Věst. čs. Společ. zool., 53: 33–47, 1989
ISSN 0042–4595

BRAIN SIZE IN BIRDS: 1. TINAMIFORMES THROUGH CICONIIFORMES

Jiří MLÍKOVSKÝ

Department of Evolutionary Biology, Czechoslovak Academy of Sciences, Sekaninova 28, 128 00 Praha 2, Czechoslovakia

Abstract. Brain size in 182 bird species and its relation to body size in 7 families of birds are estimated. The following avian orders are considered: Tinamiformes, Rheiformes, Struthioniformes, Casuariiformes, Dinornithiformes, Podicipediformes, Sphenisciformes, Procellariiformes, Pelecaniformes, Anseriformes, Phoenicopteriformes and Ciconiiformes.

Brain size is a frequently studied phenomenon in vertebrates (Jerison 1973), but the coverage of individual vertebrate groups by these studies is rather uneven, the most attention being given to mammals (Portmann 1972, Jerison 1973). Birds (class Aves) belong in this respects to the least studied groups of vertebrates.

According to Tiedemann (1810), brain size in birds was mentioned for the first time by Browne (1646) who stated (incorrectly; see Mlíkovský 1985a) that in the European Blackbird, *Turdus merula*, the brain constitutes 1.41% of its body mass. The first more detailed studies of brain-body size relationship in birds were carried out much later by Jaeger (1870) and Snell (1892). Snell (1892) was also the first to relate brain mass and body mass by an equation (see Data analysis). This application of mathematics stimulated many later workers to investigate brain-body mass relationships in various groups of vertebrates, especially mammals.

Lists of brain and body masses in birds were first published by Welcker and Brandt (1903), Hrdlička (1905) and the French neurologist Louis Lapicque and his associates (Lapicque and Girard 1905, 1906, Lapicque 1907a, b, 1908, 1909, Girard 1908, Waterlot 1912). Since then only scattered papers on brain size in birds have appeared, including especially those by Portmann and Sutter (1940), Portmann and Vischer (1943) and Portmann (1947) in Switzerland; Crile and Quiring (1940) and Graber and Graber (1962, 1965) in the U.S.A.; Skvorcova (1952, 1954, 1956, 1961) and Nikitenko (1959, 1963, 1966) in Soviet Union; and Senglaub (1957, 1963) in East Germany. The first allometric plot of brain mass versus body mass appears to be due to Brody (1945: 592). The more recent studies are due to Martin (1981, Fig. 2) and Mlíkovský (1982b, 1985a, c).

The intention of the present paper is to summarize our knowledge of the brain size in birds. Due to place limitations, evolutionary interpretation of the data at the between-family level is scheduled for a future paper. Note that use of conventional encephalization indices as commonly applied in encephalization studies is impossible here, because the slope of the brain-body mass regression varies between bird families (Mlíkovský 1985a). Such a variation is not allowed in these indices for statistical reasons (cf. Jerison 1973).

I thank Dr. Rudolf Piechocki (Halle/Saale), Dr. Gottfried Mauersberger and Dr. Burkhardt Stephan (Berlin, GDR) and Dr. Jan Hanzák and Dr. Ivan Heráň (Praha) for allowing me to study specimens under their care. To Dr. R. Piechocki I owe my debts for his advice how to measure the volumes of cava cranii.

MATERIAL

All of the skulls measured in this study were 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; and the Museum of Natural History of the Humboldt University in Berlin, East Germany. A complete list of measurements is given by Mlíkovský (1985a).

Measurements were made on 1675 skulls from 615 extant species belonging to 87 different families of birds. These measurements were supplemented by data published by other workers. Most of these authors used brain mass as a measure of brain size. In comparison with measurements applied by myself, this method is known to be much less accurate (see Dubravina 1979), especially because the avian brain is 75–80% water (Sutter 1943, Requate 1959, Graber and Graber 1965) and its mass and volume can easily change during preparation (Senglaub 1963). Measurements which were apparently incorrect for this reason and which significantly deviated from my measurements were excluded from this study. Particularly, the data by Lapicque and Girard (1905) for *Sterna hirundo* and *Pica pica*, Girard (1908) for *Sterna hirundo*, Welcker and Brandt (1903) for *Tyto alba* and *Apus apus*, Portmann and Vischer (1943) for *Rallus aquaticus*, Portmann (1947) for *Leptoptilos crumeniferos* and *Serinus canaria* and all of the data by Nikitenko (1959, 1963, 1966) were excluded.

After eliminating apparently faulty data, all of the measurements were combined. The aggregate data contains estimates of brain size in 4344 brains in 766 extant species belonging to 116 families of birds. Of them, the data on 182 species belonging to 26 families are presented in this paper. In addition, the data on brain size in 5 fossil species are presented.

Body mass was used here as a measure of body size. Unfortunately, it proved impossible to obtain body mass data for all of the species for which brain size has been determined. Data for both parameters are available for 662 extant species belonging to 71 families, of which those for 159 species belonging to 23 families are presented here.

METHODS

Measurement of brain size

I have used volume of the cava cranii as a measure of brain size (the morphological terminology of Baumel et al. 1979 is used throughout this paper). Volume has been determined using small, different sized shot particles (up to 0.5 mm in diameter). The first step was to plug all openings in the cranium, excepting the foramen magnum with plasticine. Then the cavum cranii was filled with shot up to the plane of the foramen magnum, while shaking the skull to be certain that all spaces were filled. The shot was poured into a volumetric flask and the volume determined directly. The average measuring error was 2–3% and never exceeded 10%.

Because the brain in birds completely fills the cavum cranii (with the negligible exceptions of the sinus cavernosus occipitalis and sinus foraminis magni), the volume of the cavum cranii must closely approximate the volume of the brain. Moreover, since brain density is about 1.03 $g.cm^{-3}$ (Schudnagis 1975), brain mass and brain volume have approximately equal values. All measurements were restricted to those of fully ossified, healthy adult skulls.

Body size estimation

Because body mass is rather variable in birds (see Baldwin and Kendeigh 1938 and Clark 1979 for reviews), it is difficult to determine a single "correct" or "typical" body mass for individual species. To minimize the potential bias of wrong body mass estimates I used whenever possible standard values from ornithological tables and monographs (by region or taxon). In absence of these data, as many body mass measurements as possible were compiled for each species. (Due to place limitations it is not possible to cite the source here.) Only adult, healthy birds were considered, the sexes were combined. In markedly sexual size dimorphic birds, the "typical" body mass for a species was obtained by weighting the "typical" body mass of the two sexes. Despite these efforts, variations in body mass data will remain the main bias for the calculations presented below, although their effect at the family level (which is in focus of this paper) appears negligible. The bias clearly increases toward lower taxonomic levels.

