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BRAIN SIZE IN BIRDS: 3. COLUMBIFORMES THROUGH PICIFORMES

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A b s t r a c t. Brain size in 194 bird species and its relation to body size in 7 families of birds are estimated. The following avian orders are considered: Columbiformes, Psittaciformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Coliiformes, Trogoniformes, Coraciiformes and Piciformes.

Table 1. Brain size and encephalization in Columbiformes.
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. See Mlíkovský (1988) for the calculation of these indices. 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
Columbidae (296)						
Caloenas nicobarica	1	600	2,9	0,48	−3,22	8
Goura cristata	5	2200	5,5	0,25	−10,87	2, 4, 8
Ocyphaps lophotes	2	145	1,7	1,17	24,96	1
Geophaps smithii	1		1,6			8
Phaps chalcoptera	2	300	1,7	0,57	−16,59	8
Zenaidura macroura	3	120	1,3	1,08	6,16	8
Zenaida aurita	1	130	1,23	0,95	−3,93	5
Columbigallina talpacoti	1	45	0,75	1,67	5,66	8
Scardafella squamata	1		1,0			8
Geopelia cuneata	7	40	0,52	1,30	−21,78	4—6, 8
Oena capensis	2	40	0,7	1,75	5,29	8
Turtur afer	4	60	0,9	1,50	8,05	3, 5
Streptopelia senegalensis	2	105	1,3	1,24	14,34	8
Streptopelia turtur	3	125	1,4	1,12	11,76	8
Streptopelia roseogrisea	3	115	1,1	0,96	−8,02	6
Streptopelia risoria	3	145	1,2	0,83	−11,79	4, 5
Streptopelia decaocto	4	275	1,6	0,58	−17,61	8
Columba livia (wild)	39	300	2,2	0,73	7,94	4, 7
Columba oenas	3	275	2,2	0,80	13,29	8
Columba palumbus	12	500	2,6	0,52	−3,98	4—6, 8
Ducula oceanica	1		1,9			8
Ducula lacernulata	1		2,4			8
Didunculus strigirostris	1	450	3,0	0,67	17,48	8
Raphidae (3)						
No data						

1 = Hrdlička 1905, 2 = Girard 1908, 3 = Waterlot 1912, 4 = Portmann 1947, 5 = Vaughien 1949, 6 = Senglaub 1963, 7 = Löhmer und Ebinger 1980, 8 = Mlíkovský this paper

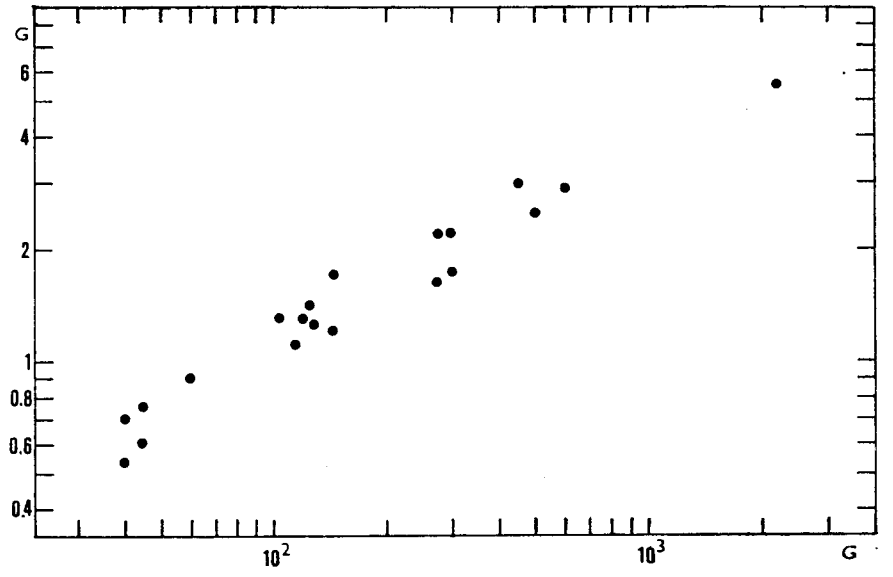

Fig. 1. Relationship between the brain size (Y axis) and the brain size (X axis) in Columbidae. See Table 1 for exact data.

