. lemerlei</i>		370	11663	XII
MNHN LAC 1961-3 (MAD 8818)	<i>H. lemerlei</i>	Beloha	350	9579	XIII
OUM 19171	<i>H. lemerlei</i>	Taolambiby	390	11867	XIV
MNHN LAC 1936-437	<i>H. lemerlei</i>		410	MD	XIV
MNHN LAC1932-75 (MAD 8819)	<i>H. lemerlei</i>		360	MD	XIV
NHM M4934	<i>H. lemerlei</i>	Itampolo-bé	375	MD	XV
NHM M4875	<i>H. lemerlei</i>		445	MD	XV
MNHN MAD 1066	<i>H. lemerlei</i>		360	13601	XV
MNHN MAD 1065	<i>H. lemerlei</i>		410	15934	XV
MNHN MAD 1070	<i>H. lemerlei</i>	Ambolisatra	400	MD	XV
NHM M82189 (VA-4)	<i>H. lemerlei</i>		370	12118	XVI
NHM M82190 (VA-3)	<i>H. lemerlei</i>	Amposa	440	17948	XVI
MNHN MAD 1076	<i>H. lemerlei</i>	Ambolisatra	345	MD	XVI
UA ANT 2	<i>H. lemerlei</i>		305	9819	XVI
PMU M3973	<i>H. lemerlei</i>	Amposa	355	MD [†]	XVI
PMU M3976	<i>H. lemerlei</i>	Amposa	360	MD	XVI
NHM M4936	<i>H. lemerlei</i>	Itampolo-bé	MD	MD	XVII

NHM M4935	<i>H. lemerlei</i>	Itampolo-bé	MD	MD	XVII
PMU M3972	<i>H. lemerlei</i>	Amposa	360	17004	XVII
PMU M3974	<i>H. lemerlei</i>	Amposa	410	MD [†]	XVII
MNHN MAD 7914	<i>H. lemerlei</i>	Lamboharana	390	14743	XVII
MNHN MAD 1080	<i>H. lemerlei</i>	Lamboharana	385	MD	XVII
MNHN MAD 7918	<i>H. lemerlei</i>	Amposa	440	MD	XVIII
L' Academi Malagache	<i>H. lemerlei</i>	Tsirave	415	14799	XVIII
MNHN LAC 1932- 589 (MAD 8815)	<i>H. lemerlei</i>	Menarandia	340	MD	XVIII
MNHN MAD 7353	<i>H. lemerlei</i>		MD	MD	XVIII
NHM M4909	<i>H. madagascariensis</i>		335	MD	VI
NHM M7093	<i>H. madagascariensis</i>	Antsirabé	380	13420	IX
ANJ1'05	<i>H. madagascariensis</i>	Anjohibe	380	13232	XIII
MNHN MAD 7352	<i>H. madagascariensis</i>	Antakara	450	MD	XIII
UA ANT 9a	<i>H. madagascariensis</i>		MD	15229	XIV
PMU M3963	<i>H. madagascariensis</i>	Masinandreina	385	9873	XIV
MNHN MAD 7701	<i>H. madagascariensis?</i>		570	MD	XIV
NHM M33359	<i>H. madagascariensis</i>		485	18562	XV
MNHN MAD 1069	<i>H. madagascariensis</i>		460	14103	XV
UA 4974	<i>H. madagascariensis</i>	Anjohibe	370	11583	XV
UA ANT 3	<i>H. madagascariensis</i>		430	12275	XV
UA ANT 4	<i>H. madagascariensis</i>		MD	MD	XV
Musee Akiba	<i>H. madagascariensis?</i>	Anjohibe	MD	MD	XV
PMU M3962	<i>H. madagascariensis</i>	Masinandreina	410	15068	XVI
NHM M5141	<i>H. madagascariensis</i>	Antsirabé	375	13318	XVII
UMZC H11001	<i>H. madagascariensis</i>	Antsirabé	485	18595	XVIII
PMU M3961	<i>H. madagascariensis</i>	Masinandreina	415	12700	XVII

PMU M3964	<i>H. madagascariensis</i>	Masinandreina	410	12833	XVIII
ANJ 175'06	<i>H. madagascariensis</i>	Anjohibe	MD	MD	Adult

ANJ, Musee Akiba, Mahajanga, Madagascar; MNHN, Muséum National d'Histoire Naturelle, Paris; LAC, Laboratoire Anatomie Comparée, MNHN, Paris (these specimens were transferred to the Institut de Paléontologie in 2008, see new accession numbers in parentheses available for some specimens); MAD, Institut de Paléontologie, MNHN, Paris; NHM, Natural History Museum, London, Palaeontology Department (VA, Vernay-Archbold Expedition); OUM, Oxford University Museum; PMU, Paleontologiska Museet, Uppsala; UA, University of Antananarivo, Madagascar; UMZC; University Museum of Zoology, Cambridge; MD, missing data (these specimens are partially damaged and not all landmarks/endocranial capacity values could be recorded). †Authors' digital landmark data corrupted but specimens complete. 'Dental group number' given in bold for specimens not classified as adult (i.e., < XI).

Supplementary Table 3. List of extant hippopotamus cranial specimens (*H. amphibius*, *C. liberiensis*).

Accession No	Species	Location	Endo- cranial capacity	Estimation cranial volume	Age code ³⁴	Dental Group ³³	Sex
UMZC H10702	<i>H. amphibius</i>	Zoo	MD	2167	0	I	
NHM ZD 1968.1460	<i>H. amphibius</i>	Zambia	230	2304	0	I	
MNHN1871- 432	<i>H. amphibius</i>	Managerie	200	2158	0	I	
MNHN1914- 258	<i>H. amphibius</i>	Managerie	150	2063	0	I	
MNHN1963- 139	<i>H. amphibius</i>	Parc Zool	180	1764	0	I	
NHM ZD 1851.12.23.4	<i>H. amphibius</i>	No Loc	MD	MD	1	I-II	
MRAC 93-022- M-0001	<i>H. amphibius</i>	Lake Chad	600	17204	2	III	
MNHN A.2211 [†]	<i>H. amphibius</i>	Senegal	MD	MD	3	III - IV	
NHM ZD 1935.9.1.398	<i>H. amphibius</i>	Namibia	660	24192	4	IV	F
NHM ZE 1962.2.14.9	<i>H. amphibius</i>	Zimbabwe	MD	22380	4	IV-V	
UMZC H10726- 8	<i>H. amphibius</i>	No Loc	MD	MD	5	V	
NHM ZE 1984.524	<i>H. amphibius</i>	West Africa	690	28586	5	IV-V	
MRAC 7813	<i>H. amphibius</i>	Zaire (Djonga)	705	21903	5	V	F
UMZC H10732	<i>H. amphibius</i>	E. Africa	650	55282	9	VII-VIII	
NHM ZE 1962.2.14.14	<i>H. amphibius</i>	Zimbabwe	795	35629	9	VII	
NHM ZD 1970.690	<i>H. amphibius</i>	Ethiopia	720	31922	9	VII	

NHM ZD 1851.11.10.12	<i>H. amphibius</i>	No Loc	865	MD	9	VII-VIII	
NHM ZD 1984.460	<i>H. amphibius</i>	No Loc	730	32240	9	VII	
MRAC 99-063- M-0004	<i>H. amphibius</i>	No Loc	735	MD	9	VII	
MRAC 98	<i>H. amphibius</i>	No Loc	780	MD	9	VII	
NHM ZD 1939.6.4.1	<i>H. amphibius</i>	S. Nigeria	810	42082	12	VIII	
NHM ZE 1961.12.11.3	<i>H. amphibius</i>	Zambia	725	34829	12	VIII	
NHM ZD 1984.458	<i>H. amphibius</i>	No Loc	770	47233	12	VIII	
NHM ZD 1932.12.27.2	<i>H. amphibius</i>	N. Nigeria	695	41073	15	IX-X	
NHM ZE 1935.10.9.2	<i>H. amphibius</i>	Botswana	880	45788	15	IX	
NHM ZD 1914.1.7.2A	<i>H. amphibius</i>	Kenya (Baringo)	820	54314	15	IX-X	
PC 21	<i>H. amphibius</i>	Tanganyika	775	42006	18	X - XI	M
NHM ZD 1924.8.3.68	<i>H. amphibius</i>	Tanzania	MD	39881	18	X	F
NHM ZD 1907.10.25.2	<i>H. amphibius</i>	Mozambique	790	38709	18	X	
NHM ZD 1874.6.4.2	<i>H. amphibius</i>	Sudan	985	62724	20	XI	
UMZC H10720	<i>H. amphibius</i>	Niger	MD	MD	20	XI	
UMZC H10743	<i>H. amphibius</i>	No Loc	855	55280	20	XI	F
UMZC H10719	<i>H. amphibius</i>	No Loc	940	60647	23	XII	M
NHM ZD 1935.3.16.26	<i>H. amphibius</i>	Zambia	825	41418	23	XII-XIII	
NHM ZE 1962.2.14.4	<i>H. amphibius</i>	Zimbabwe	850	54128	23	XII	

UMZC H10721	<i>H. amphibius</i>	Mozambique	945	53072	26	XIII	M
NHM ZD 1916.8.8.1	<i>H. amphibius</i>	Mozambique	810	55893	26	XIII	
NHM ZD 1925.9.5.1	<i>H. amphibius</i>	Nigeria	895	63281	26	XIII	M
NHM ZD 1910.9.30.1	<i>H. amphibius</i>	S. Nigeria	800	45919	26	XIII - XIV	
GM Z.32 ^{††}	<i>H. amphibius</i>	Zoo	955	54875	28	XIV	
PC 39	<i>H. amphibius</i>	Guinea	735	35376	28	XIV	F
PC 38	<i>H. amphibius</i>	Guinea	900	51527	28	XIV	M
PC 101	<i>H. amphibius</i>	Cameroons	850	59651	32	XV	M
NHM ZD 1984.525	<i>H. amphibius</i>	Gambia	980	56577	32	XV	M
NHM ZD 1984.457	<i>H. amphibius</i>	East Africa (?)	890	60167	32	XV	
UMZC H10716	<i>H. amphibius</i>	Zoo	910	50593	34	XVI	F
PC 65	<i>H. amphibius</i>	Congo	MD	43235	34	XVI	F
PC 330	<i>H. amphibius</i>	Congo (Kasindi)	870	47116	34	XVI	F
UMZC H10731	<i>H. amphibius</i>	Malawi	MD	47916	37	XVII	F
UMZC H10718	<i>H. amphibius</i>	S. Africa (Natal)	885	51258	39	XVIII	M
MNHN AE 803	<i>C. liberiensis</i>	No Loc	200?	MD	4	VI	
MNHN 1921-16	<i>C. liberiensis</i>	Ivory Coast	335	6989	10	XI	
MRAC RG 35714	<i>C. liberiensis</i>	Liberia	295	5322	10	XI	
MRAC RG 35716	<i>C. liberiensis</i>	Liberia	360	6337	14	XII	

