Original Paper

Brain, Behavior and Evolution

Brain Behav Evol 2007;69:196–219
DOI: 10.1159/000096987

Received: April 12, 2006
Returned for revision: May 3 2006
Accepted after revision: May 17, 2006
Published online: November 13, 2006

Comparative Morphology of the Avian Cerebellum: II. Size of Folia

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Key Words
Cerebellum · Evolution · Allometry · Comparative method · Birds

Abstract
Despite the highly conserved circuitry of the cerebellum, its overall shape varies significantly among and within vertebrate classes. In birds, one of the most prominent differences among orders is the relative size of the cerebellar folia. The enlargement/reduction of individual folia is thought to relate to specific behavioral differences among taxa, but this has not been adequately tested. Here, we survey variation in cerebellar folia size among 96 species of birds and test for phylogenetic effects and correlations with behavior using a combination of conventional and phylogeny-based statistics. Overall, we found that phylogenetic history accounts for a significant amount of variation in the relative size of individual folia. Order membership, in particular, accounted for more than half of the interspecific variation in folia size. There are also complex relationships among folia such that the expansion of one folium is often accompanied by a reduction in other folia. With respect to behavioral correlates: (1) we did not find any significant correlations between folia size and reliance on trigeminal input; (2) there was some evidence supporting a correlation between strong hindlimbs and an expansion of the anterior lobe; and (3) there were significant reductions in folia I–III and expansions in folia VI and VII in species classified as strong fliers. This expansion likely reflects increased visual processing requirements in species with rapid and/or agile flight. It therefore appears that folium size is a product of both phylogenetic history and behavior in birds.

Introduction

Cerebellar morphology varies immensely among vertebrate classes from sheet-like structures in some fish, amphibians and sauropsids to folded and lobuled structures in mormyrids, birds and mammals [Butler and Hodos, 2005]. Within those groups that have folded or foliated cerebella, there also exists considerable variation in the relative size of individual lobules or folia of the cerebellum. In mammals, species differences in the relative size and number of folia and lobules is thought to reflect behavioral and/or cognitive differences [Welker, 1990]. For example, the expansion of the parafloccular and medial lobes in bats and whales is thought to represent an adaptation for echolocation [Paulin, 1993]. Similarly, spider monkeys (*Ateles* spp.) have the largest lobule I of any mammal, which Larsell [1970] proposed was a reflection of its prehensile tail. Studies within species have also shown that differences in cerebellar foliation are accompanied by changes in behavior [Cooper et al., 1991; Le Roy-Dufols, 2001; Demaerel, 2002]. The primary assumption underlying all of these behavior-cerebellum

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correlations is that each folium of the mammalian cerebellum represents a discrete structural and functional unit that mediates specific sensory and/or sensorimotor projections [Welker, 1990].

In birds, similar correlations between cerebellar morphology and behavior have been suggested. For example, the enlargement of folium VII in eagles is thought to reflect their 'visual power' [Larsell, 1967]. Other proposed relationships include: enlargement of folia V and VI in 'strong flying' species; enlargement in folium VI and reliance on the trigeminal system and reduction of folia II–IV and in species with weak hindlimbs [Larsell, 1967]. More recently, Sultan [2005] suggested that the enlargement of folia IV and VI–IX reflected cognitive ability in birds based on the distribution of species in a multivariate analysis. Although there appears to be ample evidence to support a correlation between folium size and some aspects of avian behavior, two problems arise in attempting to apply these purported correlations to the functional organization of the avian cerebellum. First, the evidence for avian cerebellar folia representing discrete functional units is mixed. For example, Larsell [1967] proposed that trigeminal projections were localized in folium VI, but later studies found that most trigeminal projections actually terminate in folia V–IXab [Arends et al., 1984; Arends and Zeigler, 1989]. Similarly, the somatotopic representation proposed by Larsell [1967] is not supported by later studies [Schulte and Necker, 1998; Necker, 2001]. On the other hand, visual projections from the tecto-pontine system, tectum, pretectum and accessory optic system appear to be specific to folia of the posterior lobe [Clarke, 1974, 1977; Brecha et al., 1980; Gamlin and Cohen, 1988; Pakan et al., 2005; Pakan and Wylie, in press]. Given the lack of consensus regarding the functional organization of the cerebellar folia in birds, many of the proposed folium-behavior correlations are highly suspect and require empirical verification.

The second major problem is that the proposed correlations between folia size and behavior lack the statistical approach and phylogenetic context required to adequately evaluate them. Phylogenetic history can influence the evolution of the brain in a number of ways [Harvey and Pagel, 1991; Striedter, 2005] that might not be apparent in simple correlations or qualitative observations [see Iwaniuk et al., 1999, 2001; Iwaniuk and Whishaw, 2000]. In essence, this means that we do not know whether the enlargement of specific folia reflects behavioral differences among taxa or it reflects phylogenetic relationships and/or allometry. For example, the large VII in eagles might reflect the fact that raptors have relatively large cerebella compared to other birds rather than some feature of the visual system. There is also the possibility that there are correlated size changes among folia. That is, an evolutionary change in the size of one folium might be correlated with changes in other folia. Such concerted evolutionary changes occur among brain regions in both birds [Iwaniuk et al., 2004; Iwaniuk and Hurd, 2005] and mammals [Barton and Harvey, 2000; Finlay et al., 2001; Barton et al., 2003]. Size changes in one folium therefore might not reflect a specific behavior, but rather changes that are occurring in other parts of the cerebellum that might or might not reflect behavioral differences.

Recently, we adopted a multivariate and phylogenetic approach to understanding the evolution of the avian cerebellum within a specific clade of birds [Iwaniuk et al., 2006b]. Here, we expand on this work by comparing the relative size of folia in a broader sampling of species. First, we tested whether variation in relative folia size is significantly affected by phylogenetic history. Second, we tested whether Larsell's [1967] original conclusions could be corroborated by statistical analysis. Specifically, we examined the following: hindlimb use and folia of the anterior lobe; enlargement of folia V and VI in 'strong-fliers'; and enlargement of folium VI in species with a strong reliance on the trigeminal system.