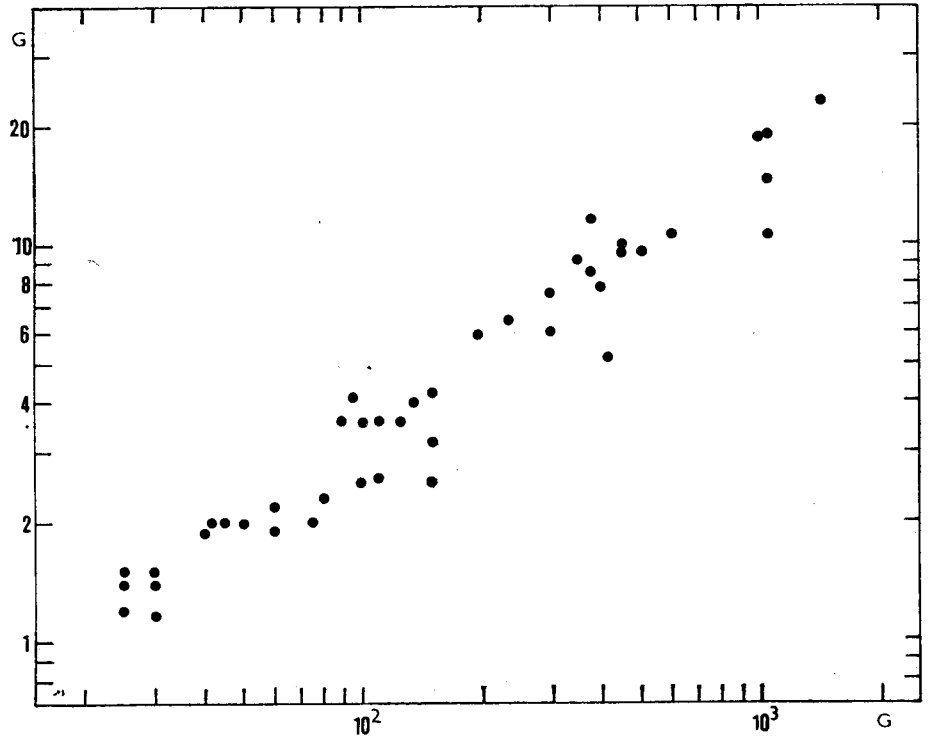

Fig. 2. Relationship between the brain size (Y axis) and the body size (X axis) in Psittacidae. See Table 2 for exact data.

INTRODUCTION

This is a continuation of my review of the brain size in birds (Mlíkovský 1989 a, b). See Mlíkovský (1989a) for the sections on Material and Methods.

RESULTS AND DISCUSSION

Columbiformes

The data on the brain size and the body size in Columbiformes are presented in the Table 1 and Figure 1. The data were sufficient for the calculation of regression equation in the family Columbidae only. Here, brain size and body size are positively correlated ($r_H = 2.052 \pm 0.236$; $p < 0.001$) and their allometrical relation is $E = 0.0855\ S^{0.556 \pm 0.309}$ ($n = 19$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -3.581$; $p < 0.001$), but does not significantly differ from the Dubois' constant ($t_s = -0.129$; $p < 0.05$).

Psittaciformes

The data on the brain size and the body size in Psittaciformes are presented in the Table 2 and Figure 2. In the Psittacidae, the only family of this order, brain size and body size are positively correlated ($r_H = 2.062 \pm 0.156$; $p < < 0.001$) and their allometrical relation is $E = 0.123\ S^{0.703 \pm 0.0463}$ ($n = 43$). The slope of this regression is significantly higher than the Dubois' constant ($t_s = 3.089$; $p < 0.01$), but does not significantly differ from the Jerison's constant ($t_s = 0.785$; $p > 0.05$).