Data analysis

Brain size may be expressed as a function of body size by the allometric equation $E = b \cdot S^a$, where E is brain size (volume or mass; cm^3 or g), S is body mass (g), a is allometric exponent or slope and b is intercept. This equation is linear after logarithmic transformation. The coefficients

Table 1. Brain size and encephalization in the "Ratitae". n = number of measured brains or cava cranii, S = body mass (g), E = brain mass (g), I_{rel} = relative brain mass (%), Q_r = coefficient of relative encephalization, Author = who measured brains or cava cranii. The figure in parentheses after the family name gives number of extant species of that family (after Wolters 1975—1982).

Taxon	n	S	E	I_{rel}	Q_r	Author
Tinamidae (46)						
Crypturellus soui	1		1.9			7
Crypturellus obsoletus	2		3.3			7
Rheidae (2)						
Rhea americana	2	20000	22.5	0.11		7
Rhea pennata	3		19.2			7
Struthionidae (1)						
Struthio camelus	10	80000	41.9	0.052		2—4, 6, 7
Dromiceidae (1)						
Dromiceius novaehollandiae	4	32500	24.9	0.077		1, 3, 5
Casuariidae (3)						
Casuarius casuarius	4	33000	31.5	0.095		1, 7
Casuarius bennetti	2		24.5			7
Casuarius uniappendiculatus	1		32.0			7
Anomalopterygidae (0)						
*Euryapteryx geranoides**	1		24.1			4
Dinornithidae (0)						
*Dinornis novaezealandiae**	1		42.1			4
Apterygidae (3)						
Apteryx australis	4	2250	11.3	0.50		4, 7
Apteryx oweni	1		7.0			7

* Quaternary species.
1 = Hrdlička 1905, 2 = Crile and Quiring 1940, 3 = Portmann 1947, 4 = Starck 1955, 5 = Cobb and Edinger 1962, 6 = Igarashi and Kamiya 1972, 7 = Mlíkovský this paper

a and b appearing in the allometric equation were determined by the reduced major-axis analysis (see Seim and Saether 1983). Calculated regression slopes were compared with predicted values, particularly 0.56 (Dubois 1897, 1913) and 2/3 ≐ 0.667 (Jerison 1961, 1973 , 1977). In the following text I shall refer to these values as Dubois' and Jerison's constant. All statistical calculations were carried out according to standard methods (Sokal and Rohlf 1969).

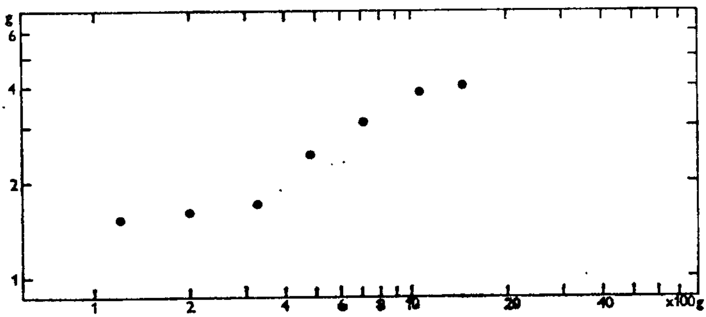


Fig. 1. Relationship between the brain size (Y axis) and the body size (X axis) in Podicipedidae. See Table 2 for exact data.

Table 2. Brain size and encephalization in Podicipediformes. See Table 1 for explanation.

Taxon	n	S	E	I_{rel}	Q_r	Author
Podicipedidae (20)						
Aechmophorus occidentalis	1	1475	4.0	0.27	−3.22	3
Podiceps griseigena	6	720	3.1	0.43	4.47	3
Podiceps major	1		4.7			3
Podiceps cristatus	15	1070	3.8	0.36	6.64	1−3
Podiceps auritus	1	480	2.4	0.50	−2.46	3
Podiceps nigricollis	1	330	1.7	0.52	−17.85	3
Podiceps dominicus	1	120	1.5	1.25	15.67	3
Tachybaptes ruficollis	22	200	1.6	0.80	−2.56	1−3

1 = Portmann and Vischer 1943, 2 = Portmann 1947, 3 = Mlíkovský this paper

The relative brain mass (I_{rel}) was calculated as

$$I_{rel} = 100\, E \,.\, S^{-1}$$

and is given in %. The relative coefficient of encephalization (Q_r) is derived from the allometric equation describing the relation between brain and body mass in individual families as follows:

$$Q_r = E \,.\, b^{-1} \,.\, S^{-1} \,.$$

This coefficient can be used only for comparison within families!

Correlations between brain size and body size were tested for significance using the Hotteling's (1953) modification of the Bravais' correlation coefficient (r_H) for samples with $n \geqq 10$ and using the Spearman's (1904) non-parametric test (r_S) for samples with $4 \leqq n < 10$. In the following, a 5% probability level is taken as significant for Type I errors (cf. Sachs 1974: 96).

Classification of birds

The sequence of families and their delimination follow Storer (1971). Since this is not a taxonomical paper, my decision to use his classification was determined by the need for clarity. It is recognized, however, that this classification now appears to be incorrect in many respects (cf. Wolters 1975−1982, Cracraft 1981, Mlíkovský 1982a, 1985b, Olson 1982, 1985).

RESULTS AND DISCUSSION

The available data on the brain size and the body size of birds are summarized

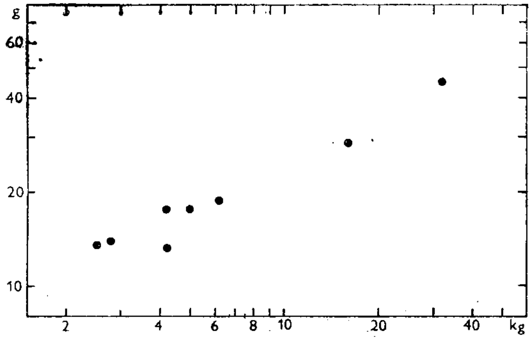


Fig. 2. Relationship between the brain size (Y axis) and the body size (X axis) in Spheniscidae See Table 3 for exact data.

in tables and, where appropriate, in figures. Whenever possible, relative brain masses (I_{rel}) and coefficients of relative encephalization (Q_r) are given.

The "Ratitae"

Data on the brain size and the body size in this diverse and probably polyphyletic group are given in the Table 1. The data do not allow the calculation of the regression equation for separate families.