Materials and Methods

Specimens

The brains of several species were obtained from wildlife sanctuaries and veterinary clinics, other researchers and museum specimens loaned to us from the Bishop Museum (Honolulu, HI), the National Museum of Natural History (Washington, DC) and the Field Museum of Natural History (Chicago, Ill., USA; table 1). For most specimens, only a single individual was measured, but it should be noted that there was little intraspecific variation for those species in which we did measure more than one individual. All birds that we collected were submersion fixed in 10% buffered formalin or 4% buffered paraformaldehyde. Specimens provided by other researchers were fixed in a similar fashion or transcardially perfused with 4% paraformaldehyde. The museum specimens were immersion fixed in 10% buffered formalin, but following adequate fixation, they were kept in 70% ethanol that was replaced on a regular basis. The specimens that were loaned to us were stored in 70% ethanol for between 2 and 62 years. Once the brains were extracted, the museum specimens were placed in 4% paraformaldehyde in 0.1 M phosphate buffer (pH = 7.4) for several days prior to processing (see below).

Following extraction, the meninges were removed and the brains weighed to the nearest milligram with an electronic balance. The brains were then bisected in the sagittal plane and the cerebellum from one half of the brain was removed by cutting

Table 1. The proportional size (folium length/total Purkinje cell length) of each folium for all 96 species surveyed. Data were derived from our own specimens and figures in Senglaub [1963], Larsell [1967] and Matochik et al. [1991]