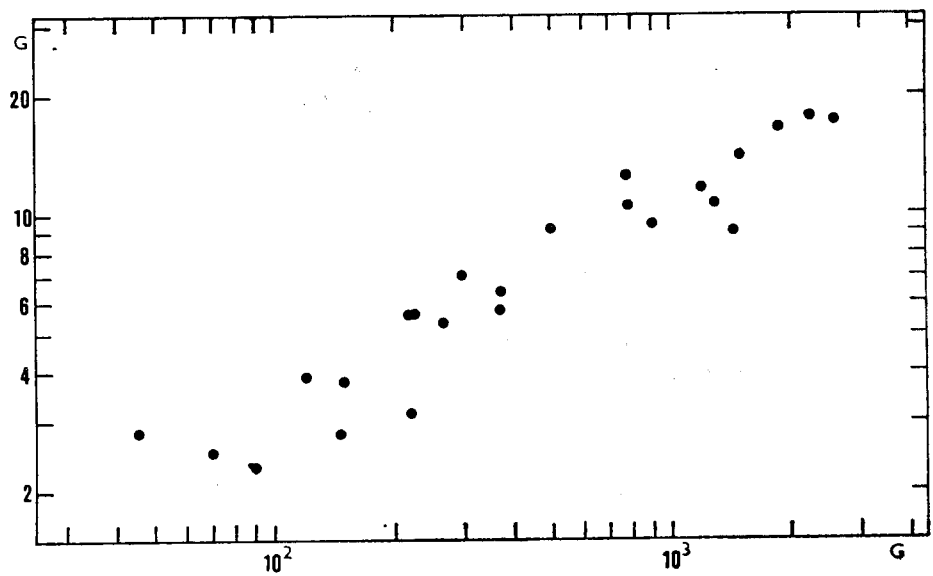

Fig. 3. Relationship between the brain size (Y axis) and the body size (X axis) in Strigidae. See Table 4 for exact data.

Table 2. Brain size and encephalisation in Psittaciformes.
See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Psittacidae (327)						
Loriculus stigmatus	1	30	1,5	5,00	11,63	8
Loriculus galgulus	1	25	1,5	6,00	26,89	8
Loriculus vernalis	1	25	1,4	5,60	18,43	8
Agapornis taranta	3	60	2,2	3,67	0,57	8
Agapornis pullarius	3	30	1,4	4,67	4,19	8
Agapornis roseicollis	3	45	2,0	4,44	11,92	8
Agapornis fischeri	2	42	2,0	4,76	17,48	5
Agapornis personatus	7	40	2,0	5,00	21,58	6—8
Forpus passerinus	4	25	1,2	4,80	1,51	8
Bolborhynchus lineola	1	50	2,0	4,00	3,93	8
Anodorhynchus hyacinthinus	1		24,5			8
Ara ararauna	3	1000	18,4	1,84	16,39	5—6
Ara chloroptera	3	1450	23,4	1,61	13,99	5—6, 8
Aratinga cunicularis	1	150	3,1	2,07	—25,58	8
Brotogeris jugularis	1	60	1,9	3,17	—13,14	1
Amazona leucocephala	7	235	6,4	2,72	12,05	1
Amazona amazonica	3	300	7,5	2,50	10,60	2—3, 8
Amazona aestiva	2	300	6,0	2,27	—11,52	6, 8
Amazona ochrocephala	12	380	9,0	2,37	12,40	1, 8
Amazona farinosa	1	380	11,5	3,03	43,62	8
Amazona versicolor	5	400	7,8	1,95	—6,04	5
Pionites leucogaster	1		5,1			8
Piocephalus robustus	1		8 0			8
Psittacus erithacus	11	350	9,0	2,57	19,09	1, 5, 8
Psittacula cyanocephala	1	80	2,3	2,88	—14,11	8
Psittacula krameri	4	110	3,6	3,27	7,47	2, 8
Psittacula eupatria	1	95	4,1	4,32	35,69	5
Psittacula alexandri	3	125	3,6	2,88	—1,76	8
Prioniturus plauturus	1		4,2			8
Prosopeia personata	1	420	5,1	1,21	—40,64	8
Alisterus scapularis	1		3,1			8
Trichoglossus haematodus	8	150	2,5	1,67	—39,99	5, 8
Eos fuscata	2	150	4,2	2,80	0,82	8
Eos squamata	1		3,8			8
Chalcopsitta atra	1	195	5,9	3,03	17,77	8
Psephotus haematonotus	1	75	2,0	2,67	—21,84	8
Platycercus eximius	4	110	2,6	2,36	—22,38	8
Platycercus elegans	2	135	4,0	2,96	3,40	8
Eunymhicus cornutus	2	100	3,6	3,60	14,92	8
Melopsittacus undulatus	19	30	1,15	3,83	—14,42	1, 3—6, 8
Strigops habroptilus	1	1050	14,5	1,38	—11,37	8
Probosciger aterrimus	1	1050	18,5	1,76	13,08	8
Calyptorhynchus magnificus	2	1050	10,3	0,98	—37,04	8
Cacatua galerita	1	450	10,0	2,22	10,89	8
Cacatua sulphurea	2	450	9,4	2,09	4,24	5, 8
Cacatua moluccensis	2	600	10,3	1,72	—6,70	1, 8
Nymphicus hollandicus	11	100	2,5	2,50	—20,19	1, 4—6, 8
Nestor meridionalis	1	510	9,5	1,86	—3,53	8
Nestor notabilis	1		15,5			8