MNHN 1921-309	<i>C. liberiensis</i>	Ivory Coast	355	7603	18	XIII
MRAC RG 31732	<i>C. liberiensis</i>	Zoo Antwerpen	385	6969	33	XVI
MRAC 77-51-M-1	<i>C. liberiensis</i>	Zoo Antwerpen	365	5923	38	XVIII

GM, Grant Museum, University College London; MNHN, Muséum National d'Histoire Naturelle, Paris, Laboratoire d'Anatomie Comparée. MRAC, Musée royal de l' Afrique Central, Tervuren, Belgium. NHM, Natural History Museum, London, Zoology Department; PC, Powell-Cotton Museum, Kent, UK; UMZC, University Museum of Zoology, Cambridge. † Juvenile cranium with cranial bones wired together without contact - biometric data unreliable. †† Specimen excluded erroneously from data presented in Figures 1 & 2 and Supplementary Table 1, but included with data presented in Table 2 and Supplementary Information. MD = missing data.

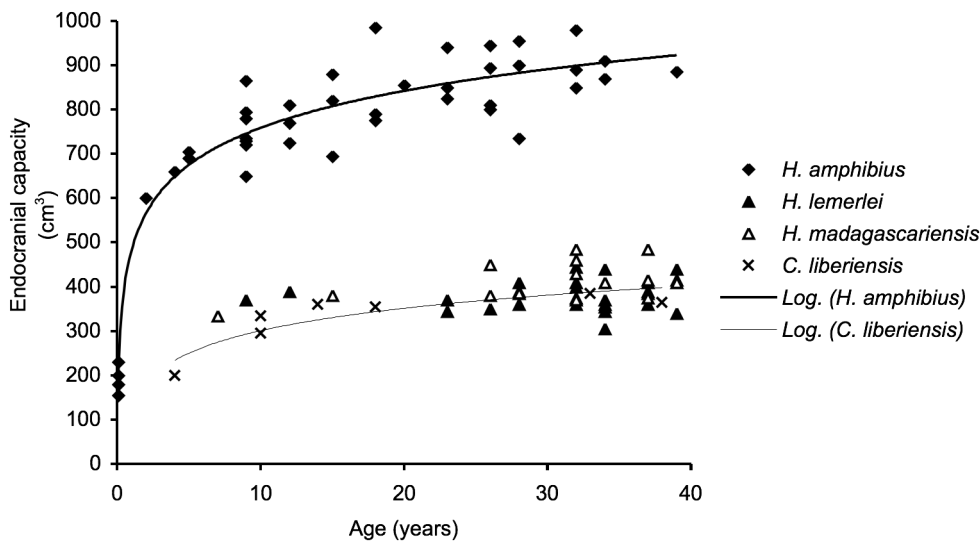
Supplementary Table 4. List of hippopotamus postcranial specimens used to estimate the body mass of the Malagasy dwarf species (see Supplementary Discussion for analysis of cranial size versus global skeletal size in hippos).

Acc. Number	species	Locality	Age Yrs	Dental Group ³³	Sex	u/r 4	u/r 7	hum 11	hum 12	tib 3	tib 4	fem 8	fem 4	GM	(GM) ³ GSV
KNM OM 2197	<i>H. amph</i>	Kenya	20	XI	F	4.80	8.90	9.50	5.90	8.30	14.60	6.20	7.20	7.75	464.66
KNM OM 2198	<i>H. amph</i>	Naivasha	23	XII	F	4.10	8.60	8.80	5.10	8.00	13.40	5.80	7.00	7.16	366.67
UMZC H10703-17	<i>H. amph</i>	Zoo	28	XIV	F	4.40	10.50	11.00	5.90	8.10	15.50	6.60	7.40	8.09	529.88
NHM ZE.1961.8.9.84	<i>H. amph</i>	Zambia Lake	34	XVI	F	5.10	9.75	10.30	6.90	9.20	16.80	6.80	8.10	8.61	637.36
FMNH 127870	<i>H. amph</i>	Nakuru	37	XVII	F	4.30	9.20	9.30	5.60	8.30	14.50	6.20	7.40	7.62	442.59
MNHN 1971-308	<i>H. amph</i>	Zoo	40	XIX	F	4.20	9.30	9.50	5.70	8.80	14.00	5.90	7.20	7.59	438.07
MNHN 1917-249	<i>H. amph</i>	Zoo Lake	21	XI	M	4.40	8.50	9.00	5.30	9.20	14.00	6.50	7.70	7.63	444.39
USNM 162979	<i>H. amph</i>	Naivasha Lake	26	XIII	M	5.20	10.20	10.40	6.50	9.20	16.20	6.70	8.20	8.58	631.54
KNM OM 6102	<i>H. amph</i>	Turkana	40	XIX	M	5.20	9.90	11.80	6.80	9.90	15.10	7.20	8.10	8.80	681.82
NHM ZE.1947.7.2.1	<i>H. amph</i>	No Loc	26	XIII	?	4.84	8.80	9.40	5.10	9.20	13.60	5.50	8.10	7.62	442.67
H. amph (adult mean)						4.65	9.37	9.90	5.88	8.82	14.77	6.34	7.64	7.95	503.09
NHM ZE.1984.524	<i>H. amph</i>	West Africa	4	IV*	?	3.36	8.20	9.00	4.37	8.25	12.41	4.23	6.79	6.50	274.47
UMZC H10702	<i>H. amph</i>	Zoo	New born	I*	F	1.48	3.89	3.36	1.76	4.00	5.42	1.90	3.01	2.84	22.89
NHM M8153	<i>H. mad</i>	Ansirabé				3.38	6.82	7.39	4.48	6.66	10.52	5.02	5.79	5.94	209.63
NHM M4796 (rt r/u)	<i>H. mad</i>	Ansirabé				2.97	6.12								
NHM M5151 (rt r/u)	<i>H. mad</i>	Ansirabé				3.01	5.90								
NHM M5151 (lt r/u)	<i>H. mad</i>	Ansirabé				2.88	6.10								
NHMM4796 (rt r/u)	<i>H. mad</i>	Ansirabé				3.11	6.04								
NHM M4794 (lt hum)	<i>H. mad</i>	Ansirabé						6.80	4.13						
NHM M4795 (rt hum)	<i>H. mad</i>	Ansirabé						6.88	3.82						
NHM M4794 (lt hum)	<i>H. mad</i>	Ansirabé						6.40	3.93						
NHM M5150 (lt hum)	<i>H. mad</i>	Ansirabé						6.88	4.25						
NHM M5150b (rt hum)	<i>H. mad</i>	Ansirabé						6.26	3.64						
NHM M4795 (rt hum)	<i>H. mad</i>	Ansirabé						6.64	3.85						
NHM M4801b (rt fem)	<i>H. mad</i>	Ansirabé										4.02	5.32		
NHM M5153 (lt fem)	<i>H. mad</i>	Ansirabé										4.03	5.22		
NHM M5153 (rt fem)	<i>H. mad</i>	Ansirabé										4.02	5.26		
NHM M4803 (lt fem)	<i>H. mad</i>	Ansirabé										4.01	5.84		
NHM M4802 (lt fem)	<i>H. mad</i>	Ansirabé										4.05	5.48		
NHM M4801a (rt fem)	<i>H. mad</i>	Ansirabé										4.78	5.93		