Order	Family	Species	I	II	III	IV	V	VI	VII	VIII	IXab	IXcd	X
Anseriformes	Anatidae	*Anas platyrhynchos*	0.0241	0.0468	0.0480	0.0614	0.1060	0.2521	0.1147	0.1669	0.0996	0.0584	0.0218
		Clangula hyemalis	0.0076	0.0325	0.0484	0.0659	0.0886	0.2077	0.1512	0.1632	0.1294	0.0742	0.0313
		Melanitta fusca	0.0110	0.0413	0.0441	0.0651	0.1226	0.2023	0.1295	0.1562	0.1198	0.0719	0.0361
		Melanitta nigra	0.0275	0.0440	0.0352	0.0524	0.1073	0.2602	0.1180	0.1486	0.1246	0.0607	0.0217
Apodiformes	Apodidae	*Apus apus*	0.0244	0.0215	0.0168	0.1021	0.1174	0.2503	0.1161	0.0973	0.1442	0.0800	0.0299
		Collocalia esculenta	0.0130	0.0180	0.0124	0.1151	0.1213	0.1572	0.1216	0.0970	0.2017	0.1013	0.0413
Apterygiformes	Apterygidae	*Apteryx australis*	0.0326	0.0484	0.0492	0.0762	0.1391	0.1742	0.1096	0.1346	0.0906	0.0642	0.0812
Caprimulgi-formes	Aegothelidae	*Aegotheles insignis*	0.0337	0.0485	0.0327	0.0770	0.0973	0.1824	0.1128	0.1451	0.1542	0.0805	0.0357
	Caprimulgidae	*Eurostopodus argus*	0.0273	0.0534	0.0341	0.0843	0.1259	0.1141	0.0961	0.1801	0.1887	0.0720	0.0240
		Nyctidromus albicollis	0.0293	0.0433	0.0250	0.0978	0.1024	0.1400	0.1140	0.1813	0.1717	0.0708	0.0244
	Nyctibiidae	*Nyctibius griseus*	0.0208	0.0409	0.0337	0.0733	0.0968	0.1676	0.1080	0.1820	0.1753	0.0754	0.0263
	Podargidae	*Podargus strigoides*	0.0369	0.0550	0.0528	0.0702	0.1617	0.1339	0.0892	0.1243	0.1109	0.1055	0.0263
	Steatornithidae	*Steatornis caripensis*	0.0339	0.0608	0.0357	0.0907	0.1602	0.0750	0.0920	0.1850	0.10035	0.1263	0.0401
Charadriiformes	Charadriidae	*Vanellus spinosus*	0.0414	0.0468	0.0662	0.1002	0.0795	0.1478	0.1180	0.1518	0.1598	0.0994	0.0471
	Laridae	*Larus argentatus*	0.0201	0.0453	0.0464	0.0759	0.1093	0.1845	0.1205	0.1141	0.1617	0.0999	0.0224
		Larus canus	0.0294	0.0383	0.0460	0.0851	0.0949	0.1513	0.1223	0.1264	0.1942	0.0919	0.0201
		Larus novaehollandiae	0.0331	0.0415	0.0425	0.0845	0.0880	0.1358	0.1362	0.1145	0.1930	0.1070	0.0240
		Larus ridibundus	0.0174	0.0316	0.0442	0.0906	0.1063	0.1493	0.1256	0.1215	0.1900	0.1006	0.0229
		Sterna paradisaea	0.0279	0.0370	0.0413	0.0906	0.0864	0.1435	0.1099	0.1167	0.1871	0.1314	0.0283
	Scolopacidae	*Actictis hypoleucos*	0.0489	0.0541	0.0497	0.0793	0.1034	0.1653	0.1031	0.1203	0.1638	0.0790	0.0331
		Limnodromus griseus	0.0430	0.0555	0.0559	0.0764	0.0826	0.1638	0.1273	0.1369	0.1442	0.0791	0.0354
		Phalaropus lobatus	0.0241	0.0556	0.0498	0.0883	0.1068	0.1217	0.1191	0.1105	0.1896	0.1114	0.0231
		Scolopax rusticola	0.0292	0.0936	0.0738	0.1056	0.1282	0.1419	0.1081	0.1111	0.0957	0.0813	0.0315
Ciconiiformes	Ardeidae	*Bubulcus ibis*	0.0377	0.0491	0.0828	0.1080	0.0795	0.1478	0.1180	0.1518	0.1248	0.0738	0.0266
Columbiformes	Columbidae	*Columba livia*	0.0307	0.0480	0.0701	0.1086	0.1245	0.1649	0.0943	0.1213	0.1050	0.0976	0.0351
		Columba palumbus	0.0295	0.0415	0.0706	0.1147	0.1183	0.1980	0.0925	0.1203	0.0904	0.0889	0.0353
		Geopelia placida	0.0477	0.0644	0.0746	0.1034	0.0975	0.1356	0.1074	0.1246	0.1121	0.1027	0.0297
		Phaps elegans	0.0405	0.0567	0.0764	0.0979	0.1042	0.1481	0.1017	0.1216	0.1202	0.0966	0.0363
		Ptilinopus superbus	0.0342	0.0539	0.0690	0.1017	0.1003	0.1889	0.1100	0.1123	0.0966	0.0989	0.0341
		Streptopelia roseogrisea	0.0239	0.0533	0.0755	0.1013	0.1086	0.1797	0.0931	0.1286	0.1026	0.1002	0.0332
Coraciiformes	Cerylidae	*Ceryle alcyon*	0.0389	0.0586	0.0339	0.0809	0.1115	0.1473	0.1414	0.1093	0.1605	0.0847	0.0330
	Dacelonidae	*Dacelo novaeguineae*	0.0394	0.0518	0.0329	0.0792	0.0915	0.1500	0.1125	0.1200	0.1755	0.1075	0.0397
Falconiformes	Accipitridae	*Accipiter fasciatus*	0.0277	0.0358	0.0442	0.0871	0.0784	0.1524	0.1451	0.1067	0.2255	0.0684	0.0288
		Aquila audax	0.0316	0.0345	0.0431	0.0617	0.1242	0.1434	0.1752	0.1235	0.1739	0.0678	0.0213
		Buteo buteo	0.0293	0.0303	0.0654	0.0771	0.0615	0.1701	0.1451	0.0992	0.2192	0.0766	0.0263
		Haliaeetus leucocephalus	0.0309	0.0442	0.0468	0.0596	0.0595	0.1888	0.1520	0.1113	0.1890	0.0895	0.0284
		Haliaeetus leucogaster	0.0253	0.0343	0.0438	0.0667	0.1032	0.2031	0.1316	0.1019	0.1899	0.0790	0.0210
	Falconidae	*Falco berigora*	0.0232	0.0347	0.0491	0.0731	0.0706	0.1935	0.1554	0.0833	0.2084	0.0716	0.0371
		Falco tinnunculus	0.0245	0.0464	0.0548	0.0750	0.0757	0.1604	0.1428	0.0913	0.2203	0.0768	0.0320
Galliformes	Phasianidae	*Bonasa umbellus*	0.0434	0.0484	0.0431	0.1366	0.1293	0.1076	0.0889	0.1197	0.1309	0.1090	0.0432
		Dendragapus obscurus	0.0350	0.0440	0.0423	0.1234	0.1281	0.1087	0.1029	0.1372	0.1285	0.1116	0.0383
		Gallus domesticus	0.0492	0.0504	0.0586	0.0834	0.1416	0.0998	0.0809	0.1448	0.1434	0.0969	0.0507
		Meleagris gallopavo	0.0175	0.0460	0.1052	0.0978	0.1545	0.0761	0.0936	0.1475	0.1567	0.0779	0.0270
		Perdix perdix	0.0260	0.0727	0.0730	0.0947	0.1131	0.0846	0.0907	0.1637	0.1375	0.1109	0.0330
		Phasianus colchicus	0.0490	0.0568	0.1164	0.0866	0.1447	0.0932	0.0776	0.1398	0.1073	0.0789	0.0497
Gruiformes	Otidiidae	*Ardeotis australis*	0.0376	0.0339	0.0422	0.0706	0.1148	0.1098	0.1106	0.1431	0.2047	0.1019	0.0308
	Rallidae	*Fulica americana*	0.0260	0.0645	0.0612	0.0787	0.1185	0.1058	0.1128	0.1393	0.1554	0.1096	0.0282
Passeriformes	Bombycillidae	*Bombycilla garrulous*	0.0392	0.0510	0.0881	0.0958	0.0960	0.1794	0.1002	0.1040	0.1470	0.0751	0.0241
	Corvidae	*Corvus corax*	0.0245	0.0464	0.0464	0.0668	0.1159	0.1630	0.0970	0.1495	0.1875	0.0820	0.0211
		Corvus corone	0.0129	0.0275	0.0565	0.1248	0.1189	0.1520	0.0920	0.1498	0.1696	0.0787	0.0173
		Corvus mellori	0.0233	0.0356	0.0484	0.0965	0.0880	0.2173	0.0932	0.1033	0.1924	0.0773	0.0247
		Corvus monedula	0.0131	0.0476	0.0696	0.1027	0.1115	0.1651	0.0881	0.1320	0.1713	0.0785	0.0205
		Garrulus glandarius	0.0378	0.0432	0.0550	0.0870	0.0910	0.1750	0.0883	0.1223	0.1765	0.1005	0.0235
		Gymnorhina tibicen	0.0247	0.0354	0.0642	0.0862	0.0905	0.1670	0.0835	0.1103	0.2177	0.0860	0.0345
	Hirundidae	*Hirundo rustica*	0.0286	0.0508	0.0615	0.0821	0.0963	0.2365	0.1037	0.1060	0.1436	0.0627	0.0283
	Menuridae	*Menura novaehollandiae*	0.0286	0.0343	0.0800	0.0832	0.1591	0.1797	0.1043	0.0928	0.1199	0.0850	0.0331
	Muscicapidae	*Erithacus rubecula*	0.0328	0.0479	0.0624	0.0899	0.1012	0.1553	0.1023	0.1257	0.1569	0.0924	0.0332
		Turdus merula	0.0307	0.0588	0.0465	0.1521	0.1101	0.1548	0.0763	0.0960	0.1385	0.1095	0.0269
	Pardalotidae	*Acanthiza pusilla*	0.0379	0.0436	0.0528	0.0787	0.1007	0.1698	0.1035	0.1063	0.1567	0.0851	0.0282
	Paridae	*Parus major*	0.0218	0.0416	0.0561	0.1036	0.0894	0.1746	0.1071	0.1166	0.1615	0.0972	0.0306

