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Brain size and foramen magnum area in crows and allies (Aves: Corvidae)

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Abstract. Allometric relations between body mass, brain size and foramen magnum dimensions were studied in the Corvidae. Numerical results are given in tables 1 and 2.

Aves, Corvidae, brain size, foramen magnum, encephalization

INTRODUCTION

Brain size is well known to be related to body size in vertebrates, including birds (Snell 1892, Jerison 1973). Early researchers believed that the slope of this relation is invariable (see Jerison 1973, 1979), but subsequent research showed that considerable variation occurs between families of mammals (Wirz 1950, Portmann 1972) and birds (Mlíkovský 1985, 1989a, b, c, 1990a), and that evolution of the brain size cannot be properly studied without detailed knowledge of brain size within higher taxa (see Mlíkovský 1985). The area of foramen magnum is less studied, although it is a useful measure of the transverse area of the spinal cord in the place where it enters brain (see Mlíkovský 1990b).

Brain size in the Corvidae is of particular interest, because crows and allies are generally considered highly intelligent birds, which was confirmed in a variety of experiments (see Krušinskij 1977). First data on the brain size of corvids were presented by Hrdlička (1905) and Lapicque & Girard (1905). Subsequent data were contributed by Girard (1908), Dosse (1937), Portmann & Sutter (1940), Portmann & Vischer (1943), Sutter (1943), Portmann (1947), Vaughien (1949), Skvorcova (1952), Spector (1956), Senglaub (1963) and Mlíkovský (1977, 1985a). Foramen magnum area in the Corvidae was measured only by Mlíkovský (1985, 1990b). Overall, these authors presented data on the brain size in 20 species and on the foramen magnum area in 6 species of the Corvidae.

In addition, I studied brain size and the foramen magnum area in this family in the Smithsonian Institution in Washington, D.C., in 1997, which resulted in the knowledge of the brain size in 71 species, and of the foramen magnum area in 69 species of the Corvidae. My previous studies were done in the Institute of Zoology of the Martin Luther University in Halle and der Saale, Germany, Natural History Museum of the Humboldt University in Berlin, Germany, and in the National Museum in Praha, Czech Republic.

MATERIAL AND METHODS

Brain size was estimated as endocranial volume. The volume was determined using small shot particles of different size, up to 0.5 mm in diameter. For detailed description of the method see Mlíkovský (1989a, see also Dubravina 1979). The avian brain almost completely fills the cavum cranii (with negligible exceptions of sinus cavernosus occipitalis and sinus foraminis magni), so that volume of cavum cranii equals volume of the brain. Brain density is ca. 1.03 g×cm^{-3} (Schudnagis 1975). Hence, brain volume nearly equals brain mass numerically.

Body size was expressed as body mass. Intraspecific variation in body mass is known to be considerable (Baldwin & Kendeigh 1939, Clark 1979). Nevertheless, standard body mass is known for many bird species (Dunning 1993, and references cited therein). Data on body mass of corvids were taken from Dunning (1993) for the purpose of the present paper.

Foramen magnum area was calculated from maximum dorsoventral and transversal diameters using the formula for the area of ellipses (Bartsch 1981). The diameters were measured with a sliding caliper to an accuracy of 0.1 mm (see Mlíkovský 1990b).

Relation between variables was studied by allometric equations $Y = ß \times X^{\alpha}$, where X is independent variable, Y is dependent variable, α is allometric exponent or slope, and ß is intercept. The coefficients a and b were determined by reduced major-axis analysis (see Seim & Saether 1983). The relative coefficient of encephalization was derived from the allometric equation as follows: $Q_r = E \times b^{-1} \times S$ (Mlíkovský 1985, 1989a).

RESULTS AND DISCUSSION

Primary data are summarized in Tab. 1. As expected, all studied variables were found to be closely correlated with each other (see Tab. 2). The relative size of both brain size and foramen magnum area to body mass decrease with increasing body size, which agrees with previous findings (Mlíkovský 1989a,b,c, 1990a,b). Body size and brain size are positively correlated also when the effect of the foramen magnum area is removed ($r=0.479$, $p=0.0003$, $n=71$).