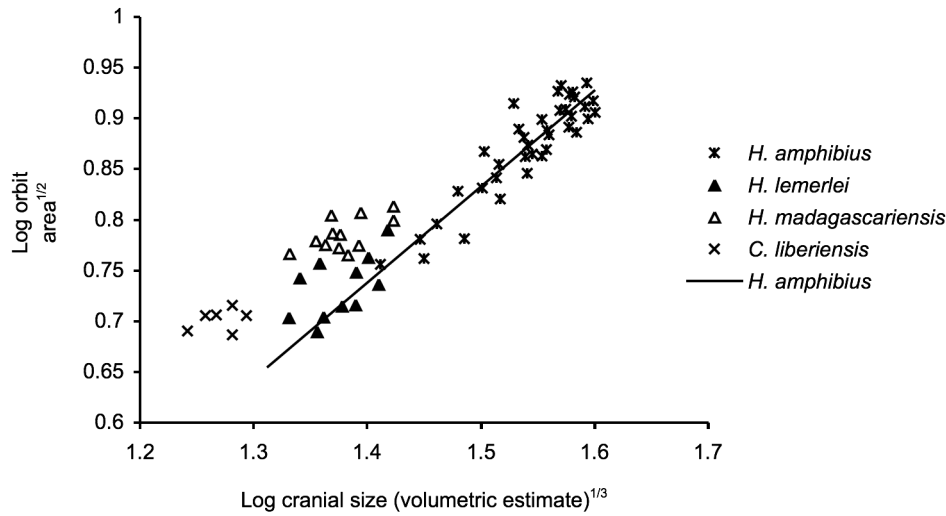
NHM M5154 (rt tib)	<i>H. mad</i>	Ansirabé						5.94	9.42					
NHM M5154 (lt tib)	<i>H. mad</i>	Ansirabé						6.38	10.03					
NHM M4804 (lt tib)	<i>H. mad</i>	Ansirabé						6.26	10.35					
<i>H. mad</i> (mean)				3.07	6.19	6.75	4.01	6.31	10.08	4.28	5.55	5.45	161.76	
NHM M4950b (lt r/u)	<i>H. lem</i>	Itampolo-bé		2.54	5.38									
NHM M4950 (lt r/u)	<i>H. lem</i>	Itampolo-bé		2.51	5.55									
NHM M4950 (rt r/u)	<i>H. lem</i>	Itampolo-bé		2.51	5.60									
NHM M4950d (rt r/u)	<i>H. lem</i>	Itampolo-bé		2.98	5.96									
NHM M4950c (rt r/u)	<i>H. lem</i>	Itampolo-bé		3.01	6.07									
NHM M4950e (rt r/u)	<i>H. lem</i>	Itampolo-bé		2.85	5.78									
NHM M4950f (lt r/u)	<i>H. lem</i>	Itampolo-bé		2.99	5.79									
NHM M4886a (lt r/u)	<i>H. lem</i>	Nosei Vey		2.75	5.02									
NHM M4886 (lt r/u)	<i>H. lem</i>	Nosei Vey		2.67	5.81									
NHM M4886c (lt r/u)	<i>H. lem</i>	Nosei Vey		2.74	5.45									
NHM M4921 (lt r/u)	<i>H. lem</i>	Nosei Vey		3.27	5.97									
NHM M4921 (rt r/u)	<i>H. lem</i>	Nosei Vey		2.94	5.97									
NHM M4860 (lt r/u)	<i>H. lem</i>	Ambolisatra		3.05	6.17									
NHM M4949 (rt hum)	<i>H. lem</i>	Itampolo-bé				5.97	3.62							
NHM M4949b (rt hum)	<i>H. lem</i>	Itampolo-bé				6.03	4.09							
NHM M4949c (rt hum)	<i>H. lem</i>	Itampolo-bé				6.27	3.67							
NHM M4949 (lt hum)	<i>H. lem</i>	Itampolo-bé				6.26	3.37							
NHM M4919 (rt hum)	<i>H. lem</i>	Nosei Vey				6.57	3.87							
NHM M4919b (rt hum)	<i>H. lem</i>	Nosei Vey				6.98	3.59							
NHM M4859 (lt hum)	<i>H. lem</i>	Ambolisatra				5.77	3.28							
NHM M4953a (rt fem)	<i>H. lem</i>	Itampolo-bé								3.95	4.22			
NHM M4953b (lt fem)	<i>H. lem</i>	Itampolo-bé								3.92	4.55			
NHM M4953c (rt fem)	<i>H. lem</i>	Itampolo-bé								3.68	4.67			
NHM M4953d (lt fem)	<i>H. lem</i>	Itampolo-bé								3.79	4.63			
NHM M4953e (lt fem)	<i>H. lem</i>	Itampolo-bé								3.89	4.40			
NHM M4862 (rt fem)	<i>H. lem</i>	Ambolisatra								4.03	4.63			
NHM M4954 (rt tib)	<i>H. lem</i>	Itampolo-bé						5.29	8.53					
NHM M4954c (rt tib)	<i>H. lem</i>	Itampolo-bé						5.82	9.08					
NHM M4954d (rt tib)	<i>H. lem</i>	Itampolo-bé						5.37	8.71					
NHM M4954b (lt tib)	<i>H. lem</i>	Itampolo-bé						5.92	8.98					
NHM M4954e (lt tib)	<i>H. lem</i>	Itampolo-bé						7.24	9.42					
<i>H. lem</i> (mean)				2.83	5.73	6.26	3.64	5.93	8.94	3.88	4.51	4.92	119.06	
NHM ZE	<i>Choer</i>	Sierra	New I*	0.89	2.18	2.73	1.19	2.49	2.89	1.35	1.84	1.80	5.86	

1908.10.22.1		Leone	born												
MNHN LAC 1948-01	<i>Choer</i>	Zoo	6	VIII*	M	2.40	4.65	5.10	3.20	4.30	7.40	3.30	3.60	4.02	65.19
NHM ZE 1952.4.1.4	<i>Choer</i>	Zoo	8	X	M	2.35	4.60	5.10	3.30	4.60	7.50	3.00	3.70	4.03	65.49
NHM ZE 1967.3.20.1	<i>Choer</i>	Liberia/zoo	10	XI	M	1.95	4.60	5.30	2.80	4.70	7.40	3.10	3.80	3.91	59.74
FMNH 135777	<i>Choer</i>	Zoo	28	XV	M	2.10	4.50	5.20	3.00	4.50	8.00	3.50	3.70	4.02	65.15
AMNH 148452	<i>Choer</i>	Zoo	33	XVI	M	2.60	4.70	5.20	3.10	4.20	7.60	3.40	4.00	4.14	70.72
MNHN 1982- 10	<i>Choer</i>	Zoo	38	XVIII	M	2.50	5.00	5.50	3.40	4.30	9.40	3.50	4.00	4.37	83.28
USNM 549277	<i>Choer</i>	Zoo	24	XIV	F?	2.10	4.70	5.10	3.20	4.10	7.35	3.30	4.00	3.99	63.46
FMNH 140919	<i>Choer</i>	Zoo	28	XV	F	2.40	4.60	5.10	3.00	4.30	7.80	3.50	4.20	4.12	70.02
RMS 1962-50	<i>Choer</i>	Zoo	28	XV	F	2.40	4.80	5.50	3.30	4.20	7.70	3.30	3.65	4.11	69.44
USNM 538815	<i>Choer</i>	Liberia	28	XV	F	2.40	4.70	5.20	3.00	4.20	8.20	3.20	4.00	4.09	68.18
AMNH 146849	<i>Choer</i>	Zoo	33	XVI	F	2.00	4.30	5.10	2.60	4.40	7.30	3.20	3.70	3.80	54.82
USNM 581892	<i>Choer</i>	Zoo	33	XVI	F	2.40	4.80	5.30	2.80	4.50	8.60	3.20	3.90	4.12	69.79
MNHN 1978- 104	<i>Choer</i>	Zoo	33	XVI	F	2.10	4.60	5.10	2.80	4.40	7.70	3.15	3.85	3.93	60.61
USNM 464982	<i>Choer</i>	Zoo	38	XVIII	F	2.40	5.00	5.40	3.20	4.60	8.30	3.40	4.30	4.29	79.22
NHM ZE 1937.11.20.1	<i>Choer</i>	Sierra Leone	10	XI		2.10	4.50	4.70	2.90	4.50	7.10	3.20	3.80	3.87	57.84
USNM 314046	<i>Choer</i>	Zoo	28	XI		2.40	4.60	5.10	2.90	4.40	7.90	3.10	3.90	4.02	65.11
NHM ZD 1914.6.21.1	<i>Choer</i>	Sierra Leone	28	XV		2.40	4.80	5.50	3.00	4.60	7.80	3.50	4.10	4.21	74.39
MNHN 1944- 146	<i>Choer</i>	Liberia/zoo	28	XV		2.00	4.10	4.80	2.70	3.90	6.80	2.90	3.40	3.59	46.39

ABBREVIATIONS. Skeletal variables taken from ref. 34: r/u 4, min. width of radial shaft in lateral-medial section (LMS); r/u 7, max. width of proximal radius in LMS; Hum 11, max. width of humeral trochlea in LMS; Hum 12, min width of humeral shaft in LMS; Fem 4, max. diameter of femur head in flexor-extensor section; Fem 8, min. width of femoral shaft in LMS; Tib 3, max distal width of tibia in LMS; Tib 4, max. proximal width of tibia in LMS. GM, geometric mean (8th root of the product of 8 variables listed above); GSV, global skeletal size variable (= GM raised to the third power, see Supplementary Discussion); FMNH, Field Museum of Natural History, Chicago; KNM, National Museums of Kenya; MNHN, Muséum National d'Histoire Naturelle, Laboratoire Anatomie Comparée, Paris; NHM, Natural History Museum, London (extant material held in the Zoology Department and subfossil material in the Palaeontology Department); UMZC, University Museum of Zoology, Cambridge; USNM, National Museum of Natural History (Smithsonian), Washington.



Supplementary Figure 1. Endocranial capacities of hippopotamus species versus age. In *H. amphibius* a rapid early phase of brain growth is evident between birth and 2 years of age. All ages are determined by dental criteria^{33,34}, with ages of subfossil specimens corresponding to those of *H. amphibius* (this does not reflect the real ages of the Malagasy hippos but it does permit a comparison of absolute brain size among the hippo taxa). One Malagasy outlier (MNHN MAD 7701) with an endocranial capacity of 570 cm³ was excluded from this analysis as its taxonomic identification is not certain. *H. amphibius* (closed diamonds; n = 41), *H. lemerlei* (closed triangles; n = 26), *H. madagascariensis* (open triangles; n = 14), *C. liberiensis* (crosses; n = 7). Best-fit, least squares logarithmic curves: bold line, $r^2 = 0.9153$ (*H. amphibius*); thin line, $r^2 = 0.7994$ (*C. liberiensis*).



Supplementary Figure 2. The relationship between orbit size and cranial size in

hippopotami. Major axis slope and 95% confidence intervals: *H. amphibius* 1.0419 (0.90 – 1.21); $r = 0.9124$; $n = 38$. Individuals aged between 2-40 years are included so the slope illustrated characterises the growth trajectory of *H. amphibius*. The small hippos (*H. lemerlei* ($n = 11$), *H. madagascariensis* ($n = 12$) and *C. liberiensis* ($n = 6$)) have relatively large eye sockets for their skull size, either deviating from (*H. madagascariensis* and *C. liberiensis*) or matching (*H. lemerlei*) the predictions based on the ontogenetic scaling of the large *H. amphibius*. In hippos the trend in orbit size does not correspond to that of brain size (see Figs 1 and 2). Orbit size variation between hippopotamus species is quite complex and has been linked to sexual dimorphism^{35,36} but this example does indicate that a reduction in brain size does not necessarily correspond to a reduction in orbit size during dwarfing. This finding is contrary to the example of *Myotragus* (see ref. 37) but comparable to that of *H. floresiensis*.