Table 1 (continued)

Order	Family	Species	I	II	III	IV	V	VI	VII	VIII	IXab	IXcd	X
	Passeridae	*Anthus trivialis*	0.0434	0.0425	0.0723	0.1015	0.0827	0.1312	0.0946	0.1974	0.1279	0.0759	0.0306
Pelecaniformes	Pelecanidae	*Pelecanus conspicillatus*	0.0334	0.0390	0.0524	0.0679	0.0900	0.1679	0.1291	0.1392	0.1868	0.0763	0.0184
	Phalacrocoracidae	*Phalacrocorax brandti*	0.0256	0.0246	0.0430	0.0708	0.0754	0.2271	0.0958	0.1008	0.1208	0.1950	0.0211
Phoenicopteri-formes	Phoenicopteridae	*Phoenicopterus ruber*	0.0249	0.0493	0.0484	0.0819	0.0836	0.2500	0.1097	0.1453	0.1351	0.0499	0.0220
Piciformes	Picidae	*Dendrocopos major*	0.0130	0.0360	0.0395	0.0751	0.1017	0.1846	0.1102	0.1445	0.1749	0.1036	0.0169
		Picus viridus	0.0094	0.0270	0.0456	0.0934	0.1224	0.1994	0.1027	0.1385	0.1439	0.1028	0.0149
Procellariiformes	Diomedeidae	*Diomedea melanophris*	0.0137	0.0267	0.0347	0.0487	0.1050	0.2578	0.1701	0.0874	0.1695	0.0686	0.0177
	Procellariidae	*Fulmarus glacialis*	0.0162	0.0217	0.0225	0.0405	0.1165	0.3302	0.1299	0.1099	0.1089	0.0826	0.0210
		Puffinus tenuirostris	0.0092	0.0258	0.0268	0.0743	0.1207	0.3065	0.1054	0.1202	0.1268	0.0721	0.0122
Psittaciformes	Cacatuidae	*Cacatua galerita*	0.0181	0.0311	0.0299	0.0792	0.1107	0.1722	0.0728	0.1169	0.1968	0.1408	0.0315
		Cacatua roseicapilla	0.0219	0.0320	0.0331	0.0585	0.1042	0.1582	0.0904	0.1385	0.2131	0.1250	0.0251
		Cacatua tenuirostris	0.0259	0.0315	0.0431	0.0592	0.1219	0.1696	0.1002	0.1154	0.2018	0.1025	0.0288
		Nymphicus hollandicus	0.0301	0.0442	0.0728	0.1067	0.0327	0.1914	0.0934	0.1067	0.1553	0.1164	0.0327
	Psittacidae	*Agapornis personata*	0.0219	0.0370	0.0561	0.0582	0.1230	0.1184	0.0956	0.1261	0.1984	0.1350	0.0303
		Alisterus scapularis	0.0177	0.0330	0.0542	0.1149	0.0953	0.1365	0.0959	0.1215	0.1915	0.1179	0.0216
		Ara chloroptera	0.0074	0.0337	0.0974	0.0614	0.1216	0.1675	0.0919	0.1546	0.1764	0.0705	0.0176
		Glossopsitta porphyrocephala	0.0348	0.0371	0.0485	0.0701	0.1293	0.1703	0.1106	0.1174	0.1242	0.1274	0.0304
		Melopsittacus undulatus	0.0287	0.0412	0.0672	0.0745	0.0696	0.2308	0.0950	0.1038	0.1450	0.1177	0.0265
		Platycercus elegans	0.0157	0.0258	0.0618	0.0529	0.0890	0.1355	0.0927	0.1219	0.2341	0.1345	0.0360
Sphenisciformes	Spheniscidae	*Aptenodytes forsteri*	0.0274	0.0595	0.0363	0.0493	0.0772	0.1845	0.1022	0.1707	0.1216	0.1326	0.0386
		Eudyptes sp.	0.0284	0.0267	0.0349	0.0434	0.1121	0.2334	0.1105	0.1204	0.1375	0.1344	0.0184
		Eudyptula minor	0.0212	0.0299	0.0357	0.0599	0.0530	0.2139	0.1276	0.1402	0.1668	0.1312	0.0207
		Pygoscelis adeliae	0.0245	0.0305	0.0622	0.0454	0.0939	0.1895	0.0899	0.1655	0.1279	0.1462	0.0244
Strigiformes	Strigidae	*Aegolius acadicus*	0.0336	0.0675	0.0621	0.0649	0.1580	0.1465	0.0937	0.1026	0.1445	0.0813	0.0452
		Asio flammeus	0.0387	0.0636	0.0683	0.0825	0.1326	0.1348	0.0839	0.1061	0.1751	0.0716	0.0429
		Asio otus	0.0349	0.0525	0.0568	0.0700	0.1489	0.1562	0.0811	0.1051	0.1685	0.0775	0.0485
		Bubo virginianus	0.0310	0.0409	0.0601	0.0775	0.1365	0.1741	0.0783	0.1094	0.1786	0.0696	0.0438
		Ninox boobook	0.0439	0.0490	0.0538	0.0762	0.1472	0.1672	0.0940	0.1089	0.1453	0.0751	0.0394
	Tytonidae	*Tyto alba*	0.0385	0.0686	0.0609	0.0774	0.1381	0.1813	0.0863	0.0970	0.1311	0.0772	0.0435
Struthioniformes	Rheidae	*Rhea americana*	0.0530	0.0379	0.0466	0.0726	0.2361	0.0996	0.0723	0.1371	0.1309	0.0748	0.0389
	Struthionidae	*Struthio camelus*	0.0450	0.0265	0.0448	0.0810	0.2475	0.1287	0.0855	0.1428	0.0917	0.0774	0.0291
Trochiliformes	Trochilidae	*Doryfera ludoviciae*	0.0101	0.0217	0.0214	0.0976	0.1322	0.2062	0.1148	0.1266	0.1470	0.0849	0.0376
		Eutoxeres condamini	0.0116	0.0229	0.0205	0.1183	0.1170	0.2185	0.1275	0.1143	0.1203	0.0925	0.0368
		Glaucis hirsute	0.0305	0.0152	0.0139	0.0899	0.1094	0.1856	0.1102	0.1072	0.2191	0.0855	0.0336
		Lampornis sp.	0.0176	0.0205	0.0209	0.1003	0.1200	0.2096	0.1120	0.1085	0.1732	0.0890	0.0284
		Sephanoides sephanoides	0.0152	0.0179	0.0169	0.1043	0.1229	0.2194	0.1076	0.1122	0.1557	0.0875	0.0405