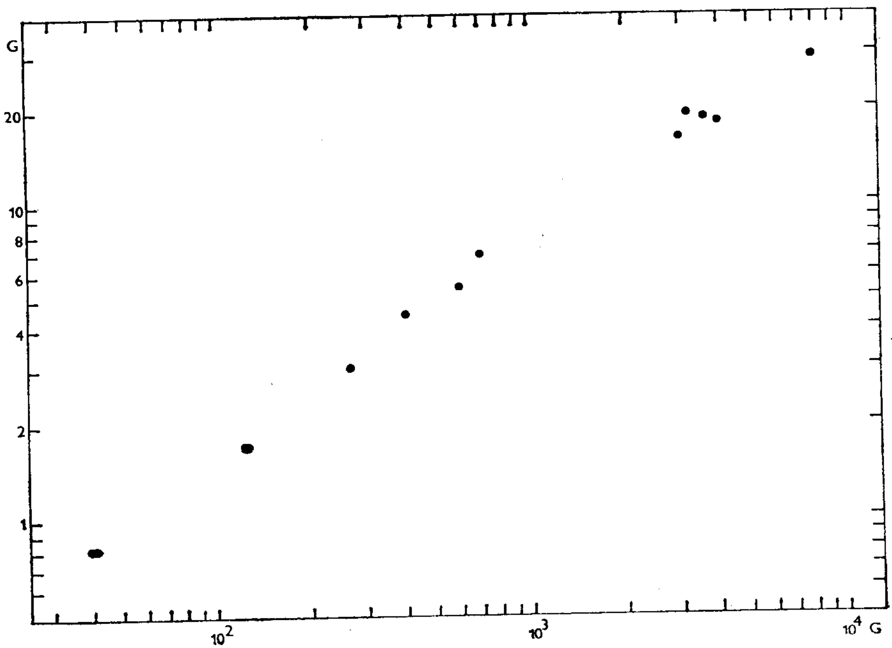


Fig. 3. Relationship between the brain size (Y axis) and the body size (X axis) in Procellariiformes. See Table 4 for exact data.

Podicipediformes

The data on the brain size and the body size in Podicipedidae, the only extant family of this order, are presented in the Table 2 and Figure 1. Brain size and body size are positively correlated ($r_S = 1.000$; $p < 0.01$) and their allometric relation is $E = 0.142\ S^{0,462 \pm 0.0525}$ (n = 7). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -3.898$; $p < 0.01$), but does not significantly deviate from the Dubois' constant ($t_s = -1.867$; $p > 0.05$).

Sphenisciformes

The data on the brain size and the body size in Spheniscidae, the only extant family of this order, are given in the Table 3 and Figure 2. Brain size and body size are positively correlated ($r_S = 0.887$; $p < 0.01$) and their allometric relation is $E = 0.287\ S^{0.481 \pm 0.0450}$ (n = 8). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -4.126$; $p < 0.01$), but does not significantly deviate from the Dubois' constant ($t_s = -1.756$; $p > 0.05$).

Table 3. Brain size and encephalization in Sphenisciformes. See Table 1 for explanation.

Taxon	n	S	E	I_{rel}	Q_r	Author
Spheniscidae (16)						
Aptenodytes forsteri	4	32000	44.3	0.14	5.08	2
Aptenodytes patagonicus	1	16000	23.5	0.18	−5.64	2
Eudyptes chrysolophus	1	4200	13.0	0.31	−18.10	2
Eudyptes crestatus	1	2500	13.5	0.54	9.15	2
Pygoscelis adeliae	2	5000	17.5	0.35	1.38	2
Pygoscelis papua	3	6200	18.5	0.30	−3.36	2
Spheniscus humboldti	2	4200	17.5	0.42	10.25	2
Spheniscus demersus	6	2800	13.8	0.49	5.66	1,2

1 = Portmann 1947, 2 = Mlíkovský this paper

Procellariiformes

The data on the brain size and the body size in Procellariiformes are given in the Table 4 and Figure 3. Because of the apparent absence of differences in the level of encephalization of individual families, this order can be treated as a unity. For the aggregate data, brain size and body size are positively correlated ($r_H = 3.260 \pm \pm 0.302$; $p < 0.001$) and their allometric relation is $E = 0.0636\ S^{0.692 \pm 0.302}$ ($n = 12$). The slope of this regression is higher both than the Jerison's constant ($t_s = 1.995$; $p < 0.05$) and than the Dubois' constant ($t_s = 10.394$; $p < 0.001$).

Pelecaniformes

The data on the brain size and the body size in this heterogenous order are given in the Table 5. The data do not allow the calculation of regression equation for individual families.

Table 4. Brain size and encephalization in Procellariiformes. See Table 1 for explanation.

Taxon	n	S	E	I_{rel}	Q_r	Author
Diomedeidae (13)						
Phoebetria palpebrata	1	3000	16.0	0.53	−1.26	2
Diomedea chrysostoma	1	3200	19.0	0.59	12.13	2
Diomedea melanophris	1	3600	18.5	0.51	0.64	2
Diomedea exulans	2	8000	28.8	0.36	−9.84	2
Procellariidae (63)						
Puffinus griseus	1	270	3.0	1.11	−2.01	1
Puffinus tenuirostris	2	600	5.4	0.90	1.50	2
Pterodroma hasitata	1		6.0			2
Daption capensis	1	425	4.4	1.04	4.99	2
Macronectes giganteus	1	4000	18.0	0.45	−8.97	2
Fulmarus glacialis	3	700	6.8	0.97	14.88	2
Hydrobatidae (21)						
Ocenites oceanicus	1	40	0.8	2.00	−2.05	2
Oceanodroma leucorrhoa	1	40	0.8	2.00	−2.05	2
Pelecanoididae (5)						
Pelecanoides urinatrix	1	125	1.7	1.36	−5.39	2

1 = Crile and Quiring 1940, 2 = Mlíkovský this paper

Table 5. Brain size and encephalization in Pelecaniformes. See Table 1 for explanation.