Relative size of the foramen magnum (all three dimensions) to the brain size decrease with increasing brain size, which agrees with previous findings (Mlíkovský 1990b), where, however, only the foramen magnum area was studied. Body size and foramen magnum area are not correlated when the effect of the brain size is removed ($r=0.197$, $p=0.157$, $n=69$).

Tab. 1. Body mass, brain size and foramen magnum dimensions in the Corvidae. n = number of measured brain volumes/foramen magnum areas, S = body mass [g], E = brain volume [mm³] = brain mass [g], FW = foramen magnum width [mm], FH = foramen magnum height [mm], FA = foramen magnum area [mm²], Q_r = relative encephalization [dimensionless]. Author = source of brain size data. All foramen magnum dimensions were measured by JM

species	n	S	E	FM	FH	FA	Q_r	source
Pica pica (Linnaeus, 1758)	22	210	6.2	6.2	4.7	22.9	1.230	2, 3, 8–10, 13, 14
Pica nuttalli (Audubon, 1837)	1	160	4.3	5.5	4.6	19.9	0.397	14
Ptilostomus afer (Linnaeus, 1766)	1	130	2.9	5.3	4.0	16.7	−0.748	14
Corvus frugilegus Linnaeus, 1758	19	440	7.9	6.8	6.2	33.1	0.166	4, 8, 12, 13
Corvus capensis Lichtenstein, 1823	2	695	8.3	6.6	5.4	28.0	−0.985	13, 14
Corvus crassirostris Rüppell, 1836	1		14.0	8.3	6.7	43.7		14
Corvus albicollis Latham, 1790	2	900	12.7	8.6	7.2	48.6	0.155	13, 14
Corvus rhipidurus Hartert, 1918	1	745	9.4	6.8	5.8	31.0	−0.634	14
Corvus cryptoleucus Couch, 1854	1	535	8.7	7.1	6.6	36.8	0.001	14
Corvus corax Linnaeus, 1758	71/46	1200	15.4	8.2	7.3	47.0	0.171	5, 6, 8, 11–14
Corvus ruficollis Lesson, 1831	2		10.1	7.2	6.1	34.5		13, 14
Corvus albus Müller, 1776	2	530	9.7	7.2	6.2	35.1	0.511	13, 14
Corvus torquatus Lesson, 1831	1		8	7.0	5.5	30.2		14
Corvus corone Linnaeus, 1758	67/3	470	8.5	6.7	5.7	30.0	0.267	2–10,12, 13
Corvus brachyrhynchos Brehm, 1822	10	450	8.7	7.3	6.2	35.5	0.509	1, 11, 13, 14
Corvus caurinus Baird, 1858	1	390	7.0	5.1	4.9	19.6	−0.046	14
Corvus ossifragus Wilson, 1812	1	285	6.7	5.7	4.5	20.1	0.679	14
Corvus imparatus Peters, 1929	1		4.4	6.1	4.8	23.0		14