Supplementary Discussion

Issues relating to estimation of body size reduction, and to the phylogeny and preservation of the Malagasy dwarf hippos

Issues relating to estimation of body size reduction

Observed body mass values

Body mass values of both species of modern hippopotamus vary enormously³⁸ and skeletal specimens of hippopotamus held in museums generally do not have associated body mass data. A value of 1495 kg (representing the mean of a pooled sex static adult sample of *Hippopotamus amphibius*)³⁹ was utilised here to estimate body mass from both cranial and postcranial elements, although it should be emphasised that these values are to provide context and were not utilised in the scaling analysis. All *H. amphibius* body mass values referred to in the main text are obtained from ref. 39 where the body masses of a post-natal series of 52 bulls and 52 cows were recorded during experimental cropping conducted in the Kruger National Park, South Africa. In ref. 39 individuals above 3 years of age were classified as adult and no further breakdown of age associated with values of mass was given. However, because physical maturity of the hippopotamus is obtained between 17-24 years of age (based on postcranial long bone epiphyseal fusion) and dental eruption is not complete until around 22 - 24 years of age^{33,34}, a mean body mass taken from individuals between 3 – 45 years of age underestimates the mass of fully grown adults of both sexes. The body mass value needs to be representative of the age distribution of crania used to estimate skull volume. Crania in dental group XI and above (equivalent to 20 yrs of age in *H. amphibius* and 10 years of age *Choeropsis liberiensis*) were classified in this study as adult (see Supplementary Table 2 & 3 and Supplementary Fig. 1). Based on a curve depicting the relationship between age and body weight of *H. amphibius* (modelled from combining separate data sets of body length and associated body weight, with ages determined by dental criteria; see <http://www.nnf.org/na/RARESPECIES/InfoSys/additionalContent/HippoAgeWeightRelationA2.pdf>) a 20 year old female hippopotamus has a predicted weight of 1200 kg and a male 1300 kg. The range of observed masses recorded from female individuals > 1200 kg and males > 1300 kg from ref. 39 is 1210 kg – 2001 kg (n = 50), with a mean value of 1495 ± 29.5 kg.

The range of body masses (180 – 275 kg)³⁸ recorded for the pygmy hippopotamus *C. liberiensis* is largely based on zoo individuals that are generally larger in body mass than wild animals. The body mass data⁴⁰ from the extinct Nigerian subspecies *C. liberiensis heslopi*⁴¹ may not be representative of other West African populations. We have utilised a mid-range value of 228 kg as we include zoo and wild crania in our static adult sample (see Supplementary Table 3), although the actual mean body mass of wild pygmy hippos is probably closer to 200 kg.

Relationship between skull size and body mass

The data given below demonstrate the validity of using cranial size as a proxy for body mass, an important underpinning of both the hippopotamus analyses themselves, and our extrapolation of the hippo findings to *H. floresiensis* where the debate has been based on the relationship between endocranial capacity and estimates of body mass rather than cranial size. First, we show that in living hippos, a volumetric estimate of cranial size is isometric to body mass. Second, to demonstrate that it is reasonable to extrapolate from the brain to skull size analysis in the dwarf hippo example, to the hominin example which has previously been

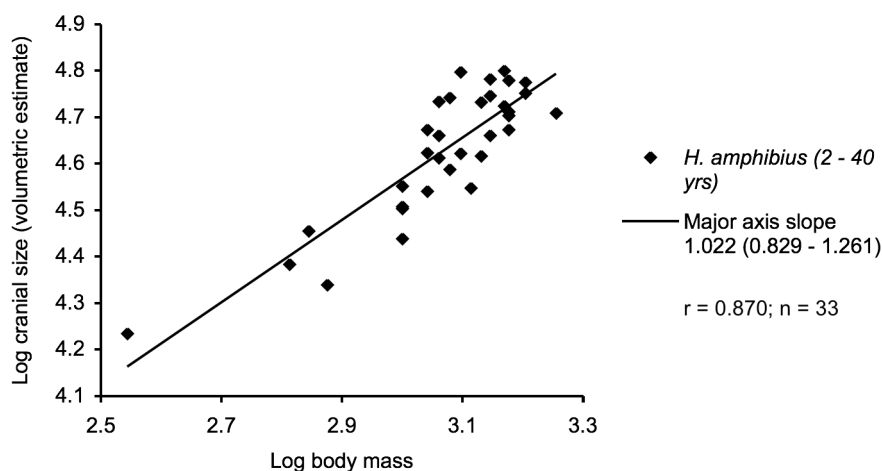
based on body mass, we show, using hominin facial variables and endocranial capacities, that a proportional change in brain size relative to cranial size, similar to that observed in the dwarf hippos, was present.

The use of cranial size (volumetric estimate) has the added, important advantage that both it and endocranial capacity can be accurately measured on the same individuals, both of modern and fossil taxa. In the case of the dwarf hippos, available cranial and postcranial material is not associated, and body mass could only be obtained by indirect estimation in any case.

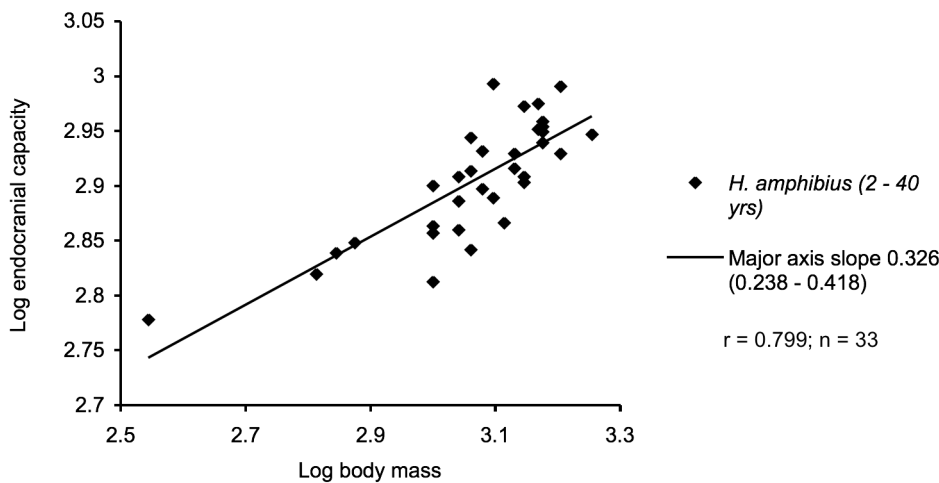
Nonetheless, as a further test of the validity of our methodology, we show that the mean body size of the fossil taxa, estimated from postcranial dimensions, is consistent, when compared to mean cranial size, with skull-body isometry across extant and extinct dwarf *Hippopotamus*.

(a) Relationship between cranial size and body mass in hippos

Estimates of body mass deduced from age (see <http://www.nmf.org.au/RARESPECIES/InfoSys/additionalContent/HippoAgeWeightRelationA2.pdf>) were allocated to the *H. amphibius* crania included in this study, using age estimates based on dental eruption and wear (Supplementary Table 3). We read male and female body mass estimates from the age/mass graph and interpolated a mass value between that of male and female for unsexed specimens. The relationship between cranial size and body mass within *H. amphibius* is approximately isometric (see Supplementary Figure 3) implying that a direct correlation exists between skull volume and body mass.

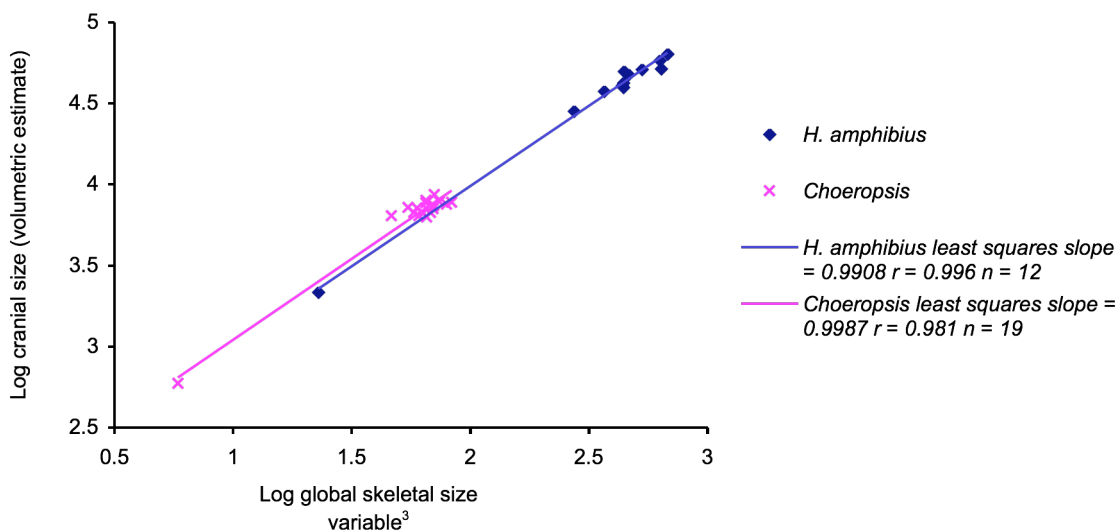


Supplementary Figure 3. The ‘late ontogenetic’ relationship between cranial size and estimated body mass in *H. amphibius*.



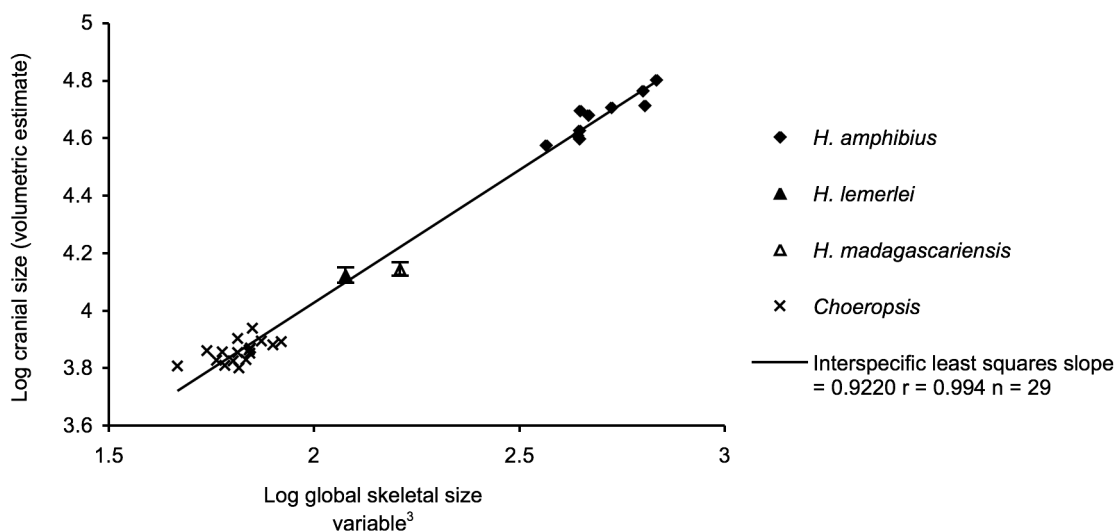
Supplementary Figure 4. The ‘late ontogenetic’ relationship between endocranial capacity and estimated body mass in *H. amphibius*. The relationship generated using estimates of body mass, and those reported using a volumetric estimate of cranial size (see main text), are similar (slope value = 0.33 versus 0.35).