Taxon	n	S	E	I_{rel}	Q_r	Author
Phaethontidae (3)						
Phaethon aethereus	2		3.3			5
Phaethon rubricauda	3		4.7			5
Sulidae (9)						
Sula bassana	5	3200	19.2	0.60		5
Phalacrocoracidae (30)						
Phalacrocorax melanoleucus	2		5.8			5
Phalacrocorax pygmaeus	4	700	4.7	0.67		5
Phalacrocorax carbo	32	2100	10.3	0.49		2, 4, 5
Phalacrocorax olivaceus	3	1150	7.5	0.65		5
Phalacrocorax capensis	1		10.0			5
Anhingidae (2)						
Anhinga anhinga	5	900	4.6	0.51		1, 5
Pelecanidae (7)						
Pelecanus occidentalis	3	3500	24.2	0.69		5
Pelecanus philippensis	1		21.5			5
Pelecanus rufescens	1		19.5			5
Pelecanus onocrotalus	2	9000	33.0	0.37		4, 5
Pelecanus erythrorhynchus	3		24.5			5
Fregatidae (5)						
Fregata magnificens	3	1500	9.2	0.61		3, 5

1 = Hrdlička 1905, 2 = Lapicque 1909, 3 = Crile and Quiring 1940, 4 = Portmann 1947, 5 = Mlíkovský this paper

Anseriformes

The data on the brain size and the body size in this order are presented in the Table 6 and Figure 4. For Anseridae, brain size and body size are positively corre-

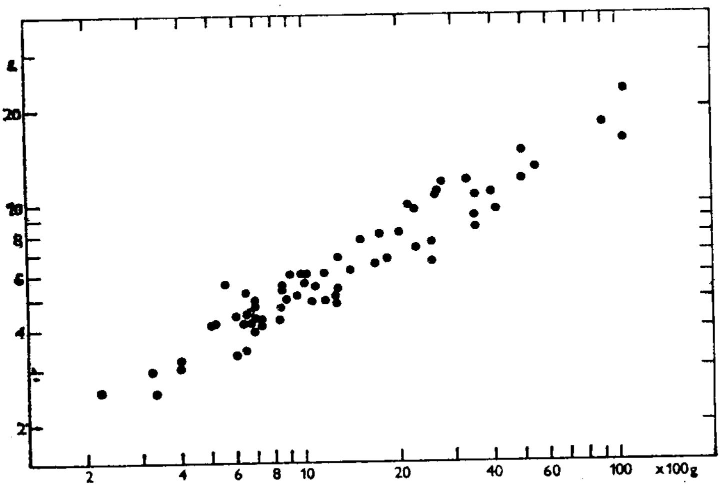


Fig. 4. Relatiosnhip between the brain size (Y axis) and the body size (X axis) in Anseridae. * = *Anseranas semipalmata*. See Table 6 for exact data.

Table 6. Brain size and encephalization in Anseriformes. See Table 1 for explanation.

Taxon	n	S	E	I_{rel}	Q_r	Author
Anhimidae (3)						
Anhima cornuta	1		8.5			15
Chauna chavaria	1		8.5			15
Chauna torquata	1		9.0			15
Anseridae (153)						
*Anseranas semipalmata**	3	2200	9.8	0.45	20.26	15
Dendrocygna arborea	1	1150	6.0	0.52	4.99	15
Dendrocygna autumnalis	2	830	4.7	0.57	−1.69	15
Dendrocygna viduata	2	700	4.9	0.70	12.50	15
Dendrocygna arcuata	1	730	4.3	0.59	−3.52	15
*Mionetta blanchardi***	2		3.0			15
Olor cygnus	2	9000	17.5	0.19	−0.62	15
Olor buccinator	1	10500	22.5	0.21	17.44	15
Olor bewickii	1	5500	12.5	0.23	−7.07	15
Cygnus olor	19	10500	15.4	0.15	−19.62	1, 7, 8, 15
Cygnus atratus	2	5000	11.8	0.24	−7.58	15
Cygnus melanocoryphus	3	4000	10.7	0.27	−5.32	15
Coscoroba coscoroba	4	3500	9.0	0.26	−14.33	15
Anser caerulescens	2	2640	10.8	0.41	19.96	15
Anser cygnoides	3	3500	10.3	0.29	−1.95	15
Anser fabalis	5	2800	11.5	0.41	23.68	15
Anser albifrons	2	2230	9.5	0.43	15.72	15
Anser erythropus	2	1850	6.7	0.36	−9.60	15
Anser anser (wild)	50	3350	11.6	0.35	13.10	8, 14, 15
Branta canadensis	3		13.7			15
Branta leucopsis	2	1760	8.0	0.45	10.92	15
Branta bernicla	4	1400	6.1	0.44	−4.15	15
Branta ruficollis	4	1280	5.1	0.40	−15.83	15
Cereopsis novaehollandiae	2	3500	8.3	0.24	−20.99	15
*Cnemiornis calcitrans****	1		15.5			15
Chloephaga picta	1	2580	6.5	0.25	−26.89	15
Chloephaga melanoptera	1	2580	7.5	0.29	−15.64	15
Alopochen aegyptiacus	4	2300	7.2	0.31	−13.77	6. 15
Tadorna tadorna	3	1100	5.5	0.50	−1.39	15
Tadorna ferruginea	2	1250	4.8	0.38	−19.75	15
Tadorna tadornoides	1	1290	5.3	0.41	−12.90	15
Plectropterus gambensis	2	5000	14.5	0.29	13.57	15
Nettapus coromandelianus	4	220	2.5	1.14	8.11	15
Amazonetta brasiliensis	2	400	3.0	0.75	−6.46	15
Aix sponsa	2	630	4.2	0.67	2.15	15
Aix galericulata	3	500	4.2	0.84	15.91	1, 6, 15
Anas sibilatrix	1	830	4.3	0.52	−10.06	15
Anas penelope	5	740	4.2	0.57	−6.46	4, 8, 15
Anas strepera	2	650	3.4	0.52	−18.71	15
Anas crecca	18	325	2.9	0.89	1.30	1, 5, 6, 8, 11−13, 15
Anas castanea	1	500	4.1	0.82	13.15	15
Anas acuta	2	900	4.4	0.49	−11.96	4, 6
Anas georgica	1	705	4.3	0.57	−1.66	15
Anas bahamensis	1	690	3.9	0.57	−9.75	15
Anas erythrorhyncha	3	600	4.4	0.73	9.91	15
Anas querquedula	10	330	2.8	0.85	−3.01	2, 4, 9, 13, 15
Anas discors	3	400	3.2	0'80	−0.22	15
Anas clypeata	4	610	3.3	0.54	−18.31	4, 15
Anas undulata	1	850	5.5	0.65	13.55	15
Anas poecilorhyncha	1	1000	6.0	0.60	13.34	15