Corvus palmarum Württemberg, 1835	1	290	5.9	6.5	4.9	25.0	0.067	14
Corvus nasicus Temminck, 1826	1	360	5.9	6.5	5.8	29.6	–0.568	14
Corvus leucognaphalus Daudin, 1800	1		8.7	6.7	5.7	30.0		14
Corvus jamaicensis Gmelin, 1789	1		7.0	6.8	5.4	28.8		14
Corvus enca (Horsfield, 1822)	1	240	6.6	6.7	4.8	25.3	1.125	14
Corvus orru Bonaparte, 1850	1	435	8.1	6.9	5.7	30.9	0.282	14
Corvus bennetti North, 1901	1	430	7.9	7.4	6.2	36	0.203	14
Corvus validus Bonaparte, 1850	1		8.7	7.7	6.0	36.3		14
Corvus tristis Lesson et Garnier, 1827	1	635	10.3	7.1	5.3	29.6	0.243	14
Corvus moneduloides Lesson, 1831	1	275	6.3	6.3	5.2	25.7	0.510	14
Corvus tropicus Kerr, 1792	1		9.9	7.6	6.2	37		14
Corvus macrorhynchos Wagler, 1827	2	490	9.7	7.6	6.6	39.4	0.740	14
Corvus splendens Vieillot, 1817	1	295	5.7	6.1	5.4	25.9	–0.140	14
Corvus monedula Linnaeus, 1758	13/0	200	4.8					14
Pyrrhocorax graculus (Linnaeus, 1766)	2	150	3.5	5.8	4.4	20	–3.803	14
Pyrrhocorax pyrrhocorax (Linnaeus, 1758)	3	300	6.1	6.6	4.5	23.3	2.146	14
Podoces hendersoni (Hume, 1871)	1	120	3.9	5.6	4.5	19.8	0.812	14
Podoces panderi Fischer, 1821	1		2.6	4.7	3.7	13.7		14
Nucifraga caryocatactes (Linnaeus, 1758)	3	160	5.4	6.2	4.7	22.9	1.413	14
Nucifraga columbiana (Wilson, 1811)	1		5.3	5.9	4.3	19.9		14
Gymnorhinus cyanocephalus Wied, 1841	1	105	2.6	5.1	4.0	16.0	–0.601	14
Cyanopica cyana (Pallas, 1776)	2	70	2.7	4.9	3.7	14.2	0.758	14
Aphelocoma caerulescens (Bosc, 1795)	1	80	2.8	5.3	4.2	17.5	0.527	14
Aphelocoma ultramarina (Bonaparte, 1825)	1	125	3.7	5.3	4.0	16.7	0.457	14
Cyanolyca argentigula (Lawrence, 1875)	1	200	2.6	4.5	3.4	12.0	–2.495	14
C. viridicyanea (Lafresnaye et Orbigny, 1838)	1	100	3.3	5.5	3.8	16.4	0.603	14
Cissilopha beecheii (Vigors, 1829)	1	195	4.3	6.2	4.5	21.9	–0.180	14
Cissilopha sanblasiana (Lafresnaye, 1842)	1	110	3.0	5.6	4.0	17.6	–0.099	14
Cissilopha melanocyanea (Hartlaub, 1844)	1	110	3.3	5.4	3.3	14.0	0.326	14
Cyanocorax yncas (Boddaert, 1783)	3	80	2.4	5.2	3.9	15.9	–0.159	14
C. mystacalis (Geoffroy-St.-Hilaire, 1835)	1		3.2	6.4	4.7	23.6		14
Cyanocorax affinis Pelzeln, 1856	1	210	3.7	6.1	4.3	20.6	–1.065	14
Cyanocorax chrysops (Vieillot, 1818)	2	155	2.7	5.7	3.2	14.3	–1.576	13, 14
Cyanocorax cayanus (Linnaeus, 1766)	1	175	4.2	5.8	4.2	19.1	0.034	14
Cyanocorax violaceus DuBus, 1847	1	260	4.7	5.9	4.2	19.5	–0.629	14
Cyanocorax cyanomelas (Vieillot, 1818)	1	220	3.8	6.1	4.7	22.5	–1.082	14
Cyanocorax caeruleus (Vieillot, 1818)	1	270	3.7	6.4	4.7	23.6	–1.803	14
Psilorhinus morio (Wagler, 1829)	1	205	5.0	6.1	5.0	24.0	0.343	14
Calocitta formosa (Swainson, 1827)	1	210	4.2	6.1	4.2	20.1	–0.501	14
Cyanocitta cristata (Linnaeus, 1758)	4	85	3.0	5.3	3.7	15.4	0.659	1, 13, 14
Cyanocitta stelleri (Gmelin, 1788)	1	130	3.4	5.4	4.1	17.4	–0.035	14
Garrulus lidthi Bonaparte, 1850	1		4.3					13
Garrulus glandarius (Linnaeus, 1758)	29	160	4.2	5.6	4.3	18.9	0.297	2–4, 6, 8–10, 12–14
Perisoreus infaustus (Linnaeus, 1758)	1	85	2.7	4.9	3.7	14.2	0.190	14
Perisoreus canadensis (Linnaeus, 1766)	1	75	2.4	4.6	3.7	13.4	0.030	14
Platylophus galericulatus (Cuvier, 1816)	1		2.5	5.1	3.7	14.8		14
Crypsirina temia (Daudin, 1800)	1		1.8	4.7	3.8	14		14
Dendrocitta formosae Swinhoe, 1863	1	105	2.4	4.9	3.6	13.9	–0.957	14
Dendrocitta occipitalis (Müller, 1835)	1		2.7	5.0	3.7	14.5		14
Dendrocitta vagabunda (Latham, 1790)	2	100	2.6	5.0	3.5	13.7	–0.459	13, 14
Urocissa erythrorhyncha (Boddaert, 1783)	5		3.2	5.9	4.2	19.5		13, 14
Urocissa caerulea Gould, 1863	1	215	4.6	6.2	4.4	21.4	–0.163	14
Cissa chinensis (Boddaert, 1783)	1	125	3.0	5.3	3.9	16.2	–0.478	14

