Acta Soc. Zool. Bohemoslov., **54: 97—106, 1990**
ISSN 0862—5247

FORAMEN MAGNUM AREA IN BIRDS

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Abstract. A review of the foramen magnum area in birds is presented. Overall, data on the foramen magnum area are given for 174 extant species belonging to 42 families of birds. Allometric relationships between the foramen magnum area and the body size and between the foramen magnum area and the brain size are estimated in 6 families of birds and in non-Passeriformes as a whole.

INTRODUCTION

Body elements are generally known to scale interspecifically with the body size (Röhrs 1959, 1961, Gould 1966). This applies also to the nervous system, particularly the brain (Jerison 1973, Szarski 1980, and many others).

In birds, allometric relationships of the brain size to the body size were recently summarized by Mlíkovský (1989 a-c, 1990). However, no such study exists thus far for the foramen magnum area in birds, although Wiedenfeld (1985) established that it is closely correlated with body mass at the interspecific level. This relation was for the first time found in mammals by Radinsky (1967) who stressed its importance for comparative neurology by pointing out that the foramen magnum area is highly correlated with, though larger than, cross-sectional area of medulla, approximately at the point where medulla oblongata transgrades into medulla spinalis. In the present paper, a first review of the foramen magnum area in birds will be presented, with special respect to the relation of the foramen magnum area to the body size and to the brain size. Anatomical nomenclature follows Baumel et al. (1979) throughout the present paper.

It should also be noted here, that foramen magnum is an important osteological feature of the occipital part of the avian skull. This region received remarkably less attention from morphologists thus far. Important exceptions are the Duijm's (1951) discussion of the inclination of foramen magnum in relation to the skull basis and the Goedbloed's (1958) comparative study of the condylus occipitalis in birds.

I thank R. Piechocki (Halle/Saale), G. Mauersberger and B. Stephan (Berlin) and J. Hanzák and I. Heráň (Praha) for permissions to study avian skulls under their care.

MATERIAL

All the skeletal material investigated in this study is from the collections of the Department of Zoology of the National Museum in Praha, Czechoslovakia; the Institute of Zoology of the Martin Luther University in Halle (Saale), East Germany;

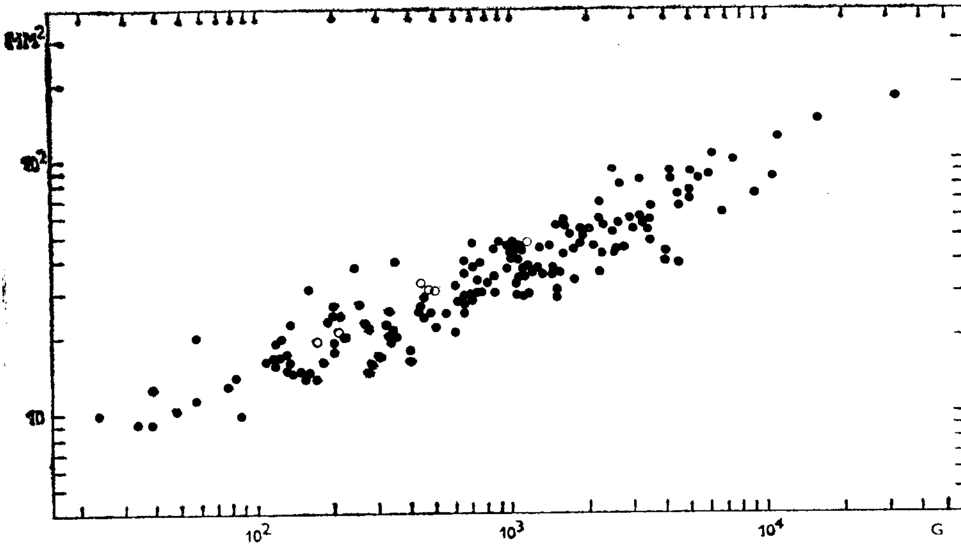

Fig. 1. Relationship between the foramen magnum area (Y axis) and the body mass (X axis) in birds. • = non-Passeriformes, o = Passeriformes. See Table 1 for exact data.

and the Museum of Natural History of the Humboldt University in Berlin, East Germany. A complete list of measurements is given by Mlíkovský (1985).