1 = Hrdlička 1905, 2 = Lapicque and Girard 1905, 3 = Girard 1908, 4 = Portmann and Vischer 1943, 5 = Portmann 1947, 6 = Senglaub 1963, 7 = Krompecher and Lipák 1966, 8 = Mlíkovský this paper

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

Taxon	n	S	E	I_{rel}	a_r	Author
Musophagidae (22)						
Corythaeola cristata	1		6,2			3
Musophaga violacea	1		3,7			3
Musophaga rossae	2		4,2			3
Tauraco erythrolophus	1		3,1			3
Tauraco livinstonii	1		2,9			3
Tauraco persa	1		2,9			3
Corythaixoides concolor	4		3,6			3
Cuculidae (130)						
Guira guira	2	120	2,0	1,67	6,10	3
Crotophaga ani	18	100	1,85	1,85	10,80	3
Centropus phasianinus	1		4,0			3
Centropus senegalensis	3	150	2,7	1,80	23,48	1
Coua caerulea	1		4,2			3
Geococcyx californianus	2	290	3,4	1,17	0,31	3
Saurothera merlini	4		2,5			3
Piaya cayana	1	110	2,0	1,82	12,42	3
Coccyzus minor	1		1,2			3
Clamator glandarius	3	135	1,8	1,33	−11,70	3
Cuculus canorus	9	120	1,6	1,33	−18,46	2, 3
Eudynamis scolopacea	3	220	2,3	1,05	−18,46	3
Rhinortha chlorophaea	1		1,3			3

1 = Waterlot 1912, 2 = Portmann 1947, 3 = Mlíkovský this paper

Cuculiformes

The data on the brain size and the body size in Cuculiformes are presented in the Table 3. The data were sufficient for the calculation of the regression equation in the family Cuculidae only.

In this family, brain size and body size are positively correlated ($r_s = 0.661$; $p < 0.05$) and their allometrical relation is $E = 0.0781\ S^{0.665 \pm 0.158}$ ($n = 8$). The slope of this regression does not significantly differ either from the Jerison's constant ($t_s = -0.010$; $p > 0.05$) or the Dubois' constant ($t_s = 0.665$; $p > 0.05$).

Strigiformes

The data on the brain size and the body size in Strigiformes are presented in the Table 4 and Figure 3. In the Strigidae, the only modern family of this order, brain size and body size are positively correlated ($r_H = 1.746 \pm 0.204$; $p < 0.001$) and their allometrical relation is $E = 0.243\ S^{0.552 \pm 0.0367}$ ($n = 25$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -3.124$; $p < 0.01$), but does not significantly differ from the Dubois' constant ($t_s = -0.218$; $p > 0.05$).

Caprimulgiformes

The data on the brain size and the body size in Caprimulgiformes are presented in the Table 5. The data do not allow the calculation of the regression equation for either of the families included.

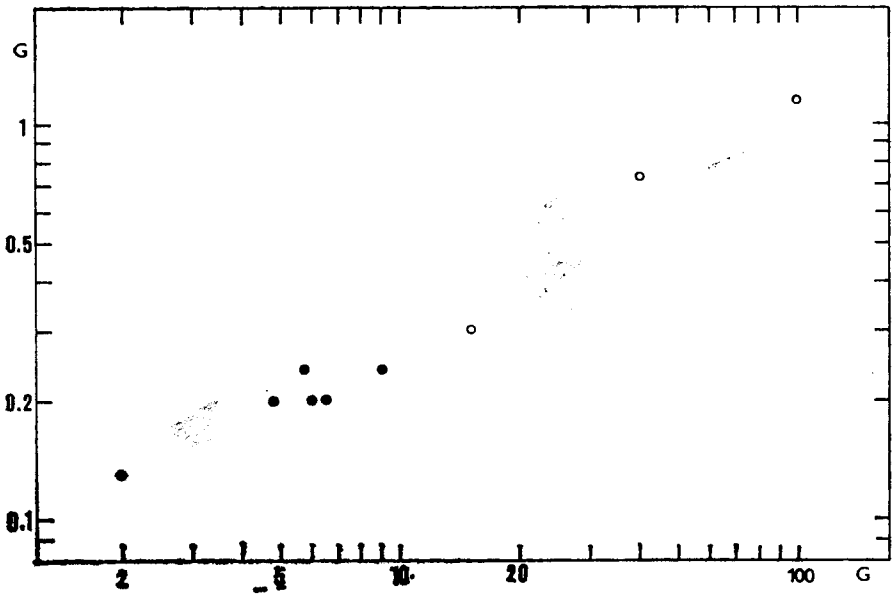

Fig. 4. Relationship between the brain size (Y axis) and the body size (X axis) in Apodidae (○) and Trochilidae (●). See Table 6 for exact data.