source: 1 – Hrdlička 1905, 2 – Lapicque & Girard 1905, 3 – Girard 1908, 4 – Dosse 1937, 5 – Portmann & Sutter 1940, 6 – Portmann & Vischer 1943, 7 – Sutter 1943, 8 – Portmann 1947, 9 – Vaughien 1949, 10 – Skvorcova 1952, 11 – Spector 1956, 12 – Senglaub 1963, 13 – Mlíkovský 1999a, 14 – Mlíkovský, this paper

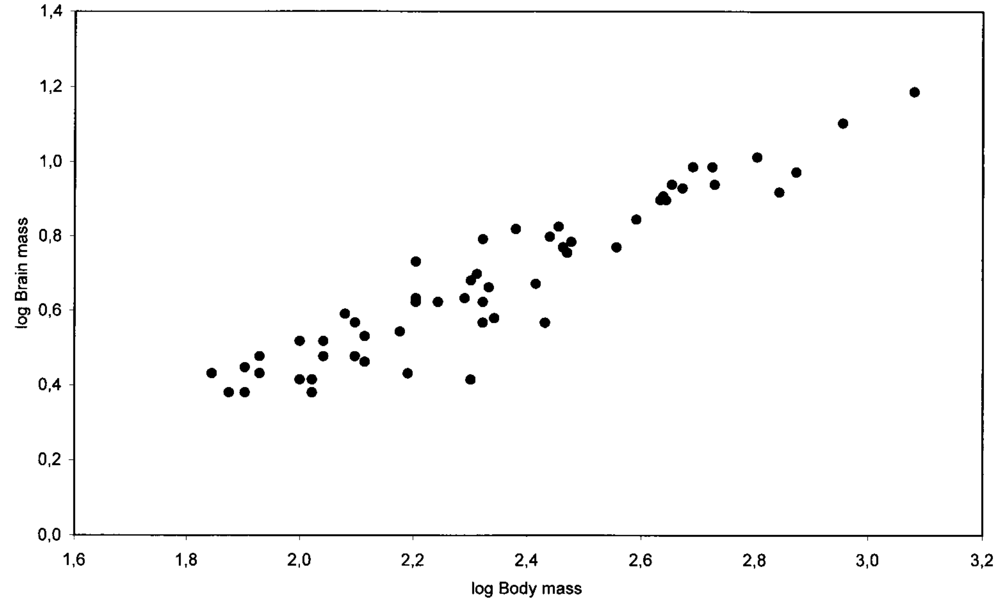

Fig. 1. Relation between body mass [g] and brain size [mass = volume; g = cm^3] in the Corvidae.