Measurements were made on 523 skulls from 166 extant species belonging to 41 different families of birds. These measurements were supplemented by the data published by Stephan (1979) on the foramen magnum in penguins. The aggregate data contains estimates of foramen magnum area in 554 skulls from 174 species belonging to 42 families of birds.

METHODS

Maximum dorsoventral and transversal diameters of foramina magna were measured with a sliding caliper to an accuracy of 0.1 mm. Using these measures, foramen magnum area was calculated according to the formula for the area of ellipses (Bartsch 1981). For methods of estimating body size and brain size see Mlíkovský (1989 a). Note that data on brain size given in the present paper may differ from those given by Mlíkovský (1989 a—c, 1990). This is because only those brain size estimates were used here when foramen magnum area was estimated for the same skull. The few exceptions are mentioned below.

Foramen magnum area was expressed as a function of body size and brain size by allometric equations $F = b \cdot S^a$ and $F = b \cdot E^a$, respectively, where F is foramen magnum area (mm^2), E is brain size (volume; cm^3), S is body size (mass; g), a is allometric exponent or slope and b is intercept. The allometric equation is linear after logarithmic tarnsformation. The coefficients a and b appearing in allometric equations were determined by the reduced major-axis analysis (see Seim and Saether 1983).

Correlations between variables were tested for significance using Olkin and Pratt's (1958) modification of the Bravais' correlation coefficient (r*). Statistical comparisons were calculated according to standard formulas (Sachs 1974). In the following, a 5% probability level is taken as significant for Type I errors (cf. Sachs 1974: 96).

Table 1. Foramen magnum area in birds. n = number of measured skulls (figures in parentheses are for brain size estimates, if different), S = body size (g), E = brain size (cm^3), F = foramen magnum area (mm^2). All measurements are by the author, except of those of the foramen magnum area in the Spheniscidae which were taken from Stephan (1979). The sequence of families follows Storer (1971), species limits are after Wolters (1975–1982)

Taxon	n	S	E	F
Tinamidae				
Crypturellus soui	1		1.9	16.5
Crypturellus tataupa	1		1.1	11.7
Podicipedidae				
Podiceps griseigena	6	720	3.05	29.8
Podiceps cristatus	9	1 070	3.8	34.0
Podiceps auritus	1	480	2.4	25.0
Podiceps nigricollis	1	330	1.7	19.2
Tachybaptes ruficollis	13	200	1.6	18.8
Spheniscidae				
Aptenodytes forsteri	4	32 000	44.3	175.7
Aptenodytes patagonicus	3(1)	16 000	28.5	142.8
Eudyptes chrysolophus	1	4 200	13.0	84.6
Eudyptes crestatus	3(1)	2 500	13.5	91.8
Pygoscelis adeliae	2	5 000	17.5	90.6
Pygoscelis papua	8(3)	6 200	18.5	107.3
Spheniscus humboldti	2	4 200	17.5	90.6
Spheniscus demersus	8(5)	2 700	13.7	81.0
Procellariidae				
Diomedea sp.	1		27.5	113.0
Fulmarus glacialis	1	700	7.0	46.9
Sulidae				
Sula bassana	3	3 200	19.5	82.8
Phalacrocoracidae				
Phalacrocorax pygmaeus	2	700	4.2	27.8
Phalacrocorax carbo	14	2 100	10.8	46.0
Anseridae				
Anseranas semipalmata[1]	1	2 200	9.5	69.1
Cygnus cygnus	1	9 000	16.0	74.2
Cygnus olor	6	10 500	14.9	86.2
Coscoroba coscoroba	2	3 500	9.25	58.1
Anser cygnoides	1	3 500	12.0	65.7
Anser fabalis	3	2 800	12.0	58.8
Anser erythropus	2	1 850	6.8	46.8
Anser anser	3	3 350	11.2	53.3
Branta leucopsis	1	1 760	8.0	44.8
Branta bernicla	2	1 400	6.1	46.6
Branta ruficollis	2	1 280	5.1	35.5

cont.