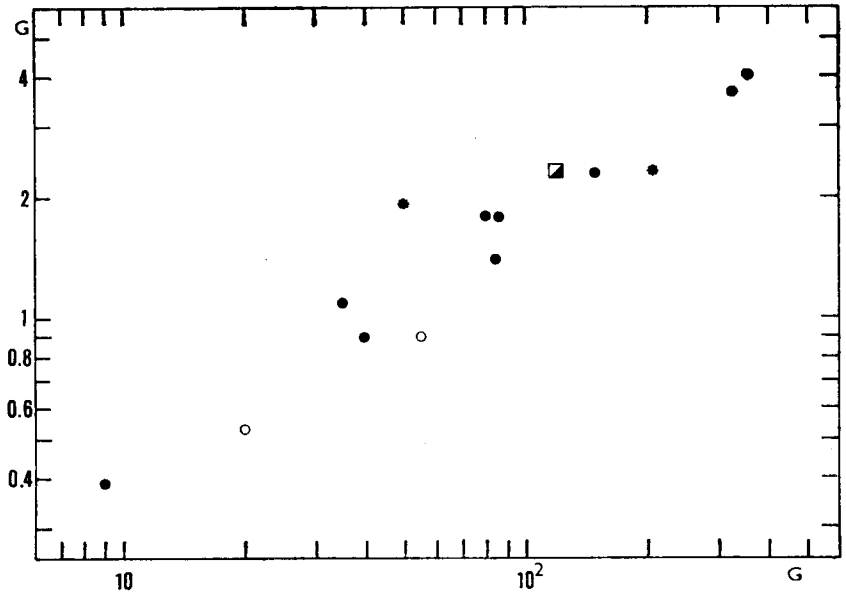

Fig. 5. Relationship between the brain size (Y axis) and the body size (X axis) in Alcedinidae (●), Meropidae (○), Momotidae (◪) and Trogonidae (*). See Tables 7 and 8 for exact data.

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

Taxon	n	S	E	I_{rel}	Q_r	Author
Strigidae (142)						
Tyto alba	36	275	6,7	2,44	24,15	1, 4, 5, 8, 11
Asio flammeus	14	370	5,7	1,54	−10,34	2, 7, 8, 11
Asio clamator	1	370	6,4	1,73	0,68	11
Asio otus	35	270	5,7	2,11	6,70	5, 7−9, 11
Strix varia	2	700	12,3	1,76	36,08	1
Strix uralensis	5	900	9,4	1,04	−9,47	11
Strix nebulosa	1	1300	10,5	0,81	−17,46	11
Strix aluco	32	500	9,2	1,84	22,56	4−5, 9, 11
Strix perspicillata	1	790	10,5	1,33	8,67	11
Otus asio	1	220	5,6	2,55	17,37	1
Otus choliba	1	145	2,8	1,93	−26,13	11
Otus scops	2	90	2,3	2,56	−21,04	5, 11
Otus leucotis	2	220	5,3	2,41	−11,08	11
Bubo poensis	1	1450	9,0	0,62	−33,39	11
Bubo virginianus	4	1500	14,9	0,99	8,24	1
Bubo bubo	47	2600	16,9	0,65	−9,38	5, 10, 11
Bubo capensis	1	1200	11,5	0,96	−5,51	11
Bubo lacteus	1	2200	17,5	0,80	2,90	11
Nyctea scandiaca	4	1900	16,0	0,84	2,01	1, 11
Surnia ulula	1	300	7,0	2,33	23,63	11
Aegolius funereus	2	150	3,8	2,53	−1,60	11
Athene noctua	23	120	4,0	3,33	17,15	3−6, 11
Glaucidium minutissimum	1	45	2,8	6,22	40,92	11
Glaucidium passerinum	2	70	2,5	3,57	−1,41	11
Ninox scutulata	1	220	3,1	1,41	−35,03	11

1 = Hrdlička 1905, 2 = Girard 1908, 3 = Dubois 1914, 4 = Portmann and Vischer 1943, 5 = Portmann 1947, 6 = Vaughien 1949, 7 = Skvorcova 1952, 8 = Senglaub 1963, 9 = Stork 1976, 10 = Piechocki, pers. communication, 11 = Mlíkovský this paper

Apodiformes

The data on the brain size and the body size in Apodiformes are presented in the Table 6 and Figure 4. The data do not allow the calculation of the regression equation for either of the families included.