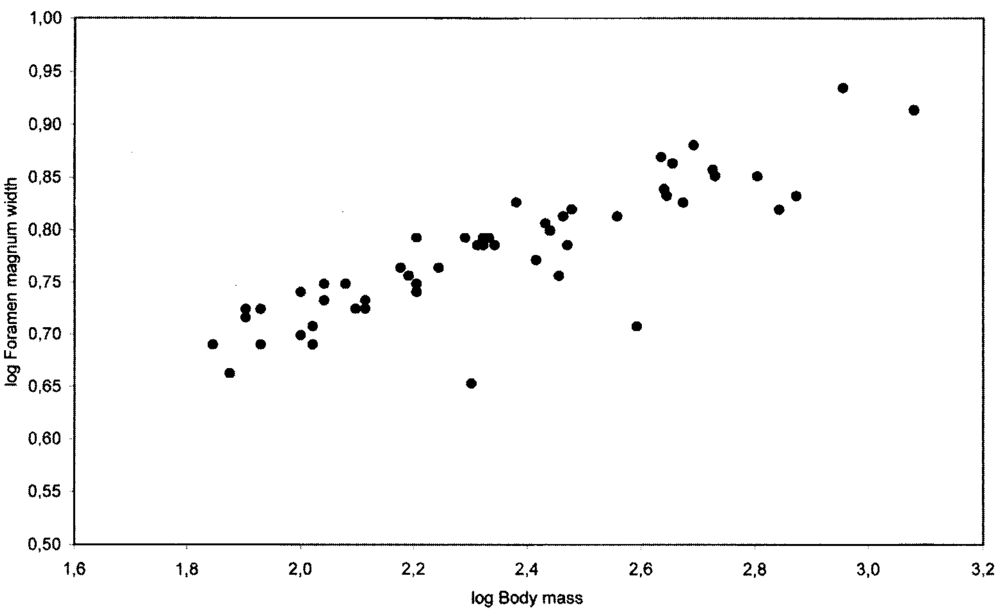

Fig. 2. Relation between body mass [g] and the width of foramen magnum [mm] in the Corvidae.

Tab. 2. Regression between individual variables. The values refer to the following equation: log Y = ß+α×logX. Standard errors for α and ß are added in each case. All correlations (r) are significant at $p < 0.001$. n = number of species

Y	X	ß	?	r	n
brain volume	body mass	−0.859±0.1030	0.660±0.0437	0.902	55
foramen magnum width	body mass	0.357±0.0388	0.181±0.0164	0.837	55
foramen magnum height	body mass	0.783±0.0481	0.253±0.0204	0.864	55
foramen magnum area	body mass	0.325±0.0785	0.436±0.0332	0.876	55
foramen magnum width	brain volume	0.597±0.0125	0.269±0.0173	0.907	71
foramen magnum height	brain volume	0.416±0.0151	0.370±0.0209	0.926	71
foramen magnum area	brain volume	0.908±0.0234	0.639±0.0325	0.939	71
foramen magnum width	foramen magnum area	0.213±0.0200	0.422±0.0148	0.903	69
foramen magnum height	foramen magnum area	−0.108±0.0200	0.578±0.0147	0.983	69
foramen magnum height	foramen magnum width	−0.288±0.0611	1.227±0.0779	0.909	69

An interesting new observation is that the shape of foramen magnum changes with both body size and brain size in a predictable manner. The slope of the regression is higher in the height that in the width of foramen magnum in both cases. This means that relative height of the foramen to its width increases with both increasing body size and brain size: Foramen magnum is flat in smallest corvids, and almost rounded in largest ones.

Evolution of encephalization within the family Corvidae has not been studied as yet. The data presented here are obscured especially by inaccurately estimated standard body masses for some species (which is indicated by outlying Q_r values; see Tab. 1). In spite of these limitations, the data indicate the following: All south-east Asian genera (*Dendrocitta* Gould, 1833, *Urocissa* Cabanis,