(b) *The relationship between cranial and postcranial size in hippos.*

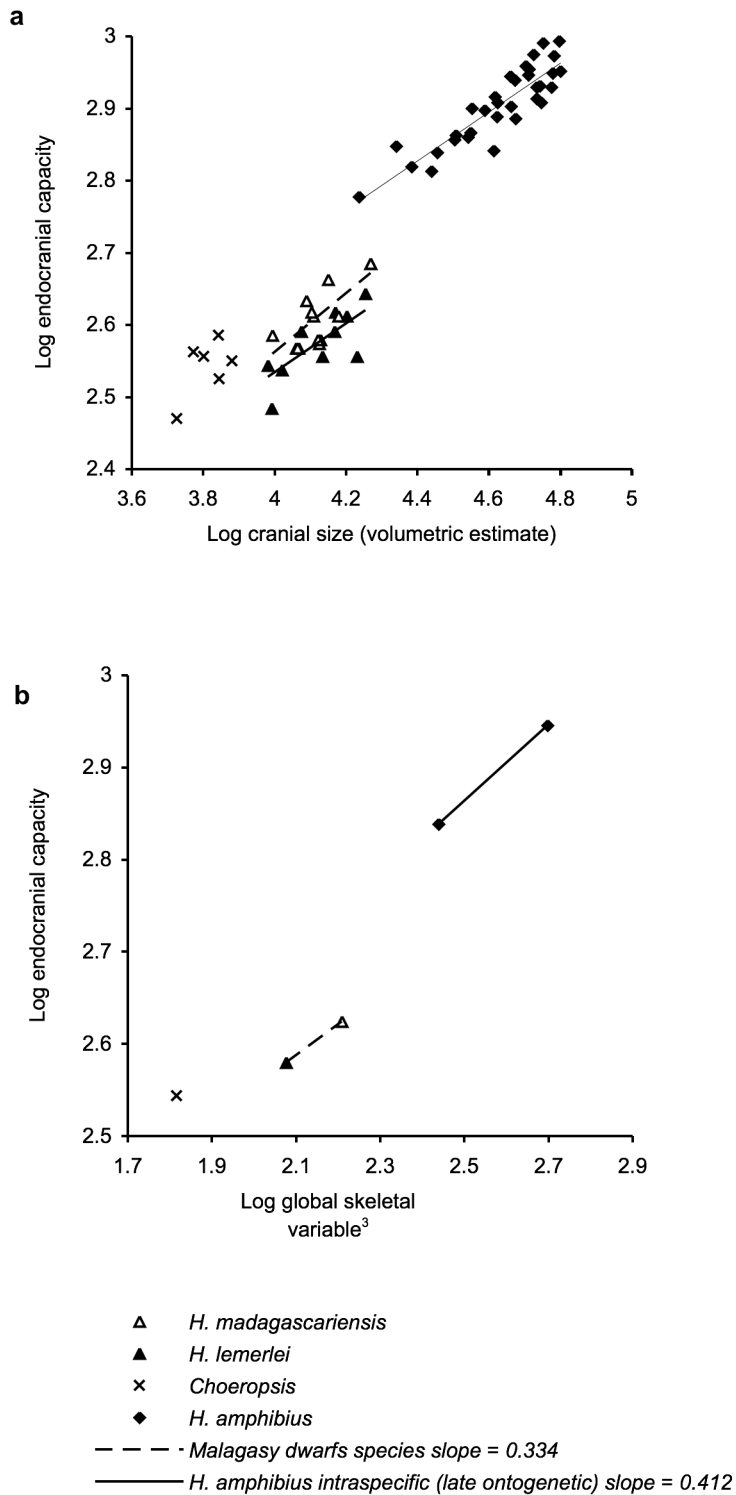


Supplementary Figure 5. The intraspecific relationship between cranial size and global skeletal size in extant hippos. We demonstrate that an exponent of 1 characterises the relationship between cranial and postcranial size within an intraspecific postnatal growth series of the two extant hippopotamus species. The skeletal data are given in Supplementary Table 4 and methods relating to the calculation of the global skeletal size variable and ageing of the hippopotami are given below. The postnatal data series consists mainly of individuals that are either adult or close to full maturity, with both species represented by a single

neonate and juvenile specimen that are denoted by an asterisk in Supplementary Table 4. In spite of the missing data the similarity of these intraspecific trends is statistically robust: ANCOVA (analysis of covariance) demonstrates that both the slope and y – intercepts of the two species do not differ significantly (test for equality of slopes $F = 0.51$, $P = 0.481$; test for equality of y – intercepts $F = 1.87$ $P = 0.183$). This demonstrates that cranial size in extant hippos scales isometrically with body size within and between species.



Supplementary Figure 6. The interspecific relationship between adult cranial size and global skeletal size for the extant and dwarf fossil species of hippopotamus. Adults of both sexes of extant hippos (see Supplementary Table 4) are plotted against global skeletal size. We do not have associated postcrania and crania for the fossil species so we have derived an estimate of global skeletal size by using the mean values for measures taken from individual skeletal elements (see Methods below, and data in Supplementary Table 4). The mean values for cranial size and standard errors (drawn on graph) are given in Table 2 of the main manuscript. The interspecific relationship across these taxa is close to 1 implying that the relationship between crania and postcrania across species is almost isometric. *H. lemerlei*, the smaller of the dwarf taxa, falls directly on the slope (i.e. it scales with the two living species), whereas the larger of dwarf species, *H. madagascariensis* has a slightly smaller cranium for its body size. This makes any estimate of reduction in brain/body size, based on brain/skull proportion, a conservative one. For a direct comparison of skeletal and cranial relationships with brain size see Supplementary Figure 7.



Supplementary Figure 7: a, taken from Figure 1 main text, the relationship between cranial size and brain size; b, the relationship between global skeletal size and brain size. Endocranial capacity (brain size) data are not available for a growth series of modern hippopotami with associated skeletons. However, to draw as close a comparison as possible with the cranial size data presented in a, for *H. amphibius* the

mean adult values (sexes pooled) for global skeletal size and brain size (see Table 2 main text) are plotted. These data are not associated but one juvenile individual (ZE. 1984.524; Supplementary Table 4) of 3 - 4 years of age with associated brain and skeletal data is added. These data are representative of the 'late ontogenetic' intraspecific scaling model of brain to body size in *H. amphibius*. If we further consider the relationship between the adult means of the fossil dwarf taxa we have an exponent of 0.33 suggesting that rather than *H. madagascariensis* having a brain dwarfed to a lesser degree than *H. lemerlei* (24 % versus 30 % reduction: see main text), in fact *H. madagascariensis* has a slightly small skull for its body size and probably exhibits the same degree of brain reduction as *H. lemerlei*. Either way, graphs **a** and **b** illustrate an analogous grade shift between *H. amphibius* and the dwarf taxa, corroborating that the latter have relatively smaller brains than would be expected from scaling *H. amphibius* to an equivalent body size.

(c) *Methods associated with Supplementary Figures 5 – 7.*

The teeth of *Choeropsis* are fully erupted by 8-10 years of age, whereas in *H. amphibius* dental eruption is complete by 22-24 years of age. However, records indicate that longevity for these species is similar at around 40 years. The physical maturity of the skeleton tends to precede dental maturity slightly, and for the purpose of this skeletal study we have classified all specimens in dental group 10 (X) as adult (see supplementary Table 4).

A global skeletal size variable⁴² is a volumetric transformation of the geometric mean of measurements from multiple skeletal elements (i.e., n^{th} root of the product of n measurements, raised to the third power). Measurements of articular surfaces and transverse sections of long bones were taken, since the geometric means of these types of measurements have been shown to scale isometrically with respect to body mass in primates⁴³ and generally in mammals bone width dimensions have been shown to correlate better with body mass than bone length dimensions⁴⁴. Eight variables from four skeletal elements (humerus, radioulna, femur and tibia) were taken from extant hippopotamus skeletons that had crania and associated long bones present, and for the subfossil taxa measurements were taken from the isolated skeletal elements (see Supplementary Table 4). The variables used are: "r/u 4" min. width of radial shaft in lateral-medial section (LMS); "r/u 7" max. width of proximal radius in LMS; "Hum 11" max. width of humeral trochlea in LMS; "Hum 12" min width of humeral shaft in LMS; "Fem 4" max. diameter of femur head in flexor-extensor section; "Fem 8" min. width of femoral shaft in LMS; "Tib 3" max distal width of tibia in LMS; "Tib 4" max. proximal width of tibia in LMS.

Although the cranial and postcranial remains of the Malagasy subfossil hippos are not known to be from associated skeletons, the size of the sample, and the restriction of each species to particular localities, makes it possible to estimate the relationship between cranial and postcranial size. The two species, *H. madagascariensis* and *H. lemerlei*, are clearly identifiable based on skull morphology, and are found to be restricted to different localities (Supplementary Table 2). At each locality there is a substantial quantity of unassociated hippopotamus postcranial bones, allowing the calculation of mean diameter values for each of the elements used in the calculation of global skeletal size variable. Because the latter combines the data from each bone type, the number of individual specimens contributing to this estimate of mean population skeletal size is substantial. These global skeletal values have been plotted against average cranial and endocranial volumes, based on a significant number of adult crania from the same sites.

(d) Estimation of body mass of dwarf hippos, *H. lemerlei* and *H. madagascariensis*

The two dwarf species, identified according to cranial evidence, were separated geographically (see Supplementary Table 2 and ref. 45). The skeletal measures of the Malagasy dwarf hippos listed are taken from isolated specimens that were not directly associated with cranial material but that co-occur with one ‘cranial species’. In the absence of an allometric analysis within extant Hippopotamidae (only 2 extant species), body mass of the extinct dwarf hippos was estimated assuming a geometric cube law for the relationship between linear dimensions and body mass^{44,46}:

$$\text{Fossil Mass} = \text{Modern Mass (FM/MM)}^3$$

FM = geometric mean of fossil postcranial measures; MM = geometric mean of modern postcranial measures.