Anas superciliosa	2	670	4.5	0.67	5.82	15
Anas luzonica	2	950	5.1	0.54	−0.92	15
Anas platyrhynchos (wild)	44	1100	6.2	0.56	11.16	2−5, 7−10, 12, 13, 15
*Euryanas finschi****	1		5.8			15
Tachyeres patachonicus	1	2620	10.5	0.40	17.11	15
Tachyeres pteneres	1	4110	9.5	0.23	−17.17	15
Rhodonessa caryophyllacea	1	880	5.0	0.57	1.29	15
Netta rufina	5	1160	4.9	0.42	−14.66	15
Aythya ferina	3	850	5.3	0.62	9.42	15
Aythya collaris	1	700	4.7	0.67	7.61	15
Aythya nyroca	3	560	5.6	1.00	42.26	2, 4
Aythya fuligula	1	660	4.2	0.64	−0.42	15
Aythya marila	4	1000	5.1	0.51	−3.66	6, 11, 15
Somateria mollissima	5	2000	8.1	0.41	4.72	8, 15
Somateria spectabilis	1	1670	6.5	0.39	−7.25	15
Clangula hyemalis	3	650	4.9	0.75	17.15	12, 15
Melanitta nigra	10	980	5.8	0.59	10.78	12, 15
Melanitta fusca	4	1500	7.1	0.47	7.44	12, 15
Bucephala clangula	1	900	6.0	0.67	20.06	15
Mergus albellus	3	650	4.4	0.68	5.20	15
Mergus serrator	5	1050	5.0	0.48	−8.04	6, 8, 15
Mergus merganser	2	1300	6.8	0.52	1.27	15

* Not included into the data set upon which the regression equation is based because of its aberrant taxonomic position.
** Early Miocene species.
*** Quaternary species
1 = Hrdlička 1905, 2 = Lapicque and Girard 1905, 3 = Lapicque and Girard 1906, 4 = Girard 1908, 5 = Timmann 1919, 6 = Crile and Quiring 1940, 7 = Portmann and Vischer 1943, 8 = = Portmann 1947, 9 = Skvorcova 1952, 10 = Senglaub 1957, 11 = Tumanov 1961, 12 = = Senglaub 1963, 13 = Werner 1973, 14 = Schudnagis 1975, 15 = Mlíkovský this paper

lated ($r_H = 1.896 \pm 0.121$; $p < 0.001$) and their allometric relation is $E = 0.121\ S^{0.547 \pm 0.0191}$ ($n = 68$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -6.265$; $p < 0.001$), but does not significantly deviate from the Dubois' constant ($t_s = -0.681$; $p > 0.05$).

The number of data allow here a few comments on the encephalization of some waterfowl tribes and genera: (1) *Anseranas*, which is phylogenetically more ancestral than other Anseridae, has a very high encephalization. (2) Dendrocygnini, another ancestral waterfowl group, are medium encephalized. (3) Swans of the genus *Olor* tend to be less encephalized than those of the genus *Cygnus*. (4) Geese (genus *Anser*) belong to highly encephalized waterfowl. (5) Tadornini are generally low encephalized. (6) *Cereopsis* has a similarly low encephalization, which may support its relationships with Tadornini (cf. Delacour and Mayr 1945, Veselovský 1970). (7) *Plectropterus*, which used to be allied with Tadornini (e.g., Verheyen 1955, Woolfenden 1961), has a markedly higher encephalization than representatives of this tribe.

Phoenicopteriformes

The data on the brain size and the body size in Phoenicopteridae, the only extant family of this order, are given in the Table 7. The data do not allow the calculation of the regression equation for this family.

Ciconiiformes

The data on the brain size and the body size in Ciconiiformes are presented in the Table 7 and Figures 5—7. The data were sufficient for the calculation of regression equations in the following ciconiiform families: Ardeidae, Plataleidae (but see below) and Ciconiidae.

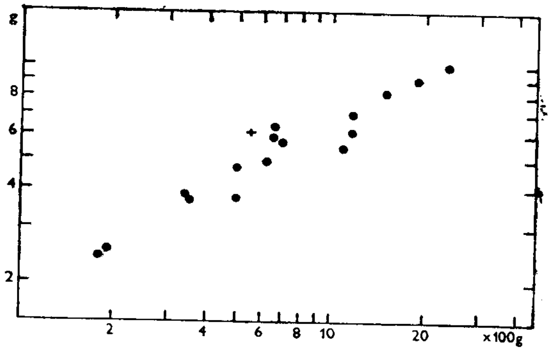
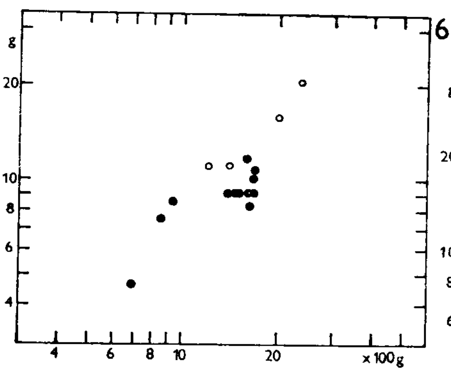


Fig. 5. Relationship between the brain size (Y axis) and the body size (X axis) in Ardeidae. + = *Cochlearius cochlearius*. See Table 7 for exact data.

In Ardeidae (Fig. 5), brain size and body size are positively correlated ($r_H = 1.721 \pm 0.423$; $p < 0.001$) and their allometrical relation is $E = 0.0875\ S^{0.626 \pm 0.423}$ ($n = 18$). The slope of this regression does not significantly deviate from either the Jerison's constant ($t_s = -0.815$; $p > 0.05$) and the Dubois' constant ($t_s = 1.323$; $p > 0.05$).

In Plataleidae (Fig. 6), brain size and body size are not significantly correlated according to my data ($r_H = 1.243 \pm 0.289$; $p > 0.05$). This is probably an artifact, caused possibly by the limited range in their body size, since this factor is known to



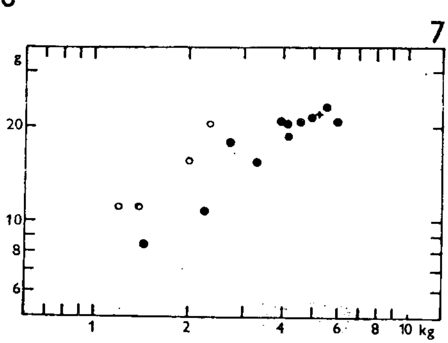


Fig. 6. Relationship between the brain size (Y axis) and the body size (X axis) in Plataleidae (●) and Myxteriini (○). See Table 7 for exact data and Figure 7 for comparison with Ciconiidae.

Fig. 7. Relationship between the brain size (Y axis) and the body size (X axis) in Ciconiidae (●), Mycteriini (○) and Balaenicipitidae (+). See Table 7 for exact data and Figure 6 for comparison with Plataleidae.

Table 7. Brain size and encephalization in Phoenicopteriformes and Ciconiiformes. See Table 1 for explanation.