For further details regarding the sources of these specimens, see Iwaniuk et al. [2006c].

through the cerebellar peduncle. This enabled us to examine the entire lateral aspect of the cerebellum prior to sectioning and use Larsell's [1967] cerebellar taxonomy appropriately (see below). The brains were then placed in 30% sucrose in 0.1 M phosphate buffer until they sank. The brains were subsequently gelatin-embedded and sectioned in the sagittal plane on a freezing stage microtome. Sections 40 μm thick were collected in 0.1 M phosphate buffered saline and mounted onto gelatinized slides. After drying, the slides were stained with thionin, dehydrated through a graded ethanol series, cleared in Hemo-D and coverslipped with Permount.

Measurements

Prior to measuring the relative sizes of individual folia, we numbered them following Larsell's [1967] cerebellar taxonomy. As shown in a representative drawing of an avian cerebellum (fig. 1), each folium is numbered in ascending order in a rostral (I) to caudal (X) direction. In total, there are eleven primary folia with IX divided into IXab and IXcd. Folia I–V and VI–IX comprise the anterior and posterior lobes, respectively [Larsell, 1967]. Folia IXcd and X comprise the vestibulocerebellum [VbC; Schwarz and Schwarz, 1986]. Primary folia are individually numbered and secondary folia alphanumerically numbered. In figure 1, for example, folia I, II and III are distinct primary folia whereas Va and Vb are the two subfolia belonging to V. According to Larsell [1967], the primary folia are identified by the presence of fissures on the exterior surface of the cerebellum. The primary fissure separates folia V and VI, and the secondary fissure separates VIII and IXab. Larsell [1967] defined individual folia and their subdivisions based upon cerebellar development in chickens *(Gallus domesticus)* and ducks *(Anas platyrhynchos)* and extrapolated this to other species. This is problematic, however, because there are species differences in how the cerebellum develops [Larsell 1967] and the pattern of cerebellar development is unknown for

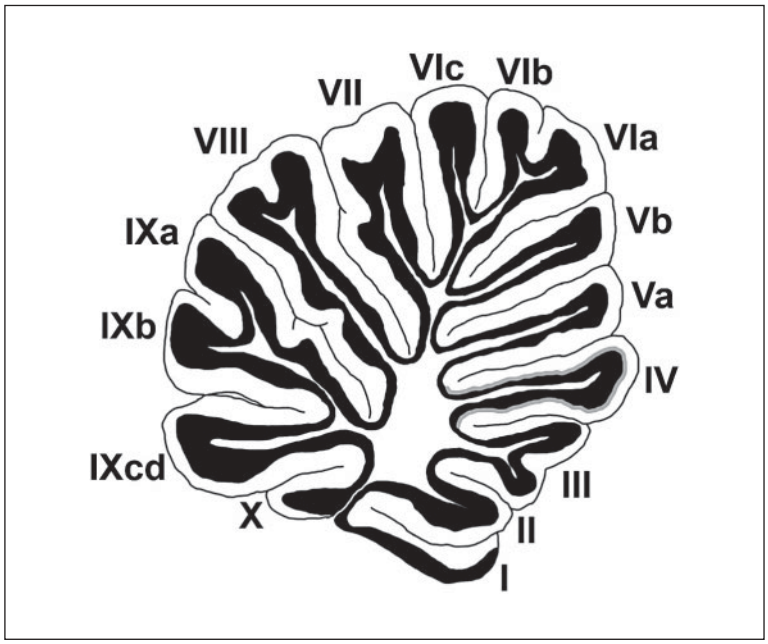


Fig. 1. A parasagittal view of the cerebellum of a 'generic' bird. Each of the folia is labeled from I through X in a rostral-caudal direction using the same terminology as Larsell [1967]. The anterior lobe consists of folia I–V, whereas the posterior lobe consists of folia VI–IXab. Folia IXcd and X comprise the vestibulocerebellum. The black areas indicate the granule cell layer. The Purkinje cell layer, which is one cell deep, sits atop the granule cell layer. The gray line indicates the Purkinje cell length for folium IV in this section.

the vast majority of species. We therefore based our divisions on branching patterns observed throughout the medio-lateral extent of the cerebellum and fissure depth. For example, moving from midsagittal to lateral pole, folia VIa, VIb and VIc coalesce into a single folium (VI), which retains deep fissures between itself and folia V and VII. In doing so, the cerebellar taxonomy reflects the branching pattern of the cerebellum more accurately than shape-based or other criteria [Iwaniuk et al., 2006b]. Using these criteria, our taxonomy follows that depicted in figures in both Larsell [1967] and Senglaub [1963], with the exception of the raptors. Although Senglaub [1963] and Larsell [1967] described a Vb in the anterior lobe of the raptor cerebellum, using both branching patterns and external morphology, we described this folium as part of VI (specifically part of VIa).

Measurements were taken of the cerebella of each specimen using the public domain NIH Image program (http://rsb.info.nih.gov/nih-image/). First, we measured the length of the Purkinje cell layer of each folium from a midsagittal section for each specimen. Next, we measured the length of the Purkinje cell layer of each folium from serial sagittal sections from the lateral pole of the cerebellum to the midsagittal section. This second measurement yielded an estimate of the volume of each folium as reflected by the Purkinje cell layer. The size of each folium represented a proportion of total Purkinje cell layer length. Therefore, any mention of size differences in folia actually reflects the size of the folium relative to the entire Purkinje cell layer.