Taxon	n	S	E	F
Cereopsis novaehollandiae	1	3 500	9.0	48.4
Chloephaga picta	1	2 580	6.5	43.6
Alopochen aegyptiacus	3	2 300	7.1	56.7
Tadorna tadorna	2	1 100	5.3	36.9
Tadorna ferruginea	2	1 250	4.8	37.4
Anas penelope	1	740	4.4	33.7
Anas strepera	2	650	3.4	28.8
Anas crecca	2	325	2.7	21.9
Anas querquedula	3	330	2.5	20.1
Anas luzonica	2	950	5.05	37.4
Anas platyrhynchos	3	1 100	5.9	44.7
Anas clypeata	2	610	3.45	28.1
Netta rufina	5	1 160	4.9	38.4
Aythya ferina	2	850	5.4	29.4
Aythya collaris	1	700	4.7	37.9
Aythya marila	1	1 000	5.3	45.3
Somateria mollissima	4	2 000	8.0	54.2
Clangula hyemalis	1	650	5.8	40.1
Melanitta nigra	8	980	5.9	43.4
Melanitta fusca	2	1 500	7.7	56.4
Bucephala clangula	1	900	6.0	47.2
Mergus albellus	1	650	4.0	35.6
Mergus serrator	2	1 050	5.1	33.6
Mergus merganser	2	1 300	6.7	45.4
Phoenicopteridae				
Phoenicopterus ruber	2	3 000	10.8	54.1
Ardeidae				
Botaurus stellaris	3	1 150	6.5	29.4
Ixobrychus minutus	1	170	1.6	13.8
Nycticorax nycticorax	2	650	5.15	24.9
Ardeola ibis	2	340	3.7	20.8
Ardeola ralloides	2	180	2.2	16.1
Ardea cinerea	8	1 500	8.25	31.1
Egretta garzetta	2	500	3.35	22.2
Casmerodius albus	1	1 100	6.0	29.2
Threskiornithidae				
Plegadis falcinellus	2	690	4.45	28.6
Platalea leucorodia	2	1 700	10.75	51.2
Ciconiidae				
Ciconia nigra	4	2 700	11.9	45.3
Ciconia abdimii[2]	1(2)	1 450	8.25	37.2
Ciconia episcopus	1	2 250	10.5	42.8
Ciconia ciconia	14	3 300	15.4	55.9
Cathartidae				
Coragyps atratus	2	1 900	10.0	49.5
Vultur gryphus	1	11 000	31.5	122.5
Sarcoramphus papa	1	4 500	21.0	72.3

cont.