Taxon	n	S	E	I_{rel}	Q_r	Author
Phoenicopteridae (5)						
Phoenicopterus ruber	18	3000	10.7	0.36		1, 5, 8
Phoenicopterus minor	10	1500	7.2	0.48		3, 6, 8
Phoenicopterus jamesi	3		9.3			8
Ardeidae (63)						
Botaurus stellaris	5	1150	6.1	0.53	−15.41	5, 8
Botaurus lentiginosus	2	625	4.9	0.78	−0.47	1, 8
Ixobrychus minutus	8	170	1.6	0.94	−26.57	5, 8
Ixobrychus sturmii	1		3.7			8
Tigrisoma mexicanum	1	1160	7.0	0.60	−3.45	8
Nyctanassa violacea	1	660	6.3	0.95	23.68	8
Nycticorax nycticorax	4	650	5.9	0.91	16.94	1, 8
Nycticorax caledonicus	1	700	5.6	0.80	5.96	8
*Cochlearius cochlearius**	2	550	6.1	1.11	34.23	8
Ardeola ibis	5	340	3.8	1.12	13.00	8
Ardeola ralloides	5	180	2.4	1.33	6.27	8
Butorides striatus	6	190	2.4	1.32	2.73	2, 8
Ardea melanocephala	2		7.8			8
Ardea cinerea	19	1500	8.1	0.54	−4.89	4, 5, 8
Ardea herodias	2	2200	10.0	0.45	−7.61	1
Ardea coccoi	2	1900	9.0	0.47	−8.85	8
Egretta garzetta	11	500	3.7	0.74	−13.58	4, 5, 8
Egretta caerulea	2	350	3.7	1.06	8.05	1
Egretta rufescens	1		3.5			1
Egretta alba	4	1100	5.5	0.50	−21.58	3, 5, 8
Egretta intermedia	1	500	4.7	0.94	9.78	3
Balaenicipitidae (1)						
Balaeniceps rex	1	5100	22.5	0.44		8
Scopidae (1)						
Scopus umbretta	4	320	3.9	1.22		3, 8
Plataleidae (31)						
Threskiornis moluccus	1	1670	9.0	0.54		8
Threskiornis melanocephalus	1	1470	9.0	0.61		8
Threskiornis aethiopicus	3	1400	9.0	0.64		8
Nipponia nippon	2		10.0			8
Geronticus eremita	3	1630	8.2	0.50		8
Geronticus calvus	1	1630	9.0	0.55		8
Pseudibis papillosa	1	1470	9.0	0.61		8
Plegadis falcinellus	3	690	4.6	0.67		8
Plegadis chihi	1	700	4.6	0.66		1
Eudocimus ruber	1	935	8.5	0.91		8
Eudocimus albus	1	850	7.5	0.88		8
Platalea ajaja	2	1600	11.3	0.71		8
Platalea leucorodia	3	1700	10.8	0.64		8
Platalea alba	1	1670	10.0	0.60		8
Mycteriini (6)						
Mycteria americana	3	2350	22.3	0.95		1, 8
Mycteria ibis	4	2000	15.4	0.77		8
Anastomus oscitans	1	1400	11.0	0.79		8
Anastomus lamelligerus	2	1200	11.0	0.92		8
Ciconiidae (13)						
Ciconia nigra	4	2700	11.8	0.44	−10.30	8
Ciconia abdimii	2	1450	8.3	0.57	7.42	8
Ciconia episcopus	4	2250	10.8	0.48	−4.04	8

Ciconia maguari	1	4200	20.5	0.49	6.76	8
Ciconia boyciana	2	4000	20.9	0.52	13.49	7, 8
Ciconia ciconia	25	3300	15.3	0.46	−2.05	3, 5, 8
Ephippiorhynchus asiaticus	2	4050	18.3	0.45	−1.68	8
Ephippiorhynchus senegalensis	3	6000	20.7	0.35	−20.56	8
Leptoptilus javanicus	2	4500	21.5	0.48	5.55	8
Leptoptilus dubius	1	5500	26.0	0.47	7.49	8
Leptoptilos crumeniferus	2	5000	22.8	0.46	2.28	8

* Not included into the data set upon which the regression equation is based because of its aberrant taxonomic position.
1 = Hrdlička 1905, 2 = Waterlot 1912, 3 = Crile and Quiring 1940, 4 = Portmann and Vischer 1943, 5 = Portmann 1947, 6 = Spector 1956, 7 = Schüz 1965, 8 = Mlíkovský this paper

significantly lower the Bravais' correlation coefficient and its derivatives (Smith 1980). For this family I believe, then, that we commit the Type II error, i. e. we reject a correct null hypothesis if we dispute correlation between the brain size and the body size in it. Nonetheless, this mathematical result prevents us from calculating a meaningful regression equation relating the brain size and the body size in Plataleidae.

In Ciconiidae (Fig. 7) (without Mycteriini — see below), brain size and body size are positively correlated ($r_H = 1.870 \pm 0.316$; $p < 0.001$) and their allometrical relation is $E = 0.0152\ S^{0.856 \pm 0.0778}$ ($n = 11$). The slope of this regression significantly deviates from both the Jerison's constant ($t_s = 2.434$; $p < 0.05$) and the Dubois' constant ($t_s = 3.805$; $p < 0.01$).

The tribe Mycteriini with two living genera (*Mycteria* and *Anastomus*) is usually included in the family Ciconiidae in current classifications of birds (Kahl 1972, 1979, Wood 1983, 1984), but it shares various characters with Plataleidae (see Sibley and Ahlquist 1972 for review). The Mycteriini have markedly higher encephalization than proper Ciconiidae (Figure 7), but they appear to fit Plataleidae reasonably well in this respect (Figure 6). This may indicate that Mycteriini are plataleids which evolved toward storks (Ciconiidae).

REFERENCES

Baldwin, S. P., S. C. Kendeigh, 1938: Variations in the weight of birds. *Auk*, 55: 416—467.
Baumel, J. J., A. S. King, A. M. Lucas, J. E. Breazile, H. E. Evans, eds., 1979: Nomina anatomica avium. London: Academic Press, xxv + 637 pp.
Brody, S., 1945: Bioenergetics and growth. New York: Reinhold.
Browne, — 1646: Popular errours. London. (fide Tiedemann 1810)
Clark, G. A., 1979: Body weight in birds: a review. *Condor*, 81: 193—202.
Cobb, S., T. Edinger, 1962: The brain of the Emu (Dromaeus novaehollandiae, Lath.). 1. Gross anatomy of the brain and pineal body. *Breviora* (Mus. Comp. Zool.), 170: 1—18.
Cracraft, J., 1981: Toward a phylogenetic classification of the Recent birds of the world (class Aves). *Auk*, 98: 681—714.
Crile, G., D. P. Quiring, 1940: A record of the body weight and certain organ and gland weights in 3690 animals. *Ohio J. Sci.*, 40: 219—259.
Delacour, J., E. Mayr, 1945: The family Anatidae. *Wilson Bull.*, 57: 3—55.
Dubois, E., 1895: De verhanding van het gewicht der hersenen tot de grootte van het lichaam bij de zoogdieren (On the relationship between the brain weight and body size in vertebrates). *Verh. kon. Akad. Wet. Amsterdam*, (2) 5: 1—41.
Dubois, E., 1913: On the relation between the quantity of brain and the size of the body in vertebrates. *Proc. kon. Akad. Wet. Amsterdam*, 16: 647—668.
Dubravina, N. B., 1979: Ispol'zovanie ob"ema mozkovoj korobki dlja ocenki vesa mozga mlekopitajuščich (The use of the endocranial volume for determining the brain weight in