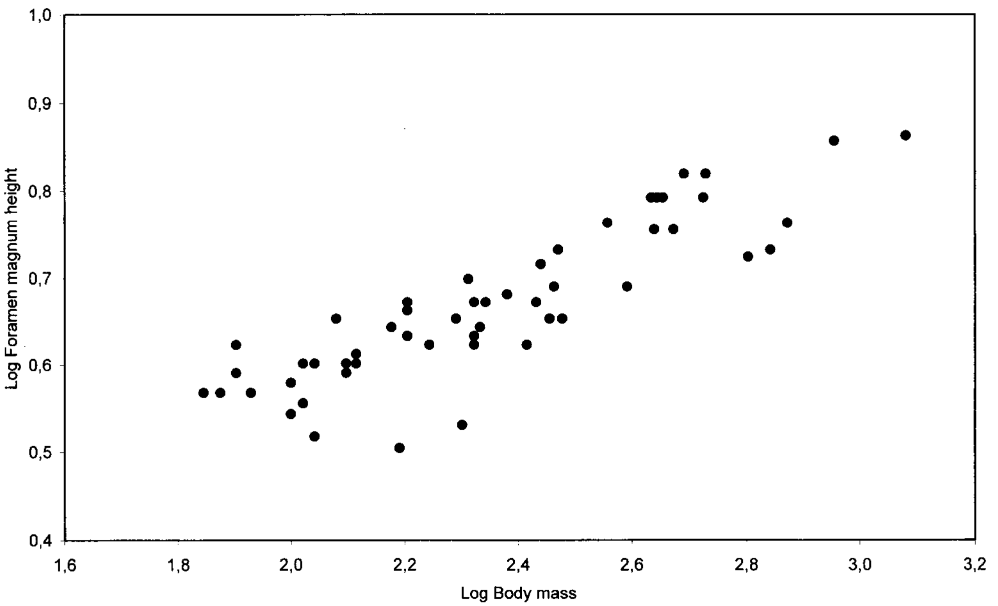

Fig. 3. Relation between body mass [g] and the height of foramen magnum [mm] in the Corvidae.

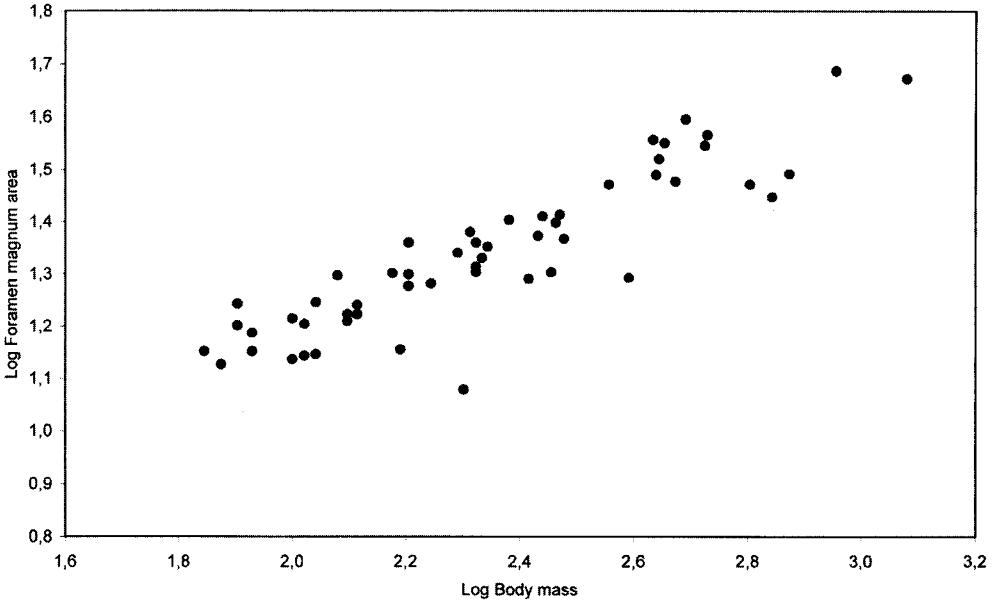

Fig. 4. Relation between body mass [g] and foramen magnum area [mm^2] in the Corvidae.