Taxon	n	S	E	F
Accipitridae				
Gyps fulvus	1	7 500	26.5	100.3
Gypaetus barbatus	2	6 000	24.25	88.7
Haliaeetus albicilla	41	5 000	19.0	75.9
Haliaeetus leucocephalus	2	5 000	18.25	70.0
Milvus milvus	3	1 100	8.2	45.4
Milvus migrans	8	850	7.25	45.0
Pernis apivorus	3	750	7.1	39.6
Accipiter gentilis	10	1 000	7.95	46.0
Accipiter nisus	7	200	2.9	24.5
Buteo lagopus	5	1 000	9.0	45.7
Buteo buteo	12	1 000	8.4	46.2
Aquila chrysaetos	3	4 500	17.3	66.7
Aquila clanga	1	2 200	11.5	58.4
Aquila pomarina	2	1 600	10.75	55.1
Circus aeruginosus	5	600	5.8	31.9
Circus cyaneus	8	450	4.6	29.2
Pandion haliaetus	1	1 600	9.0	56.7
Falconidae				
Falco peregrinus	1	800	6.2	32.6
Falco columbarius	3	190	2.8	23.3
Falco tinnunculus	3	200	4.0	26.4
Falco vespertinus	1	160	2.7	31.3
Falco subbuteo	1	240	3.6	37.9
Cracidae				
Crax alector	1		7.0	44.2
Phasianidae				
Tetrastes bonasia	1	400	1.7	17.7
Lyrurus tetrix	1	1 050	3.7	29.2
Tetrao urogallus	2	4 500	5.6	39.0
Pavo cristatus	1	4 000	5.0	40.7
Chrysolophus pictus	1	600	2.7	21.2
Phasianus colchicus	6	1 500	3.7	29.1
Crossoptilon auritus	1	1 750	5.9	34.2
Gallus gallus (wild)	1	850	3.1	35.2
Perdix perdix	[illegible]	400	1.75	15.9
Coturnix coturnix	1	90	0.7	9.2
Meleagris gallopavo (wild)	1	4 000	6.0	43.6
Rallidae				
Porzana porzana	1	80	1.0	12.3
Gallinula chloropus	1	280	1.9	15.5
Fulica americana	1	430	2.9	25.4
Fulica atra	4	650	3.4	27.4
Heliornithidae				
Heliornis fulica	1	135	1.4	22.5

cont.

Taxon	n	S	E	F
Gruidae				
Grus grus	3	5 500	18.5	83.6
Anthropoides virgo	5	2 500	9.4	42.9
Balearica pavonina	4	3 250	13.0	58.6
Psophiidae				
Psophia crepitans	1	1 000	5.8	41.1
Otididae				
Otis tarda	17	6 600	10.6	62.0
Haematopodidae				
Haematopus ostralegus	1	550	4.0	24.8
Recurvirostridae				
Recurvirostra avocetta	1	340	1.9	20.5
Charadriidae				
Vanellus vanellus	1	200	2.2	20.5
Scolopacidae				
Scolopax rusticola	4	330	2.4	25.2
Philomachus pugnax	1	155	1.4	13.8
Gallinago gallinago	2	130	1.35	17.0
Lymnocryptes minimus	1	60	0.9	19.6
Numenius arquata	1	760	4.4	29.4
Actitis hypoleucos	1	50	0.7	9.9
Laridae				
Larus canus	2	450	3.7	24.0
Larus ridibundus	1	300	2.8	16.7
Sterna hirundo	1	135	1.7	15.7
Alcidae				
Cepphus grylle	2	430	3.05	26.0
Uria aalge	1	1 050	5.4	40.9
Gaviidae				
Gavia stellata	1	1 600	6.0	42.8
Gavia arctica	10	2 500	7.5	52.3
Columbidae				
Goura cristata	1	2 200	5.7	35.8
Zenaidura macroura	1	120	1.1	15.5
Streptopelia turtur	1	125	1.4	16.3
Streptopelia decaocto	1	275	1.4	14.5

cont.