The body mass range estimates given in Table 2 for the Malagasy dwarf hippos assume a modern body mass range of 1210 - 2001 kg for *H. amphibius* (see supplementary discussion above of observed body mass values and ref. 39). For calculation of the geometric mean of skeletal measures, see data given in Supplementary Table 4 and supplementary discussion of the methods, above. The estimated body mass for the dwarf hippos using a mean body mass of 1495 kg for *H. amphibius* (mean of a pooled sex static adult sample, see supplementary discussion, above, of observed body mass) is 482 kg for *H. madagascariensis* and 355 kg for *H. lemerlei*. If we compare the body mass estimates based on cranial size given in Table 1, that of *H. lemerlei* (374 kg) is very similar to the value estimated from the postcranium, whereas that based on the cranium of *H. madagascariensis* (394 kg) underestimates body mass slightly. This corroborates the findings above (see Supplementary Figs 6 and 7) suggesting that *H. madagascariensis* has a slightly smaller skull for its body size.

(e) The relation between skull size and body mass in humans

In modern hippos, the degree of reduction in brain size observed relative to skull size can be extrapolated, based on the data above, to infer brain-size changes relative to overall body mass; but can the same rationale be applied to humans, given their disproportionately large brain?

Supplementary Table 5 (see below) gives the endocranial capacity predictions based on the hippo dwarfism model (see main text) of some *Homo erectus* (*sensu lato*) (African = *ergaster*) specimens using basicranial length (Basion – Nasion) and orbital area as a proxy for skull size. The *Homo* cranial remains from Dmanisi, Georgia are included within *H. erectus* (see refs 47, 48). Juvenile and adolescent cranial specimens, such as D2700^{48,49} and KNM-WT15000, have not been included as growth of the face is not complete. Endocranial capacity, basicranial length and/or orbital area are preserved in only four adult *H. erectus* specimens, Sangiran 17, KNM-ER 3883, KNM-ER 3733 and D3444 (see Supplementary Table 5). In primates cranial indicators of body mass have been difficult to isolate and orbital area has generally been considered one of the best cranial predictors of body mass in humans^{50,51}. However, as it has been suggested that one of the effects of insular dwarfism in mammals is a reduction in orbital area as well as a reduction in brain size³⁷, we have here also considered basicranial length. Basicranial length (Basion – Nasion) is representative of the interface between the facial- and neurocranium and has been considered a suitable estimator of skull size in primates^{52,53}.

Supplementary Table 5. Estimates of brain size in *H. floresiensis* based on the hippo dwarfism model, using *H. erectus* (and one *H. habilis*) cranial variables as a proxy for body mass and body mass estimates.

Species/ specimen	Body mass (kg) ^{49,51,54}	Endocranial capacity (cm ³) ^{47,51,54}	Basi- cranial length: basion- nasion (cm) ^{48,54, 55}	(Basi- cranial length: basion- nasion) ³	Orbital area (cm ²) ^{47,54, 55}	(Orbital area) ^{3/2}	<i>H. floresiensis</i> endocranial capacity prediction based on hippo dwarfing model (cm ³)	
							Cranial variables (proxy for body size)	<i>H. floresiensis</i> body mass estimate 29 kg 23 kg
Sangiran 17 Asian <i>H.</i> <i>erectus</i>	76	1004	11.2 ⁵⁵ 11.5 ⁴⁸	1405 1521			499 484	
					15.48	60.91	548	499 464
KNM-ER 3883 African <i>H.</i> <i>erectus</i>	57.5	804	10.1 ⁵⁵ 10.2 ⁴⁸	1030 1061			450 444	
					14.76	56.71	456	444 405
KNM-ER 3733 African <i>H.</i> <i>erectus</i>	59.2	850	10.3 ⁵⁵ 10.7 ⁴⁸	1093 1225			458 440	
					15.17	59.09	476	464 423
D3444 Dmanisi <i>H.</i> <i>erectus</i>	40	650						
					12.16	42.40	409	405 378
ER 1813 <i>H.</i> <i>habilis</i>	35	509	8.4	593			342 356	
					9.9	31.20		335 310
LB1 <i>Homo</i> <i>floresiensis</i>	23 (16 - 29)	405 (380 - 430)	8.1 ⁵⁴	531				
					9.92	31.24		

H. erectus basicranial length values taken from refs 48 and 55, orbital dimensions from refs 47 and 55 and body mass estimates and endocranial capacity values from refs 47, 49 and 51. *H. habilis* values from refs 51 and 55. *H. floresiensis* values from ref. 54 (see main text for endocranial capacity estimates and associated references).

If the hippo model is applied to the Asian *H. erectus* skull (San 17) with a skull size equivalent to 1405 – 1521 cm³ (basicranial length)³ and endocranial capacity of 1004 cm³, that reduced its skull size by 62 – 65 % to 531 cm³ (see LB1 Table above), an endocranial capacity of 693 – 713 cm³ (69 – 71 % of original value) would be predicted from scaling (skull size)^{0.35}. If the brain were reduced by a further 30% of that value, as in the case of the Malagasy hippo *H. lemerlei*, an endocranial capacity of 484 – 499 cm³ would result. If orbital area (height x breadth)^{3/2} is used as proxy for skull size instead, using the same analogy as above, a slightly larger endocranial capacity of 555 cm³ is predicted for San 17 (see Table above). In contrast, if we

consider the smaller of the two African *H. erectus* skulls (KNM-ER 3883) with a skull size equivalent to $1030 - 1061 \text{ cm}^3$ (basicranial length)³ and an endocranial capacity of 804 cm^3 , that reduced its skull size by 48 -50 % to 531 cm^3 , an endocranial capacity of $635 - 643 \text{ cm}^3$ (79 – 80 % of original value) would be predicted from scaling (skull size)^{0.35}. If the brain size was reduced by a further 30 % of that value, as an effect of insular dwarfism, an endocranial capacity of $444 - 450 \text{ cm}^3$ would result. If orbital area is used as alternative proxy for skull size, using the same analogy as above, a similar endocranial capacity of 456 cm^3 is predicted (see Supplementary Table 5). Furthermore, if we consider the Dmanisi cranium D3444 with an orbit size equivalent to 42.40 (orbital area)^{3/2} and a cranial capacity of 650 cm^3 , that reduced its size by 26% to 31.24 (orbital area)^{3/2} a cranial capacity of 585 cm^3 (90% of original value) would be predicted from scaling (orbit size)^{0.35}. If the brain was reduced by a further 30% of that value, as an effect of insular dwarfism, an endocranial capacity of 409 cm^3 would be predicted.

Finally, if *H. habilis* (cranium ER 1813) were considered ancestral to *H. floresiensis*, a scaling hypothesis equivalent to that of the hippo example would not need to be invoked, as the endocranial predictions in Supplementary Table 5 are lower than the endocranial capacity value of *H. floresiensis*. In this example most of the reduction can be explained by scaling (body mass)^{0.35} (e.g., body mass reduced by 34% - 35 kg to 23 kg), which gives a endocranial capacity value of 443 cm^3 , close to the upper estimate for LB1- 430 cm^3 (i.e., this is an expectation of body size adjustment and not necessarily island dwarfism). However, if LB1's endocranial capacity is 405 cm^3 and body mass 29 kg then scaling (body mass)^{0.35} gives an endocranial capacity prediction of 478 cm^3 (15 % larger than the endocranial capacity of LB1) and body size adjustment alone can not account for such a difference in size.

This substitution of cranial variables for body mass in *H. erectus* generates roughly equivalent values of endocranial capacity as those predicted using body mass (see Supplementary Table 5). This suggests that inferences drawn from the scaling of hippopotamus skull size during dwarfing can justifiably be extrapolated to hominin scaling models that primarily consider body mass estimates. However, endocranial capacity predictions derived from cranial measures compare more closely with those that are estimated using a body mass value of 29 kg for *H. floresiensis* (the upper end of its estimated range) rather than 23 kg (the median value) (see Supplementary Table 5).

Choice of scaling model

Island mammals include some of the most extreme examples of body size adjustment. The striking parallel developments of form that characterise island mammals, such as deer, hippos, and elephants, are all associated with a reduction in body size⁵⁶. Body size decrease (dwarfism) and increase (gigantism) on islands has been shown to be rapid, species evolving faster than their mainland counterparts⁵⁷. This kind of body size adjustment is an example of rapid 'phyletic' evolution (evolution within a lineage or population *sensu* Boucot⁵⁸). In a classic piece of work by Lande⁵⁹ it was recognised that the allometric regression slope of brain weight against body weight observed between closely related species (e. g., phyletic dwarfism) fell in the same range (0.2 – 0.4) as that observed between individuals within a population. In other words intraspecific scaling exponents should best model phyletic dwarfism in the context of brain-body relationships. However, confusion about different kinds of intraspecific brain size allometry persists. This is because the divide between static adult data and growth data is blurred (i. e., biological specimens are often difficult to age with precision) and in the case of the brain that matures very slowly over much of postnatal development these two types of allometric exponent tend to be fairly similar. However, one of the most striking features of insular dwarfs is that they are not geometrically-scaled models of their larger ancestors, and many of the allometric (size related) shape changes that accompany dwarfism result from the truncation of growth⁶⁰ (see example of *H. madagascariensis* cranial data in Supplementary Fig. 8). This

relatively simple ‘paedomorphic’ change in development, where the adult features of the dwarf resemble the juvenile features of the ancestor, can generate vast differences in the organism’s form. This pervasive trend of ‘ontogenetic scaling’⁶¹ where animals scale in an analogous fashion to how they grow, has to be taken into account if we are to understand the dwarfing process.

The brain, however, poses a special challenge in this context as brain development and maturation are completed early relative to other parts of the skull, and growth is usually rapid initially and then slows down. Usually in precocial mammals the earlier rapid phase of brain growth occurs prenatally and the point of inflection occurs at or around birth^{62,63}. However, in hippos the rapid early phase of ‘foetal’ growth continues after birth for about two years (see Supplementary Fig. 1), a condition coincidentally similar to that observed in humans where it has been described as ‘secondary altriciality’⁶⁴. The important point relevant to modelling island dwarfism is that the exponent calculated from the later, slower phase of brain growth should be distinguished from larger exponent values calculated from data combining early and late phases of brain growth (i. e., both could be derived from postnatal ontogenetic data). In this study both types of exponent, ‘late ontogenetic’ and ‘ontogenetic’, were utilised to predict the effects of scaling or developmental allometry. The static adult exponent was not considered to be meaningful in this context as it does not characterise the developmental allometry associated with the late phase of brain development. However, the static adult exponent (0.35 - 0.4) for *H. amphibius* is given in Supplementary Table 1, demonstrating that the value is similar to the ‘late ontogenetic’ exponent but weakly correlated by comparison (see discussion of regression models beneath Supplementary Table 1). This apparent correspondence of ‘static adult’ and ‘growth’ allometry is attributable to the slow rate of growth and early maturation of the brain postnatally. However, if the scaling of other skeletal variables (e.g., the face) were to be considered, where most of the growth occurs postnatally, the difference between ‘static adult’ and ‘growth’ allometries would be much larger and outcomes of the scaling predictions very different (see example of hippo cranial scaling below). This is why studies that lack growth data are not able to predict accurately the potential effects of scaling.