In order to expand the number of species sampled, we compared measurements of relative folia size from midsagittal sections with that derived from the entire cerebellum. Analyses of covariance (ANCOVAs) yielded a significant relationship between the midsagittal and volume measures at two levels: within species and among folia ($F = 3336.43$; d.f. = 1, 469; $p < 0.01$); and within folia and among species ($F = 952.98$; d.f. = 1, 505; $p < 0.01$). Thus, midsagittal measures are significantly correlated with volume measures both within and among species. This significant relationship allowed us to double the number of species sampled from 48 to 96 species by including data derived from illustrations of midsagittal sections in the literature [Senglaub, 1963; Larsell, 1967; Matochik et al., 1991].

Statistical Analyses

We first assessed whether the proportional measures of relative folium size (see above) were affected by allometry. Least-squares linear regressions were performed on the proportional size of each folium and three scaling variables: brain volume, cerebellar volume and brain-cerebellar volume [see Iwaniuk et al., 2006c]. Only two folia were significantly affected by allometry: IV and X (p's < 0.01). The amount of variation explained by allometry for both of these folia was relatively low ($r^2 = 0.27$, 0.09, respectively). We therefore analyzed the residuals from allometric equations as well as the original proportions for folia IV and X. Only the proportions were analyzed for all remaining folia.

To assess the extent that phylogenetic history might affect relative folium size, we conducted both nested ANOVAs of taxonomic ranks and a randomization test for phylogenetic signal [Blomberg et al., 2003]. Nested ANOVAs were performed in the R statistical package [R Development Core Team, 2004] on all folia with three taxonomic ranks: order, family and genus (see table 1). The analysis of Blomberg et al. [2003], however, provided a more specific test of whether there was significant phylogenetic signal in our data. We used the PDAP software package (available from T. Garland Jr.) to test for phylogenetic signal using the independent contrasts approach. A phylogeny of all 96 species was constructed based on inter-ordinal relationships in Sibley and Ahlquist [1990], with additional resolution provided by other studies [Christidis et al., 1991; Dimcheff et al., 2002; Kennedy and Page, 2002; Shapiro et al., 2002; Wink et al., 2004; Altshuler et al., 2004; Barker et al., 2004]. We then calculated the variance of each folium across this

tree using independent contrasts analysis [Felsenstein, 1985] as implemented in PDTREE (a program within the PDAP package). A randomization test was then performed to determine whether the true variance in the data is smaller than 95% of the variance in a randomized data set. The randomized data set was created by randomly shuffling the original data across the phylogenetic tree 1000 times, regardless of its hierarchical organization, in PDRANDOM. Finally, the variances of these randomized data sets were calculated in PDERROR and the 95% confidence interval calculated. If a significant phylogenetic signal is present for a given data set, the variance of the original data will be less than 95% of the variance of the randomized data.

We also examined correlations among folia. First, we constructed a correlation matrix relating the relative size of each folium to that of every other folium. This was subsequently repeated using independent contrasts analysis [Felsenstein, 1985] as implemented in PDTREE. Default branch lengths were all set at one because the tree was reconstructed from several sources, but for each comparison we checked that the contrasts were adequately standardized [Garland et al., 1992]. When the contrasts were correlated with the branch lengths (i.e., not standardized), we tested various unequal branch length models until the contrasts were standardized and then performed the pair-wise correlations. Second, we performed a hierarchical cluster analysis to assess how similar species were to one another in multivariate space. The cluster analysis provides a representation of the similarity and dissimilarity among species in multivariate space that is easier to interpret than other multivariate methods, such as principal component analysis, and includes all of the inherent variation. Cluster analyses were performed using the hierarchical cluster function (hclust) algorithm [Murtagh, 1985] in R [R Development Core Team, 2004]. We used the Ward's linkage method because it optimizes the minimum variance within clusters [Ward, 1963] and has been used in previous analyses [Rehkämper et al., 2003; Iwaniuk et al., 2006b].