Taxon	n	S	E	F
Psittacidae				
Forpus passerinus	1	25	1.0	9.5
Agapornis pullarius	1		1.4	10.7
Anodorhynchus hyacinthinus	1		24.5	59.7
Psittacus erithacus	1	350	8.0	39.6
Psittacula alexandri	3	125	3.6	19.5
Trichoglossus haematodus	4	150	2.4	14.6
Platycercus eximius	1	110	2.5	16.0
Platycercus elegans	1	135	3.7	14.7
Cuculidae				
Clamator glandarius	1	135	1.7	14.3
Cuculus canorus[2]	1(9)	120	1.6	15.6
Strigidae				
Tyto alba	1	275	5.0	21.4
Asio otus	6	270	6.0	21.8
Strix aluco	10	500	9.0	30.3
Bubo poensis	1	1 450	9.0	36.1
Bubo virginianus	1	1 500	18.5	47.1
Bubo bubo	22	2 600	17.4	56.9
Bubo capensis	1	1 200	11.5	36.8
Nyctea scandiaca	1	1 900	18.0	53.4
Athene noctua	1	120	4.5	18.7
Ninox scutulata	1	220	3.1	20.2
Apodidae				
Apus apus	1	40	0.8	12.2
Alcedinidae				
Alcedo atthis	1	40	0.8	8.7
Coraciidae				
Coracias garrulus	1	160	1.8	14.2
Upupidae				
Upupa epops	1	60	1.3	11.0
Ramphastidae				
Ramphastos tucanus	1		5.0	24.5
Picidae				
Dendrocopos major	3	85	2.4	13.7
Picus viridis	1	200	3.9	24.7
Dryocopus martius	1	250	8.0	26.7
Jynx torquilla	1	35	0.8	8.3

cont.

Taxon	n	S	E	F
Eurylaimidae				
Cymbirhynchus macrorhynchus	1		1.4	14.8
Cotingidae				
Pyroderus scutatus	2		4.45	23.3
Tyrannidae				
Colonia colonus	1		1.3	12.0
Corvidae				
Corvus corax	41	1 150	14.5	47.7
Corvus americanus	1		9.0	23.7
Corvus corone	3	470	8.7	31.2
Corvus frugilegus	2	440	7.5	33.1
Garrulus glandarius	2	170	3.95	19.4
Pica pica	1	210	5.2	21.1

1) Excluded from the calculations for the family Anseridae.
2) Brain size and foramen magnum area estimated on different skulls.

RESULTS

The data were sufficient for calculation of regression equations in 6 families of birds and in non-Passeriformes as a whole (Figure 1, Table 1). The results are presented below.

In Spheniscidae, foramen magnum area is positively correlated with both body size ($r^* = 0.976$, $p < 0.001$) and brain size ($r^* = 0.975$, $p < 0.001$). Their allometric relations are $F = 6.792\ S^{0.313 \pm 0.0328}$ and $F = 16.232\ E^{0.631 \pm 0.0651}$, respectively ($n = 8$). When the effect of body size is removed by the partial correlation analysis, foramen magnum area and brain size ceaze to be correlated ($r^*_{FE.S} = 0.497$, n.s.).

In Ardeidae, foramen magnum area is positively correlated with both body size ($r^* = 0.988$, $p < 0.001$) and brain size ($r^* = 0.990$, $p < 0.001$). Their allometric relations are $F = 2.472\ S^{0.353 \pm 0.0251}$ and $F = 10.852\ E^{0.525 \pm 0.0332}$, respectively ($n = 8$). Foramen magnum area and brain size are positively correlated even when the effect of the body size is removed ($r^*_{FE.S} = 0.794$, $p < 0.05$).

In Anseridae, foramen magnum area is positively correlated with both body size ($r^* = 0.885$, $p < 0.001$) and brain size ($r^* = 0.943$, $p < 0.001$). Their allometric relations are $F = 2.443\ S^{0.395 \pm 0.0329}$ and $F = 12.449\ E^{0.675 \pm 0.0427}$, respectively ($n = 34$). Foramen magnum area and brain size are positively correlated even when the effect of the body size is removed ($r^*_{FE.S} = 0.704$, $p < 0.001$).

In Accipitridae, foramen magnum area is positively correlated with both body size ($r^* = 0.980$, $p < 0.001$) and brain size ($r^* = 0.984$, $p < 0.001$). Their allometric relations are $F = 3.266\ S^{0.375 \pm 0.0199}$ and $F = 11.674\ E^{0.642 \pm 0.0308}$, respectively ($n = 17$). Foramen magnum area and brain size are marginally positively correlated even when effect of the body size is removed ($r^*_{FE.S} = 0.468$, $p < 0.1$).