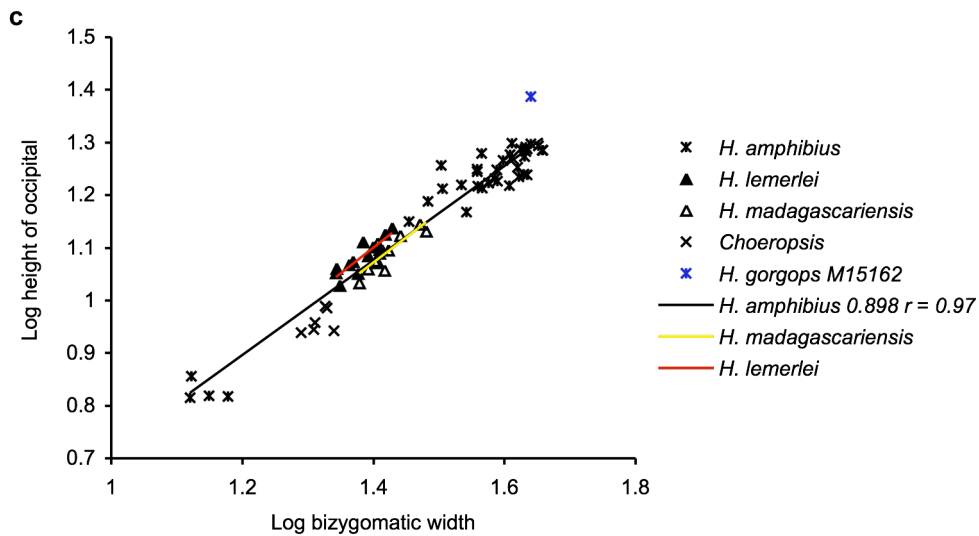
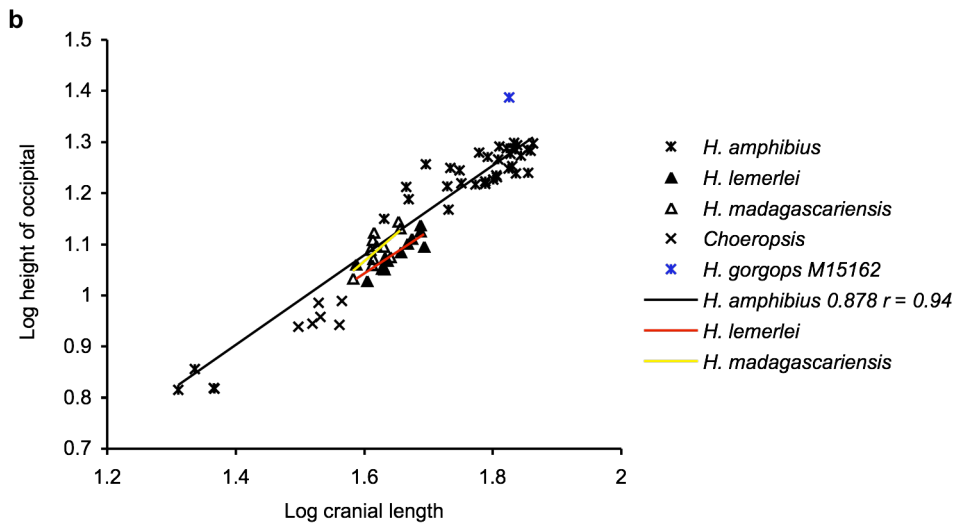
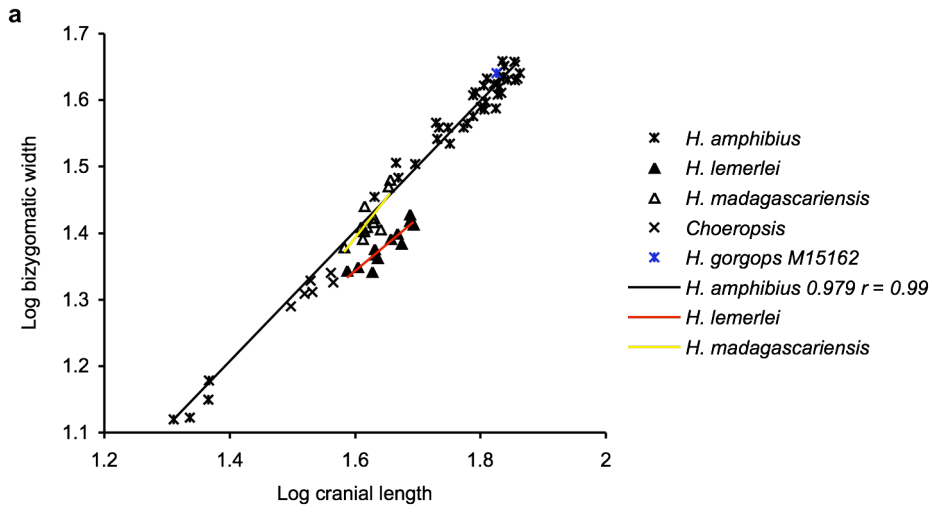
The results presented here (Figs 1 and 2, main text) demonstrate that the island dwarf hippos do not scale ontogenetically relative to *H. amphibius*, regardless of which ontogenetic model is adopted, but do demonstrate that that ontogenetic trajectories have changed in position or elevation (slopes identical but y -intercept values different). This kind of vertical readjustment of identical scaling trends when comparing species has been described as a grade shift^{62,65} or a lateral shift⁶¹. In this context, it implies that a change early in development (or earlier than that represented by the data) occurred, causing the ‘dwarf species’ to have a lower ratio of brain to skull size than the ancestral species, regardless of its eventual adult size. This study demonstrates that predictions based on intraspecific brain-body scaling trends in mammals (ontogenetic or static adult) do not conform to the developmental adjustment of brain size shown to be associated with the process of dwarfism of mammals on islands. This implies that although there are several plausible theories to potentially explain the small brain of *Homo floresiensis*, it is mechanistically possible to achieve a lower ratio of brain to body size via the process of insular dwarfism.

Issues relating to duration and rate of brain growth (see also above)

In ‘phyletic dwarfs’ we suggest that a reduction in the duration of rapid early brain growth could potentially explain a “grade shift” to a lower brain-body ratio as demonstrated by the change in ratio of brain to cranial volume in Fig. 1. Similarly, a “grade shift” to a higher brain-body ratio, (e.g., chimpanzee - human) has been attributed to a prolonged phase of early rapid brain growth (see above and ref. 64). Duration, in this context, is referring only to the earlier, more rapid phase of brain growth that precedes the slower ‘late

ontogenetic' phase. When studies (such as refs 66, 67) attribute the larger brain of modern humans, relative to that of the chimpanzee, to growth rate differences rather than to duration, they are referring to the duration of the entire postnatal period (birth to adulthood). In humans and chimps this includes both early rapid and late slower phases of growth. These growth phases are not treated separately in refs 66 and 67, accounting for the apparent contrast between our (and see ref. 68) and their interpretations of the same data. As the earlier rapid phase of brain growth (often referred to as foetal or prenatal) continues in humans until roughly 18 months after birth but only continues in chimps to around 6 months (post birth), the brain size difference between the species is attributable to differences in growth velocity that occur within the first 18 months. After the first 18 months of life, the brains of both chimp and human are not substantially different in terms of growth rate (see ref. 66) therefore the point when the brain stops growing (the duration of the slower 'late ontogenetic' phase) is going to have relatively little effect (compared to the duration of the early rapid growth phase) on terminal brain size.

Issues relating to the scaling of cranial variables and the effects of growth allometry.



Supplementary Figure 8. A comparison of the intraspecific relationships among the hippopotamus cranial variables used to estimate cranial volume (cranial length, bizygomatic width and height of occipital) for the extant *H. amphibius* (n = 37), the Malagasy dwarf hippopotamus taxa (*H. lemerlei*, n = 12; *H. madagascariensis*, n = 12), the extant pygmy hippo (*Choeropsis liberiensis*, n = 6) and *H. gorgops* (n = 1).

To evaluate the effect of growth allometry and shape differences among the taxa, the *H. amphibius* exponent derived from a postnatal ontogenetic series is given: **a**, the relationship between bizygomatic breadth and cranial length is approximately isometric, *H. madagascariensis* scales ontogenetically and isometrically with respect to these variables, *H. lemerlei* does not scale ontogenetically (trajectory shifted laterally) and has a proportionately narrower cranium for its length; **b**, the relationship between height of occipital and cranial length is negatively allometric (0.87), *H. madagascariensis* scales ontogenetically but has a proportionately taller cranium for its length due to the effect of negative allometry, *H. lemerlei* does not scale ontogenetically (trajectory shifted laterally) and the cranium is proportionate in its height - length ratio relative to *H. amphibius* due to the effect of negative allometry; **c**, the relationship between occipital height and bizygomatic breadth of the cranium is negatively allometric (0.89), *H. madagascariensis* scales ontogenetically but has a proportionately taller cranium relative to its breadth compared to *H. amphibius* due to the effect of negative allometry. *H. lemerlei* does not scale ontogenetically (trajectory shifted laterally) and has a proportionately taller cranium relative to its breadth compared to *H. amphibius*, the shape difference exaggerated further by the effect of negative allometry.