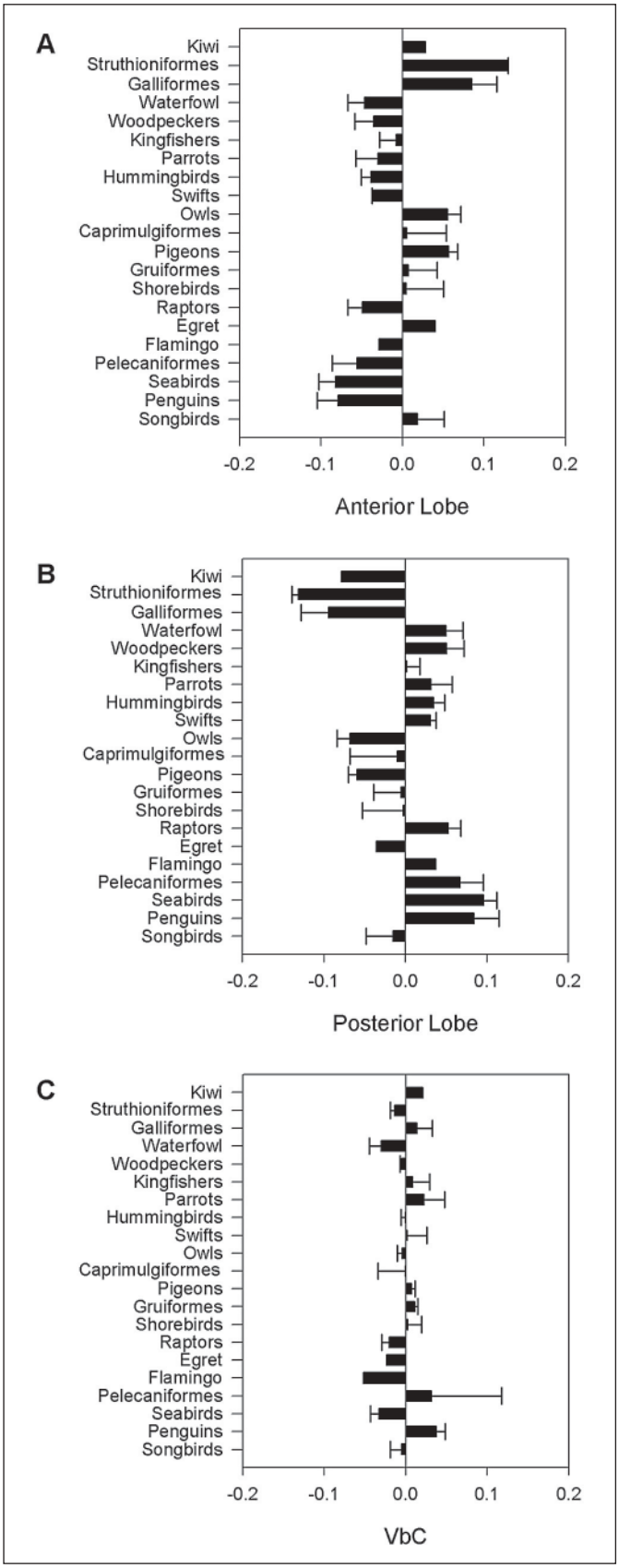
Lastly, we tested whether trigeminal-reliant species, strong fliers and species with large hindlimb musculature ('strong hindlimbs') had enlarged or reduced cerebellar folia. Trigeminal-reliant essentially means that the species use tactile cues from the face and/or beak during feeding. We assumed that species such as the Greater Flamingo *(Phoenicopterus ruber)*, shorebirds (Scolopacidae) and waterfowl [Dubbeldam, 1990] that are specialized for filter and tactile feeding rely heavily upon the trigeminal system. Given that two groups of folia receiving trigeminal input have been identified, one comprised of folia VIII and IXab [Arends and Zeigler, 1989] and a second comprised of folia IV–VI [Arends et al., 1984], we tested for differences in both of these combinations of folia as well as individual folia, anterior and posterior lobes and VbC. Strong-fliers were defined as those taxa highlighted by Larsell [1967], waterfowl and raptors, as well as hummingbirds, swifts, the Arctic Tern *(Sterna paradisaea)*, seabirds (Procellariiformes), penguins (Sphenisciformes) and the Barn Swallow *(Hirundo rustica)*, all of which spend most of their lives on the wing (albeit the penguins under water) or, in the case of the waterfowl, are rapid long-distance fliers. Lastly, to test the hypothesis that walking ability and hindlimb musculature is correlated with the anterior lobe [Larsell, 1967; Iwaniuk et al., 2006b], we classified several taxa as having strong hindlimbs based on locomotor and prey capture behaviors: the ratites, two of the three diving ducks (both *Melanitta* species), raptors, owls, chicken-like birds (Galliformes) and the largely terrestrial Australian Bustard *(Ardeotis australis)* and Superb Lyrebird *(Menura novaehollandiae)*.

For all comparisons of behavior and folium size, we performed two types of analysis: one using conventional statistics and the second using phylogenetically-based approaches. ANOVAs were used to test for significant differences between behavioral categories for all primary folia and several combinations of folia. The calculated F's of these ANOVAs were then compared with both conventional critical F's and phylogeny-corrected critical F's [Garland et al., 1993; Pellis and Iwaniuk, 2002; Iwaniuk, 2004; Iwaniuk and Arnold, 2004; Iwaniuk et al., 2005, 2006a]. This method simulates multiple data sets across a phylogenetic tree to a yield a phylogeny-corrected null distribution from which a phylogeny-corrected critical F can be calculated [Garland et al., 1993]. The simulations and null distribution were calculated in PDSIMUL and PDANOVA (both programs within PDAP) respectively. We constrained the simulations to biologically realistic values by setting the limits just above and below the largest and smallest values in our data set and assumed a gradual model of evolutionary change (i.e., along branches of the tree). In order to use these phylogeny-corrected F distributions, we provide F ratios rather than t tests for all comparisons.

Results

Major Divisions of the Cerebellum

The size of both the anterior and posterior lobes varied tremendously among taxa (fig. 2A, B). At one end of the spectrum, the Little Penguin *(Eudyptula minor)* had the largest posterior lobe and smallest anterior lobe of the species surveyed. Conversely, the Ring-necked Pheasant *(Phasianus colchicus)* had the smallest posterior lobe and largest anterior lobe. VbC size was far less variable (fig. 2C), but there were still relatively large differences between species at opposite ends of the distribution. For example, the Brandt's Cormorant *(Phalacrocorax brandti)* had the largest VbC and it was almost three times larger than that of the Greater Flamingo *(Phoenicopterus ruber)*, the species with the smallest VbC. Nested ANOVAs revealed that most of the variation in size of the anterior lobe, posterior lobe and VbC occurred at the order level (all $p's < 0.0001$) and a significant difference was detected among orders for all three divisions (anterior: $F = 12.60$, d.f. = 20, 85, $p < 0.0001$; posterior: $F = 13.12$, d.f. = 20, 75, $p < 0.0001$; VbC: $F = 4.12$, d.f. = 20, 75, $p < 0.0001$). At the order level, the seabirds (Procellariiformes) had the smallest anterior lobe and largest posterior lobe whereas the ratites had the largest anterior lobe and smallest posterior lobe (fig. 2A, B). With respect to the VbC, the penguins (Sphenisciformes) had the largest VbC and the aforementioned flamingo (Phoenicopteriformes) had the smallest VbC (fig. 2C).



Phylogenetic Effects

The randomization test of Blomberg et al. [2003] revealed that significant phylogenetic signal was present in at least eight of the eleven folia (table 2). Only the absolute proportional size of folium IV and not relative folium IV (i.e., residuals from allometric analysis described above) exhibited a significant phylogenetic signal. A significant phylogenetic signal was not, however, detected in the size of folia V and VIII. Thus, for at least eight folia, species that are more closely related to one another tend to be similar.

The nested ANOVAs indicated that most of the variation was accounted for by orders rather than families or genera (table 3). Although not shown, we came to a similar conclusion when species were classified according to infraorder/parvorder following Sibley and Ahlquist [1990]. Thus, phylogenetic history, and in particular order membership, plays a significant role in the evolution of differences in relative size of the cerebellar folia.