In Trochilidae, brain size and body size are only marginally correlated ($r_s = 0.643$; $p < 0.1$). This clearly appears to be an artifact, caused by small number of included species and by restricted range of body size. Nevertheless, calculation of the regression equation is meaningless until the bias is removed.

Coliiformes

The data on the brain size and the body size in Coliiformes are presented in the Table 7. They do not allow the calculation of the regression equation for the Coliidae, the only family included.

Trogoniformes

The data on the brain size and the body size in Trogoniformes are presented in the Table 7 and Figure 5. The data do not allow the calculation of the regression equation for the Trogonidae, the only modern family included.

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

Taxon	n	S	E	I_{rel}	Q_r	Author
Steatornithidae (1)						
Steatornis caripensis	2		3,3			2
Podargidae (12)						
Podargus strigoides	1		4,7			2
Aegothelidae (7)						
No data						
Nyctibiidae (5)						
No data						
Caprimulgidae (78)						
Hydropsalis brasiliana	1		1,6			2
Macropsalis creagra	1		1,1			2
Caprimulgus europaeus	4	80	0,94	1,18		1—2
Semiophorus vexillarius	1	70	1,0	1,43		2

1 = Portmann 1947, 2 = Mlíkovský this paper

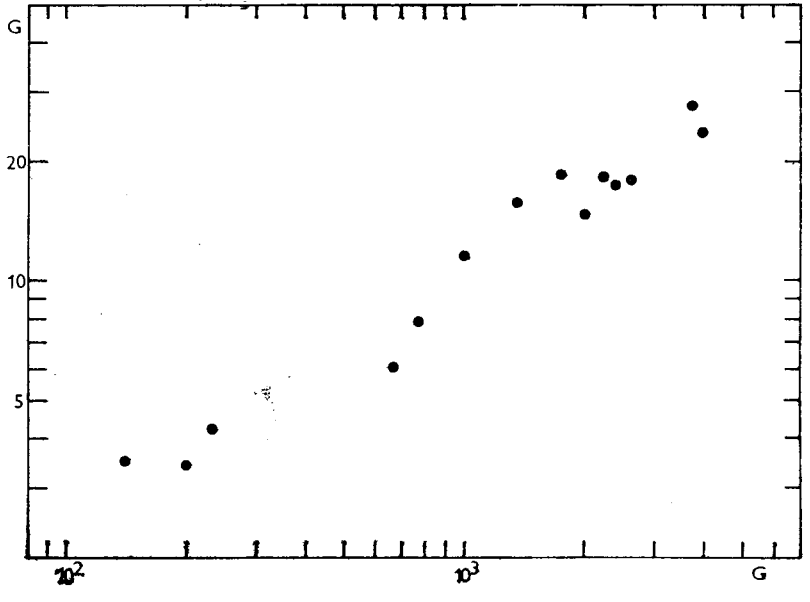

Fig. 6. Relationship between the brain size (Y axis) and the body size (X axis) in Bucerotidae. See Table 8 for exact data.

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

Taxon	n	S	E	I_{rel}	A_r	Author
Hemiprocnidae (4)						
No data						
Apodidae (82)						
Apus melba	11	100	1,13	1,13		5, 8
Apus apus	26	40	0,72	1,80		4—8
Cypsiurus parvus	1	15	0,3	2,00		2
Trochilidae (317)						
Glaucis hirsuta	1	6 5	0,20	3,08		8
Colibri coruscans	1	9,0	0,24	2,67		8
Amazilia tzacatl	1	4,8	0,20	4,17		3
Lampornis amethystinus	1	6,0	0,20	3,08		1
Clyptolaema rubricauda	1		0,28			8
Ocreatus underwoodi	1		0,14			8
Aglaiocercus kingi	1		0,22			8
Aglaiocercus coelestis	1		0,22			8
Heliothryx barroti	1	5,7	0,24	4,21		8
Mellisuga minima	1	2,0	0,13	6,50		1

1 = Lapicque 1908, 2 = Waterlot 1912, 3 = Crile and Quiring 1940, 4 = Portmann and Vischer 1943, 5 = Portmann 1947, 6 = Skvorcova 1952, 7 = Senglaub 1963, 8 = Mlíkovský this paper

Coraciiformes

The data on the brain size and the body size in Coraciiformes are presented in the Table 8 and Figures 5—6. The data were sufficient for the calculation of the regression equations in the families Alcedinidae and Bucerotidae only.