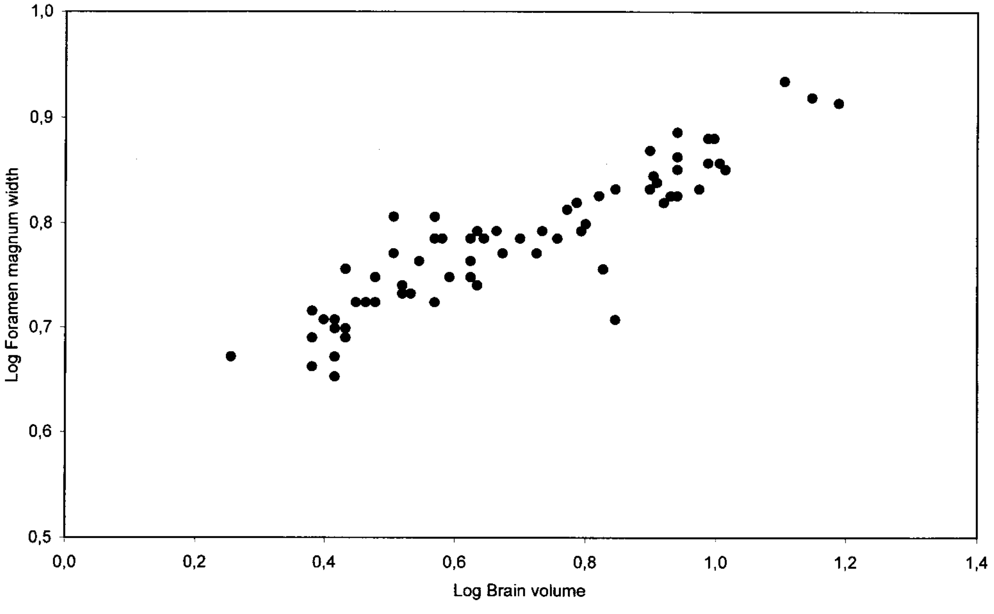

Fig. 5. Relation between brain size [mass = volume; g = mm^3] and the width of foramen magnum [mm] in the Corvidae.

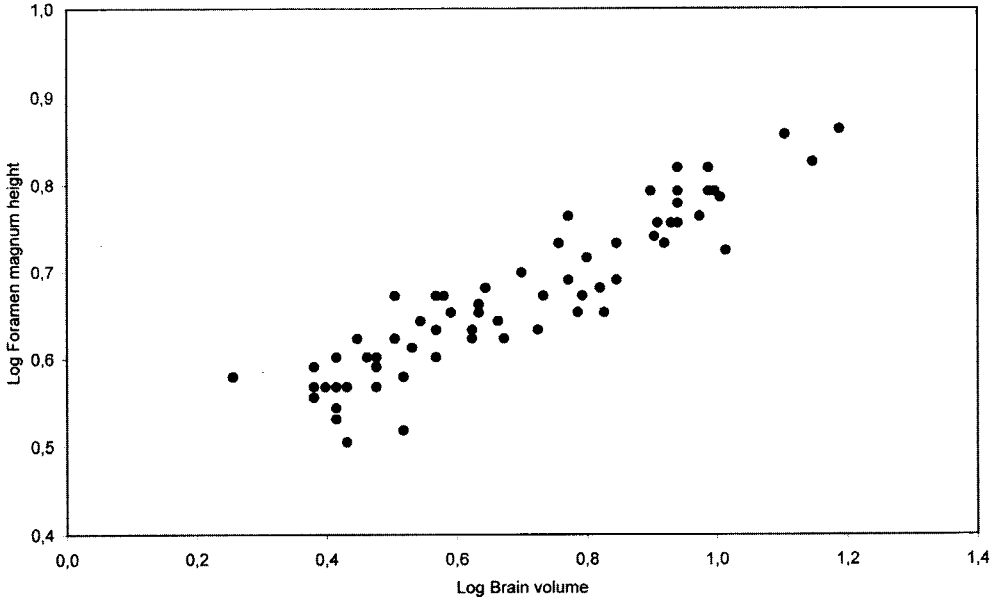

Fig. 6. Relation between brain size [mass = volume; g = mm^3] and the height of foramen magnum [mm] in the Corvidae.