mammals). In: V. S. Bezel', ed., Primenenie količestvennych metodov v èkologii (The application of quantitative methods in ecology): 101–109. Sverdlovsk: AN SSSR.
Girard, P., 1908: Facteurs dont dependent la masse, la forme et la composition chimique quantitative de l'encéphale chez les oiseaux. Paris: Épinal, 68 pp.
Graber, R. R., J. W. Graber, 1962: Weight characteristics of birds killed in nocturnal migration. *Wilson Bull.*, 74: 74–88.
Graber, R. R., J. W. Graber, 1965: Variation in avian brain weights with special reference to age. *Condor*, 67: 300–318.
Hotteling, H. 1953: New light on the correlation coefficient and its transforms. *J. roy. statist. Soc. (B)*, 15: 193–232.
Hrdlička, A., 1905: Brain weight in vertebrates. *Smithson. misc. Coll.*, 48: 89–112.
Igarashi, S., T. Kamiya, 1972: Atlas of the vertebrate brain. Tokyo: University of Tokyo Press.
Jaeger, G., 1870: Ueber Wachsthumsbedingungen. *Z. wiss. Zool.*, 20: 565–596.
Jerison, H. J., 1961: Quantitative analysis of evolution of the brain in mammals. *Science*, 133: 1012–1014.
Jerison, H. J., 1973: Evolution of the brain size and intelligence. New York: Academic Press, xiv + 482 pp.
Jerison, H. J., 1977: The theory of encephalization. *Ann. New York Acad. Sci.*, 299: 146–160.
Kahl, M. P., 1972: A revision of the family Ciconiidae (Aves). *J. Zool.*, 167: 451–461.
Kahl, M. P., 1979: Family Ciconiidae. In: E. Mayr, G. W. Cottrell, eds., Check-list of birds of the world, 1: 245–252. 2nd ed. Cambridge: Museum of Comparative Zoology.
Lapicque, L., 1907a: Tableau général des poids encéphalique en fonction du poids du corps. *C. R. Acad. Sci. Paris*, 144: 1459–1462.
Lapicque, L., 1907b: Tableau général des poids somatique et encéphalique dans les espéces animales. *Bull. Mém. Soc. Anthropol. Paris*, (5) 8: 248–261.
Lapicque, L., 1908: Limite supériure de la proportion d'encéphale par rapport au poids du corps chez les oiseaux. *C. R. Acad. Sci. Paris*, 147: 1421–1423.
Lapicque, L. 1909: Le poids de l'encéphale dans les différents groupes d'oiseaux. *Bull. Mus. natl. Hist. nat. Paris*, 15: 408–412.
Lapicque, L., P. Girard, 1905: Poids de l'encéphale au fonction du poids du corps chez les oiseaux. *C. R. Acad. Sci. Paris*, 140: 1057–1059.
Lapicque, L., P. Girard, 1906: Poids des diverses parties de l'encéphale chez les oiseaux. *C. R. Soc. biol. Paris*, 61: 30–33.
Martin, R. D., 1981: Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature*, 293: 57–60.
Mlíkovský, J., 1982a: Towards a new classification of birds. In: V. D. Il'ičev, V. M. Gavrilov, eds., XVIII Congressus internationalis ornithologicus, Abstracts of symposia and poster presentations: 248–251. Moskva: Nauka.
Mlíkovský, J., 1982b: Encephalization of birds. In: V. D. Il'ičev, V. M. Gavrilov, eds., XVIII Congressus internationalis ornithologicus, Abstracts of symposia and poster presentations: 251. Moskva: Nauka.
Mlíkovský, J., 1985a: Velikost mozku a encefalizace jako evoluční problém (Brain size and encephalization as an evolutionary problem). Unpublished CSc. Thesis, Praha, Czechoslovak Academy of Sciences, 326 pp.
Mlíkovský, J., 1985b: Towards a new classification of birds. In: V. D. Il'ičev, V. M. Gavrilov, eds., Acta XVIII congressus internationalis ornithologici: 1145–1146. Moskva: Nauka. (reprinted from Mlíkovský 1982a).
Mlíkovský, J., 1985c: Encephalization of birds. In: V. D. Il'ičev, V. M. Gavrilov, eds., Acta XVIII congressus internationalis ornithologici: 1145–1146. Moskva: Nauka. (reprinted from Mlíkovský 1982b).
Nikitenko, M. F., 1959: Sravnitel'naja charakteristika razmerov i stroenija golovnogo mozga u nekotorych vidov vorob'inych (Comparative characteristics of the brain size and structure in some passerine species). *Dokl. AN SSSR*, 125: 945–948.
Nikitenko, M. F., 1963: Golovnyj mozg i puti ego èvoljucii u pozvonočnych (The brain and ways of its evolution in vertebrates). *Usp. sovr. Biol.*, 56: 442–465.
Nikitenko, M. F., 1966: Osnovnye čerty adaptacii k vodnomu obrazu žizni i stroenie golovnogo mozga u čistikovych ptic (Basic aspects of the adaptation to water habits and the brain structure in Alcidae). *Ž. obšč. Biol.*, 26: 464–474.
Olson, S. L., 1982: A critique of Cracraft's classification of birds. *Auk*, 99: 733–739.
Olson, S. L., 1985: The fossil record of birds. In: D. S. Farner, J. R. King, eds., Avian biology, 8: 79–238. New York: Academic Press.