In Alcedinidae, brain size and body size are positively correlated ($r_s = 0.967$; $p < 0.01$) and their allometrical relation is $E = 0.0964\ S^{0.639 \pm 0.0339}$ ($n = 9$). The slope of this regression is significantly higher than the Dubois' constant ($t_s = 2.330$; $p < 0.05$), but does not significantly deviate from the Jerison's constant ($t_s = -0.816$; $p > 0.05$).

Table 7. Brain size and encephalization in Coliiformes and Trogoniformes.
See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Coliidae (6)						
Colius striatus	1	55	1,1	2,00		1
Urocolius indicus	2	60	1,2	2,00		1
Trogonidae (39)						
Trogonurus cucurui	1	50	1,9	3,80		1
Priotelus temnurus	1		1,2			1
Pharomachrus moccino	1	205	2,3	1,12		1

1 = Mlíkovský this paper

Table 8. Brain size and encephalization in Coraciiformes.
See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Alcedinidae (91)						
Ceryle rudis	3	80	1,7	2,13	7,23	2, 5
Chloroceryle amazona	1		3,6			5
Chloroceryle americana	1	35	1,1	3,14	17,67	5
Streptoceryle torquata	2	325	3,7	1,14	−4,71	5
Streptoceryle alcyon	1	150	2,6	1,73	9,74	5
Dacelo novaeguineae	2	360	4,1	1,14	−1,09	1
Halcyon smyrnensis	2	95	1,8	1,89	1,73	5
Todiramphus chloris	2	85	1,4	1,65	−15,05	5
Alcedo atthis	7	40	0,9	2,25	−11,60	4—5
Ispidina picta	3	9	0,39	4,33	−0,64	2
Todidae (5)						
No data						
Momotidae (9)						
Momotus momota	1	120	2,3	1,92		5
Meropidae (25)						
Merops apiaster	3	55	0,89	1 62		4—5
Merops nubicus	1		0,9			5
Merops albicollis	3	20	0,53	2,65		2
Coraciidae (11)						
Coracias garrulus	6	160	2,2	1,38		5
Eurystomus glaucurus	1		1,8			5
Brachypteraciidae (5)						
No data						
Leptosomatidae (1)						
No data						
Upupidae (1)						
Upupa epops	12	60	0,98	1,63		4—5
Phoeniculidae (6)						
No data						
Bucerotidae (46)						
Tockus erythrorhynchus	2	140	3,25	2,32	16,82	5
Tockus monteiri	1	200	3,2	1,60	−9,39	5
Tockus alboterminatus	2	235	4,2	1,79	6,76	5
Rhyticeros undulatus	1	2250	18,5	0,82	3,74	5
Rhyticeros plicatus	1	1750	18,5	1 06	22,74	5
Anthracoceros malayanus	1	1000	11,5	1,16	10,94	5
Bycanistes fistulator	3	765	8,3	1,08	−4,21	5
Bycanistes bucinator	1	670	6,0	0,90	−24,33	5
Bycanistes cylindricus	2		11,5			5
Bycanistes subcylindricus	13		14,3			5
Ceratogymna elata	2	2000	14,8	0,74	−10,20	5
Ceratogymna atrata	1	1350	15,5	1,15	22,33	5
Buceros rhyticeros	2	2400	17,8	0,74	−4,40	5
Buceros bicornis	2	2600	17,8	0,68	−9,38	5
Bucorvus abyssinicus	4	4000	23,4	0,59	−10,70	5
Bucorvus cafer	4	3800	27,3	0,72	7,82	3, 5

1 = Hrdlička 1905, 2 = Waterlot 1912, 3 = Crile and Quiring 1940, 4 = Portmann 1947, 5 = Mlíkovský this paper