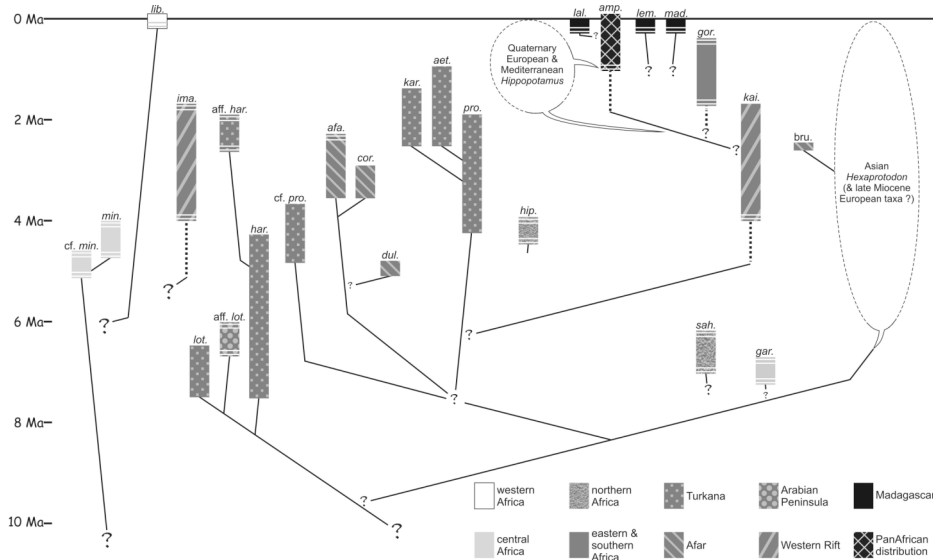
The cranium of *H. madagascariensis*, although not geometrically scaled relative to *H. amphibius* (shape differences present), is ontogenetically scaled suggesting that this variation is correlated with size. *H. lemerlei*, in contrast, has a different-shaped cranium relative to that *H. amphibius* and this variation is not correlated to size. However, although adult *H. lemerlei* cranial ratios differ from those of *H. amphibius*, the differences in the three dimensions cancel each other out so that, combined as a volumetric estimate, they do not produce a relatively larger/smaller cranium and these shape difference cannot account for the relative reduction in brain size reported. The Malagasy dwarf species are from different geographical regions of Madagascar and their external cranial dimensions exhibit adaptations to different ecological niches. Finally, the inclusion of an *H. gorgops* specimen (NHM M15162) provides no evidence that either dwarf taxon has a more similar cranial shape to *H. gorgops* than to *H. amphibius*.

Issues relating to the phylogeny and preservation of dwarf hippos

Malagasy hippos and their unique preservation

A summary diagram (adapted from ref. 69) of hippopotamine past diversity and overview of the current phylogeny is provided below. In spite of the fossil diversity of hippopotamids, represented by more than 40 species³⁶, many of these taxa are incompletely known from fragmentary skeletal remains, and even in the rare examples of fossil taxa that have complete crania preserved, these specimens do not constitute a growth series where modelling of scaling trends (such as demonstrated in this paper using the modern *H. amphibius*) are possible. The Malagasy hippos represent an extraordinary exception to this rule, not just amongst hippopotamus fossil taxa but among dwarf island mammals in general (see list of complete cranial specimens in Supplementary Table 2). For example with the exception of *Myotragus* (see main text), most Mediterranean island dwarf mammalian remains, although incredibly abundant, are not represented by complete crania necessary to determine the endocranial capacity. This is why other examples of dwarf hippopotami, such as the Cypriot pygmy hippo⁷⁰, cannot serve as a model to test scaling hypotheses

associated with brain size. Likewise, although it would be desirable to have data, comparable to that of the extant *H. amphibius*, for the extinct Pleistocene *H. gorgops* (see discussion below), an ontogenetic series is not preserved and the large, heavily mineralised cranial specimens that do exist have braincases filled with sediment (it is not logistically feasible to transport and scan such fossil material that can be over 80 cm in length).



Supplementary Figure 9. Phylogenetic relationships between African hippopotamines with temporal and geographic placement (adapted from ref. 69).

aet.: aff. *Hippopotamus aethiopicus*; *afa.*: aff. *H. afarensis*; *aff. har.*: *Archaeopotamus aff. harvardi*; *aff. lot.*: *A. aff. lothagamensis*; *amp.*: *H. amphibius*; *bru.*: *Hexaprotodon bruneti*; *cf. min.*: *Saotherium cf. mingozi*; *cf. pro.*: aff. *Hip. cf. protamphibius*; *cor.*: aff. *Hip. coryndonae*; *dul.*: aff. *Hip. dulus*; *gar.*: *Hex. garyam*; *gor.*: *Hip. gorgops*; *har.*: *A. harvardi*; *hip.*: *Hex. ? hipponensis*; *ima.*: *Hex. ? imaguncula*; *kai.*: *Hip. kaisensis*; *kar.*: aff. *Hip. karumensis*; *lal.*: *Hip. laloumena*; *lem.*: *Hip. lernelei*; *lib.*: *Choeropsis liberiensis*; *lot.*: *A. lothagamensis*; *mad.*: *Hip. madagascariensis*; *min.*: *S. mingozi*; *pro.*: aff. *Hip. protamphibius*; *sah.*: *Hex. ? sahabiensis*.

[Note that in the most recent systematic revision of the family Hippopotamidae³⁶, several African taxa that had previously been assigned to *Hexaprotodon* were reclassified as aff. *Hippopotamus* prior to the completion of further taxonomic work. However, the genus *Hippopotamus* can be distinguished by a suite of apomorphic characters that are absent in taxa referred to as aff. *Hippopotamus*.]

Phylogenetic context

The current phylogeny, focusing on the African representatives of the subfamily Hippopotaminae, is outlined in Supplementary Fig. 9 adapted from ref. 69 and is based on the first cladistic revision of the group³⁶. The living pygmy hippopotamus (*Choeropsis liberiensis*) represents a lineage distinct from all other hippopotamids, diverging from its closest relatives before 5 Ma. In spite of the much greater past diversity of hippopotamine taxa attributed to three other genera (*Saotherium*, *Hexaprotodon* and *Hippopotamus*) the tetraprotodont (4 incisor teeth) genus *Hippopotamus*, with derived anterior dentition (including the extant *H. amphibius*, and *H. gorgops*, *H. kaisensis* from Africa, the Malagasy species and the

Quaternary European and Mediterranean *Hippopotamus* species), can be distinguished relatively easily from other hippopotamines and the monophyly of this taxon is well supported^{36,69}. However, the number of species and the relationships within the genus are not clearly established. The earliest record of the genus is from a poorly known African species *H. kaisensis* (the most complete specimen is a fragment of a tetraprotodon lower jaw). In Africa, by the basal Pleistocene, *H. gorgops* had become the most ubiquitous hippopotamus, replacing all other large hippopotamids. By the Middle Pleistocene, *H. amphibius*, dentally a little more advanced than *H. gorgops*, but cranially more archaic, appears to have supplanted the earlier species in Africa, where it is still common today. Several Pleistocene *Hippopotamus* spp. also colonised Europe and Western Asia prior to their final extinction by the Holocene. The European *Hippopotamus* spp. (excluding the Mediterranean island examples), though generally larger in body size, are morphologically very similar to *H. amphibius* and considerable debate exists over the synonymy of some of these fossil specimens with *H. amphibius*⁷¹.

Three species of recently extinct *Hippopotamus* have been described from Madagascar^{45,72}. All hippopotamus material that has been dated is of Holocene age⁷³ and no established earlier fossil record of hippopotamus exists on the island. A 'dwarf' species, *H. lemerlei* from the island's coastal lowlands, is more amphibious and expresses marked sexual dimorphism⁴⁵. Another dwarfed species, *H. madagascariensis*⁴⁵, is known from the island's central highlands. A third species, *H. laloumena*⁷², from Mananjary on the East coast of Madagascar, known only from a mandible and some metapodials, is close in size to the smallest *H. amphibius* and was initially described as a subspecies of the latter, *H. amphibius standini*⁷⁴. *H. lemerlei* and *Hip madagascariensis* both possess upper canines with a very shallow posterior groove and lower canines with strong and convergent ridges, features considered to be apomorphic traits of *Hippopotamus*³⁶. The precise timing and number of immigration events that led to the colonisation and diversity of hippopotamus species on Madagascar is not known. However, the founder ancestor or ancestors were derived from the genus *Hippopotamus*. It is conceivable that another member of the genus *Hippopotamus* could have been ancestral to the dwarf taxa but several lines of evidence support the initial colonisation of Madagascar by *H. amphibius*.

- *H. laloumena* is morphologically indistinguishable from a young adult female *H. amphibius* (the Type specimen housed in l'Académie malgache, Antananarivo, was compared to a large sample of modern *H. amphibius* specimens by E. W.; data unpublished and see ref. 72). This specimen is heavily mineralised, precluding the possibility of its direct dating but suggesting that a colony of *H. amphibius* (or a species almost identical) was established on the east coast of the island historically, probably earlier than the Holocene judging from the extent of its fossilisation. The character state separating *H. amphibius* and *H. gorgops* used in the cladistic analysis of ref. 36 is not shared by the Malagasy taxa which group with *H. amphibius*. The most striking characteristics that distinguish *H. gorgops* from *H. amphibius*, that were not coded in ref. 36's analysis, are the extreme elevation of the orbits (periscopic eyes) and raised occipital crest (see Supplementary Fig. 8 b and c) which neither dwarf taxa have. In other ways the basicranial structure and cranial proportions of *H. amphibius* and *H. gorgops* are very similar.
- The Malagasy dwarf hippos can be distinguished from each other by a suite of cranial characteristics that can be linked with adaptations to different lifestyles and diet⁴⁵. *H. lemerlei*, a highly specialised amphibious species, does share with *H. gorgops* one character (thickened supraorbital margins), but there is variation within *H. lemerlei* in this feature, pointing towards their parallel evolution, a phenomenon commonly reported in highly derived insular dwarf mammals^{56,75}. Equally, *H. lemerlei* has an extremely long narrow cranial form that separates it from *H. madagascariensis*, *H. amphibius* and *H. gorgops*. The skull proportions of *H. madagascariensis* are clearly more similar to *H. amphibius*, but with orbital rim elevation completely absent in some specimens.

- The last records of *H. gorgops* are from Africa approximately 0.6 Ma⁶⁹, which precludes the possibility of ancient DNA analysis. Although the date of origin of the Malagasy species is unknown, there is currently no evidence of their pre-dating the Holocene.

Ongoing analyses of morphology and ancient DNA of hippos should shed further light on the timing of colonisation of hippos on Madagascar but there is good evidence to support the idea that a species of *Hippopotamus* founded the original population, and all continental species of *Hippopotamus* are morphologically very similar and closely related³⁶.

Supplementary notes

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