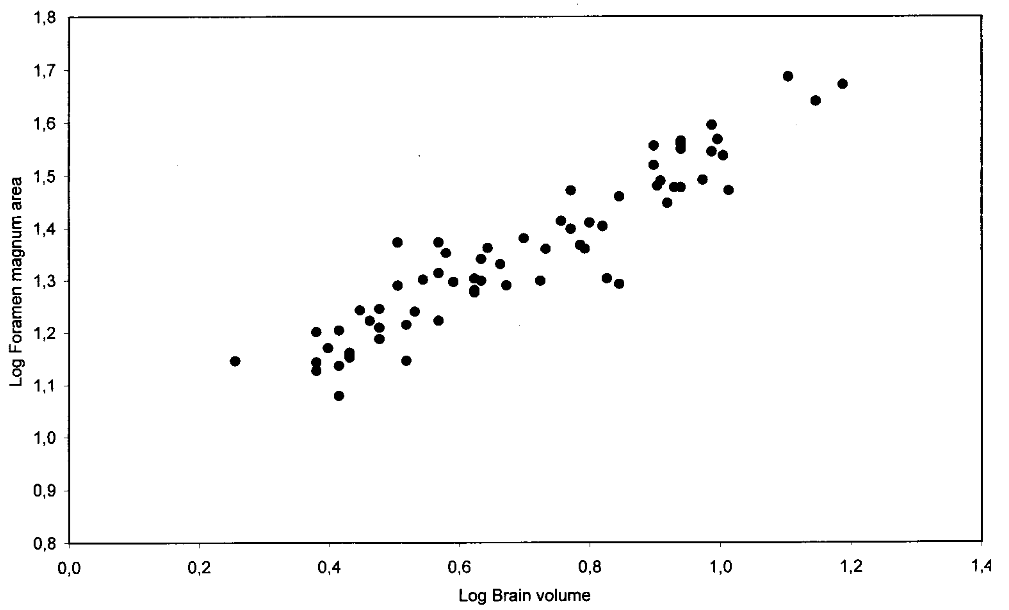

Fig. 7. Relation between brain size [mass = volume; g = mm^3] and foramen magnum area [mm^2] in the Corvidae.

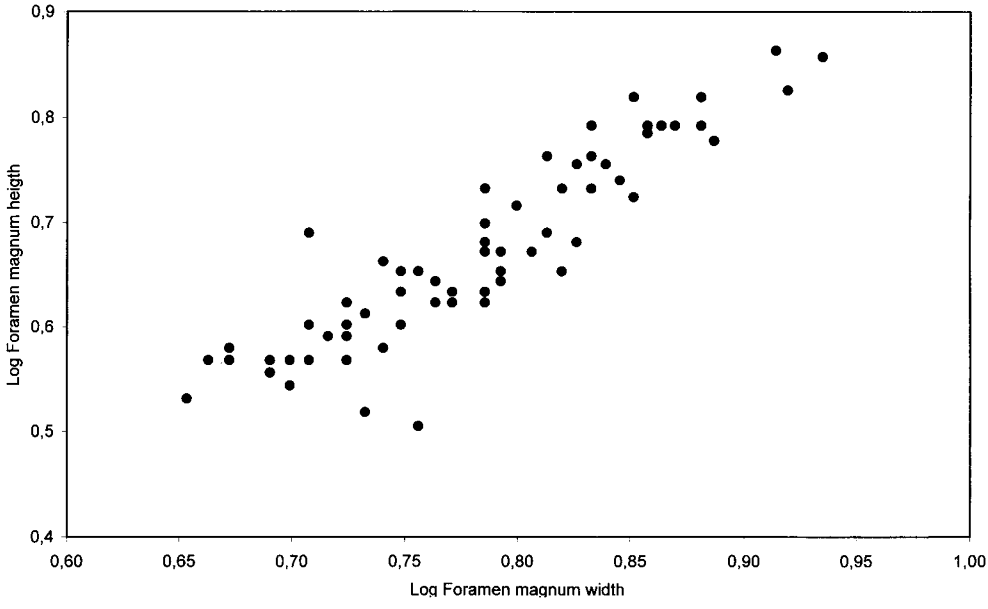

Fig. 8. Relation between the width and height of foramen magnum [mm] in the Corvidae.

1851, and *Cissa* Boie, 1826) and the African genus *Ptilostomus* Swainson, 1837 have very low encephalization (Q_r<–0.4). Most Holarctic genera (*Pica* Brisson, 1760, *Podoces* Fischer, 1821, *Nucifraga* Brisson, 1760, and *Cyanopica* Bonaparte, 1850) have high encephalization (Q_r>+0.1), while both species of the genus *Pyrrhocorax* Tunstall, 1771 fall far outside the predicted range (see Tab. 1). The encephalization of *Corvus* Linnaeus, 1758 species ranges widely (probably as the result of insufficiently known body masses of some species), but most species fall in the range Q_e = +0–0.6, being thus comparable to the Holarctic genera. Neotropic genera of the Corvidae have highly variable encephalization, which is difficult to interpret without additional data. Further analysis of the evolution of encephalization within the family Corvidae depends on the clarification of the phylogeny of corvid genera.

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