Portmann, A., 1947: Etudes sur la cérébralisation chez les oiseaux. II. Les indices intercérébraux. *Alauda*, 15: 1—15.
Portmann, A., 1972: La cérébralisation des mammifères. In: P.—P. Grassé, ed., *Traité de zoologie*, XVI(4): 385—417. Paris: Masson.
Portmann, A., E. Sutter, 1940: Über die postembryonale Entwicklung des Gehirns bei Vögeln. *Rev. suisse Zool.*, 47: 195—202.
Portmann, A., L. Vischer, 1943: Organgewichte bei Vögeln. *Rev. suisse Zool.*, 50: 277—282.
Requate, H., 1959: Federhauben bei Vögeln. Eine genetische und entwicklunspsychologische Studie zum Problem der Parallelbildungen. *Z. wiss. Zool.*, 162: 191—313.
Sachs, L., 1974: Angewandte Statistik. Berlin: Springer, xx + 548 pp.
Schudnagis, R., 1975: Vergleichend quantitative Untersuchungen an Organen, insbesondere am Gehirn von Wild- und Hausform der Graugans (Anser anser Linnaeus, 1758). *Z. Tierzücht. Züchtungsbiol.*, 92: 73—105.
Schüz, E., 1965: Von "Oshima", vom Schwarzschnabelstorch und von der Lebensdauer der Störche. *Beitr. Vogelk.*, 10: 329—333.
Seim, E., B.-E. Saether, 1983: On rethinking allometry: which regression model to use? *J. theor. Biol.*, 104: 161—168.
Senglaub, K., 1957: Vergleichend metrische und morphologische Untersuchungen an Organen und am Kleinhirn von Wild-, Gefangenschafts- und Hausenten. *Gegenbaurs morphol. Jb.*, 100: 11—62.
Senglaub, K., 1963: Das Kleinhirn der Vögel in Beziehung zu phylogenetischer Stellung, Lebensweise und Körpergrösse, nebst Beiträge zum Domestikationsproblem. *Z. wiss. Zool.*, 169: 1—63.
Sibley, C. G., J. Ahlquist, 1972: A comparative study of the egg-white proteins of non-passerine birds. *Bull. Peabody Mus. nat. Hist.*, 36: i-vi, 1—276.
Skvorcova, T. A., 1952: Veličina i osobennosti stroenija mozga nekotorych vidov ptic v sootnošenii s drugimi organami i v svjazi s obrazom žizni i dvigatel'noj aktivnost'ju (Brain size and peculiarities of the brain structure in some bird species in relation to other organs and in connection with life habits and locomotor activity). Unpublished Ph. D. Thesis, Leningrad, Leningrad State University.
Skvorcova, T. A., 1954: O sootnošenii veličiny i nekotorych osobennostej stroenija mozga djatlov s ich dvigatel'noj aktivnost'ju (On the relatioship of the brain size and some peculiarities of the brain structure of woodpeckes to their locomotor activity). *Dokl. AN SSSR*, 94: 345—348.
Skvorcova, T. A., 1956: Nekotorye osobennosti stroenija mozga sinic v svjazi s ich obrazom žizni i dvigatel'noj aktivnost' ju (Some peculiarities of the brain structure in tits in the connection with their life habits and locomotor activity). *Dokl. AN SSSR*, 107: 907—910.
Skvorcova, T. A., 1961: Osobennosti veličiny i stroenija mozga ptic v svjazi s obrazom žizni (Peculiarities of the brain size and structure in birds in connection with their life habits). Tez. vsesojuzn. S"ezda Anat. Gistol. Embriol., 6(1): 477—479.
Smith, R. J., 1980: Rethinking allometry. *J. theor. Biol.*, 87: 97—111.
Snell, O., 1892: Die Abhängigkeit des Hirngewichtes von dem Körpergewicht und den geistigen Fähigkeiten. *Arch. Psychiatrie*, 23: 436—446.
Sokal, R. R., F. J. Rohlf, 1969: Biometry. San Francisco: Freeman, 776 pp.
Spearman, C., 1904: The proof and measurement of association between two things. *Amer. J. Psychol.*, 15: 72—101.
Spector, W. S., ed., 1956: Handbook of biological data. Philadelphia; Saunders, xxxv + 584pp.
Starck, D., 1955: Die endokraniale Morphologie der Ratiten, besonders der Apterygidae und Dinornithidae. *Gegenbaurs morphol. Jb.*, 96: 14—72.
Storer, R. W., 1971: Classification of birds. In: D. S. Farner, J. R. King, eds., Avian biology, 1: 1—18. New York: Academic Press.
Strel'nikov, I. D., 1970: Anatomo-fiziologičeskie osnovy vidoobrazovanija pozvonočnych (Anatomical-physiological bases of speciation in vertebrates). Leningrad: Nauka, 368 pp.
Sutter, E., 1943: Über das embryonale und postembryonale Hirnwachstum bei Hühnern und Sperlingsvögeln. *Denkschr. schweiz. naturforsch. Ges.*, 75: 1—110.
Tiedemann, F., 1810: Zoologie. II. Anatomie und Naturgeschichte der Vögel. Vol. 1. Heidelberg: Mohr und Zimmer, viii + 735 pp.
Timmann, O., 1919: Vergleichende Untersuchungen an Wild- und Hausenten. *Zool. Jb. allg. Zool.*, 36: 621—656.
Tumanov, —, 1961: quoted after Strel'nikov 1970.
Verheyen, R. (1955): La systématique des Ansériformes basée sur l'ostéologie comparée. *Inst. roy. Sci. nat. Belgique, Bull.*, 31(35): 1—18, (36): 1—16, (37): 1—22, (38): 1—16.

Veselovský, Z., 1970: Zur Ethologie der Hühnergans (Cereopsis novaehollandiae Lath.). *Z. Tierpsychol.*, 27: 915–945.
Waterlot, G., 1912: Détermination de poids encéphalique et de grandeur oculaires chez quelques vertébrés du Dahomey. *Bull. Mus. natl. Hist. nat.*, 1912: 491–494.
Welcker, H., A. Brandt, 1903: Gewichtswerte der Körperorgane bei dem Menschen und den Tieren. *Arch. Anthropol.*, 28: 1–89.
Werner, C. F., 1973: Grössen- und Lagebeziehungen der Kopforgane bei Gänsen und Enten (Anseriformes). *Zool. Jb. Anat.*, 90: 373–388.
Wolters, H. E., 1975–1982: Die Vogelarten der Erde. Hamburg: Paul Parey, xx + 748 pp.
Wood, D. S., 1983: Phenetic relationships within the Ciconiidae (Aves). *Ann. Carnegie Mus.*, 52: 79–112.
Wood, D. S., 1984: Concordance between classifications of the Ciconiidae based on behavioral and morphological data. *J. Ornithol.*, 125: 25–37.
Woolfenden, G. E., 1961: Postcranial osteology of the waterfowl. *Bull. Florida State Mus.*, 6: 1–129.

Received September 24, 1987; accepted June 9, 1988