Table 9. Brain size and encephalization in Piciformes.
See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Galbulidae (15)						
Galbula galbula	1	21	0,6	2,86		6
Bucconidae (32)						
No data						
Capitonidae (81)						
Megalaima virens	1		2,2			6
Trachyphonus margaritatus	2		1,2			6
Eobucco bourcierii	1	34	1,1	3,24		6
Idicatoridae (16)						
No data						
Ramphastidae (33)						
Selenidera maculirostris	1		3,0			6
Ramphastos tucanus	3		5,3			6
Ramphastos toco	2		6,3			6
Ramphastos sulphuratus	1		4,8			6
Ramphastos vitellinus	2	350	4,7	1,34		6
Picidae (204)						
Dendrocopos major	36	85	2,8	3,29	−1,55	2−6
Dendrocopos medius	4	70	2,3	3,29	−7,39	3, 5, 6
Dendrocopos minor	4	22	1,2	5,45	8,38	4−6
Picoides tridactylus	4	65	3,2	4,92	35,68	5
Melanerpes formicivorus	1	75	2,5	3,33	−4,07	6
Centurus aurifrons	1	55	2,2	4,00	4,82	6
Centurus superciliaris	3	85	2,6	3,06	−8,58	6
Colaptes cafer	1	110	2,7	2,45	−20,70	6
Picus canus	6	110	3,6	3,27	5,73	3, 5−6
Picus viridis	15	200	4,4	2,20	−14,86	1−6
Dryocopus lineatus	1	180	4,3	2,39	−10,45	6
Dryocopus martius	6	250	7,7	3,08	27,50	3, 6
Jynx torquilla	9	35	0,9	2,57	−41,21	2−3, 6

1 = Girard 1908, 2 = Portmann and Vischer 1943, 3 = Portmann 1947, 4 = Vaughien 1949, 5 = Skvorcova 1954, 6 = Mlíkovský this paper

In Alcedinidae, brain size and body size are positively correlated ($r_s = 0.967$; $= 2.207 + 0.277$; $p < 0.001$) and their allometrical relation is $E = 0.102\ S^{0.669 \pm 0.0367}$ ($n = 14$). The slope of this regression is significantly higher than the Dubois' constant ($t_s = 2.970$; $p < 0.01$), but does not significantly differ from the Jerison's constant ($t_s = 0.064$; $p > 0.05$).

Piciformes

The data on the brain size and the body size in Piciformes are presented in the Table 9 and Figure 7. The data were sufficient for the calculation of the regression equation only in the family Picidae.

In this family, if Jynx is excluded from calculations (see below), brain size

and body size are positively correlated ($r_H = 1.612 \pm 0.302$; $p < 0.001$) and their allometrical relation is $E = 0.128\ S^{0.698 \pm 0.0751}$ ($n = 12$). The slope of this regression does not significantly deviate from both the Jerison's constant ($t_s = 0.417$; $p > 0.05$) and the Dubois' constant ($t_s = 1.838$; $p > 0.05$).

Considerable differences in encephalization between the picid subfamilies are worth mentioning. The ancestral Jynginae, represented here by *Jynx torquilla*,

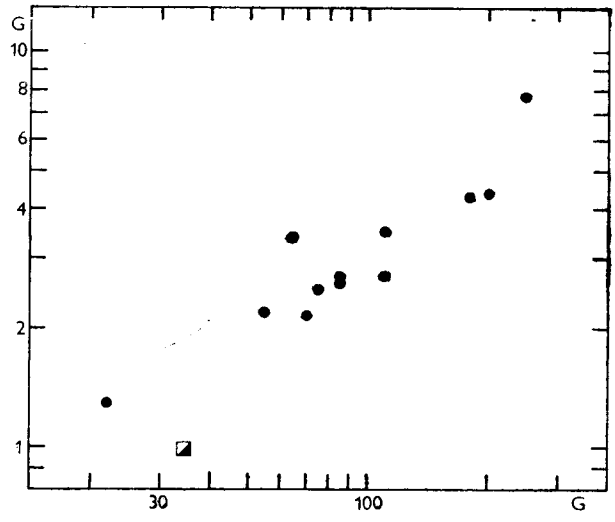

Fig. 7. Relationship between the brain size (Y axis) and the body size (X axis) in Picidae. ◪ = *Jynx torquilla*. See Table 9 for exact data.

are markedly less encephalized than the derived Picinae, to which belong all other studied picid species (see Table 9 and Figure 7). This agrees well with the more primitive structural organization of the jyngine brain (Brandis 1896, Dennler 1919, Ruge 1971). Unfortunately, no data were available on encephalization and/or brain morphology of the Picumninae, another ancestral picid subfamily.

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