In Phasianidae, foramen magnum area is positively correlated with both body size ($r^* = 0.958$, $p < 0.001$) and brain size ($r^* = 0.969$, $p < 0.001$). Their allometric relations are $F = 1.585\ S^{0.404 \pm 0.0411}$ and $F = 11.528\ E^{0.728 \pm 0.0633}$, respectively ($n = 11$). The correlation between foramen magnum area and brain size approaches significance even when effect of the body size is removed ($r^*_{FE.S} = 0.622$, $p < 0.1$).

In Strigidae, foramen magnum area is positively correlated with both body size ($r^* = 0.977$, $p < 0.001$) and brain size ($r^* = 0.966$, $p < 0.001$). Their allometric relations are $F = 2.523\ S^{0.391 \pm 0.0317}$ and $F = 7.577\ E^{0.664 \pm 0.0653}$, respectively ($n = 10$). Foramen magnum area and brain size are positively correlated even when effect of the body size is removed ($r^*_{FE.S} = 0.784$, $p < 0.05$).

In non-Passeriformes as a whole, foramen magnum area is positively correlated with both body size ($r^* = 0.932$, $p < 0.001$) and brain size ($r^* = 0.954$, $p < 0.001$). Their allometric relations are $F = 1.799\ S^{0.439 \pm 0.0128}$ and $F = 11.601\ E^{0.649 \pm 0.0653}$, respectively ($n = 159$). Foramen magnum area and brain size are positively correlated even when effect of the body size is removed ($r^*_{FE.S} = 0.811$, $p < 0.001$).

DISCUSSION

As expected, foramen magnum area was found to be correlated both with body size (see also Wiedenfeld 1985) and with brain size, which itself is known to be closely related to body size in birds (Mlíkovský 1989 a-c, 1990 . Because the relation between foramen magnum area and brain size could have been caused by common dependence on the body size, I removed its effect using partial correlation analysis. The results showed that even after this removal, foramen magnum area and brain size are positively correlated. The only exception found was the Spheniscidae (penguins), but I consider this an artifact, because in this family foramen magnum area and brain size were measured on different skulls, which fact may well have obscured the subtle partial correlation between foramen magnum area and brain size in this family. This finding means that higher encephalized birds possess also relatively larger foramen magnum and, hence, relatively more massive medulla than less encephalized birds.

Another point of interest was whether the correlations between the three studied variables are equal, or differ from each other. Comparisons (performed for non-Passeriformes as a whole) revealed that the brain size is more closely correlated with the body size than the foramen magnum area ($z = 18.011$, $p < 0.001$), but no such difference was found between r^*_{FE} and r^*_{FS} ($z = 1.827$, n.s.), which indicates that foramen magnum area is equally well correlated with body size as with brain size. Not surprizingly, $r^*_{FE.S}$ is significantly lower than r^*_{FE} ($z = 6.613$, $p < 0.001$) which reflects the removed effect of the body size in $r^*_{FE.S}$. After this removal, brain size explains approximately 66 % of the observed variability (the value was 91 % before this removal). Taken together, body size and brain size explain 95 % of the observed variability of the foramen magnum area in birds.

SUMMARY

(1) Data on the foramen magnum area in 174 extant species belonging to 42 different families of birds, and the relations of the foramen magnum area to the body size and the brain size in 6 families and in non-Passeriformes as a whole were presented.

(2) Foramen magnum area was found to be closely correlated both with the body size and with the brain size; the degree of correlation was similar in both cases.

(3) Foramen magnum area was found to be less closely correlated with the body size than the brain size.

(4) Positive correlation between the foramen magnum area and the brain size was found to hold even after the effect of the body size is removed. It means that higher encephalized birds possess a relatively more massive medulla than less encephalized ones.

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Received March 16, 1989; accepted December 14, 1989