Table 2. Variances of the actual data (True variance) on the phylogenetic tree and the lower 95% interval of the variances calculated from randomizing the data across the phylogenetic tree (Randomized variance)

Folium	True variance	Randomized variance
I	$\mathbf{1.11 \times 10^{-4}}$	1.54×10^{-4}
II	$\mathbf{1.55 \times 10^{-4}}$	2.60×10^{-4}
III	$\mathbf{1.10 \times 10^{-4}}$	1.91×10^{-4}
IV (absolute)	$\mathbf{1.49 \times 10^{-4}}$	2.93×10^{-4}
IV (relative)	2.60×10^{-4}	1.61×10^{-4}
V	6.73×10^{-4}	5.00×10^{-4}
VI	$\mathbf{1.05 \times 10^{-4}}$	1.12×10^{-4}
VII	$\mathbf{2.10 \times 10^{-4}}$	2.20×10^{-4}
VIII	4.04×10^{-4}	2.93×10^{-4}
IXab	$\mathbf{2.13 \times 10^{-4}}$	6.63×10^{-4}
IXcd	$\mathbf{1.49 \times 10^{-4}}$	2.85×10^{-4}
X (absolute)	$\mathbf{1.75 \times 10^{-4}}$	2.10×10^{-4}
X (relative)	$\mathbf{2.40 \times 10^{-5}}$	3.77×10^{-5}

True variances less than 95% of the randomized variance are shown in bold.

Fig. 2. Bar graphs indicating the variation in relative size of: **A** anterior lobe; **B** posterior lobe; and **C** vestibulocerebellum (VbC). The bars represent the average value of each order normalized to the average among all species and the error bars indicate their standard deviations.

Clear differences among orders can also be observed from examining qualitative features of the cerebellar morphology, as shown by the midsagittal sections depicted in figure 3. The Ruffed Grouse (*Bonasa umbellus*, fig. 3B), Northern Saw-whet Owl (*Aegolius acadicus*, fig. 3F), doves (fig. 3G), American Coot (*Fulica americana*, fig. 3H) and Cattle Egret (*Bubulcus ibis*, fig. 3J) all represent the 'typical' avian cerebellar morphology, with eleven major folia. Many other species have more foliated cerebella (e.g., fig. 3D, I, K, L), but these are generally larger birds, as the degree of foliation is correlated with cerebellar volume, brain volume and body mass [Iwaniuk et al., 2006c]. This is best demonstrated within the Corvida (fig. 3K): the cerebellum of the small Brown Thornbill *(Acanthiza pusilla)* is much 'simpler' than those of the larger members of this infraorder. The gruiforms (fig. 3H) provide a similar example with the large (4,450 g) Australian Bustard having a much more foliated cerebellum than the smaller (651 g) American Coot *(Fulica americana)*. Within orders, there are similarities with respect to the overall appearance of the cerebella folia that goes beyond simple measurements of size. For example, all the ducks (fig. 3A) have an elongated cerebellum that is almost triangular in shape. All of the parrots (fig. 3D), raptors (fig. 3I), larger corvids (fig. 3K) and seabirds [fig. 3L; Iwaniuk et al., 2006c] have a highly elaborated posterior lobe consisting of numerous sub-folia. The hummingbirds (fig. 3E) have a cerebellum with a markedly reduced folium III, which is shared by the closely related swifts and some caprimulgiforms [Iwaniuk et al., 2006b]. This morphology is also shared, to some ex-

Table 3. The results of nested ANOVAs of relative folium size performed on three taxonomic ranks: order, family and genus

Folium	Rank	F	d.f.	p
I	Order	7.26	20, 13	<0.01
	Family	1.40	21, 13	0.27
	Genus	2.06	41, 13	0.08
II	Order	10.82	20, 13	<0.01
	Family	3.10	21, 13	0.02
	Genus	2.05	41, 13	0.08
III	Order	24.18	20, 13	<0.01
	Family	3.13	21, 13	0.02
	Genus	5.24	41, 13	<0.01
IV (absolute)	Order	5.97	20, 13	<0.01
	Family	0.85	21, 13	0.64
	Genus	1.52	41, 13	0.21
IV (relative)	Order	2.83	20, 13	0.03
	Family	0.81	21, 13	0.68
	Genus	1.93	41, 13	0.10
V	Order	17.25	20, 13	<0.01
	Family	3.12	21, 13	0.02
	Genus	2.27	41, 13	0.06
VI	Order	12.65	20, 13	<0.01
	Family	1.91	21, 13	0.12
	Genus	1.11	41, 13	0.44
VII	Order	17.34	20, 13	<0.01
	Family	2.77	21, 13	0.03
	Genus	1.77	41, 13	0.13
VIII	Order	9.81	20, 13	<0.01
	Family	4.09	21, 13	0.01
	Genus	1.06	41, 13	0.48
IXab	Order	24.77	20, 13	<0.01
	Family	9.88	21, 13	<0.01
	Genus	6.50	41, 13	<0.01
IXcd	Order	17.56	20, 13	<0.01
	Family	7.45	21, 13	<0.01
	Genus	2.18	41, 13	0.07
X (absolute)	Order	16.80	20, 13	<0.01
	Family	4.63	21, 13	0.01
	Genus	2.25	41, 13	0.06
X (relative)	Order	7.68	19, 10	<0.01
	Family	4.99	20, 10	0.01
	Genus	1.59	31, 10	0.22

Table 4. Results of ANOVAs performed on each folium using order membership as a categorical variable (all $p < 0.01$)

Folium	F	d.f.	r^2
I	4.08	20, 75	0.39
II	5.21	20, 75	0.47
III	5.87	20, 75	0.51
IV (absolute)	5.72	20, 75	0.50
IV (relative)	2.53	20, 75	0.24
V	8.25	20, 75	0.60
VI	10.58	20, 75	0.67
VII	10.64	20, 75	0.67
VIII	5.41	20, 75	0.48
IXab	4.34	20, 75	0.41
IXcd	5.80	20, 75	0.50
X (absolute)	6.69	20, 75	0.55
X (relative)	3.19	19, 61	0.34

The degree of freedom for folium X (relative) is less than that of the other comparisons because of a correction for allometry (see Methods).

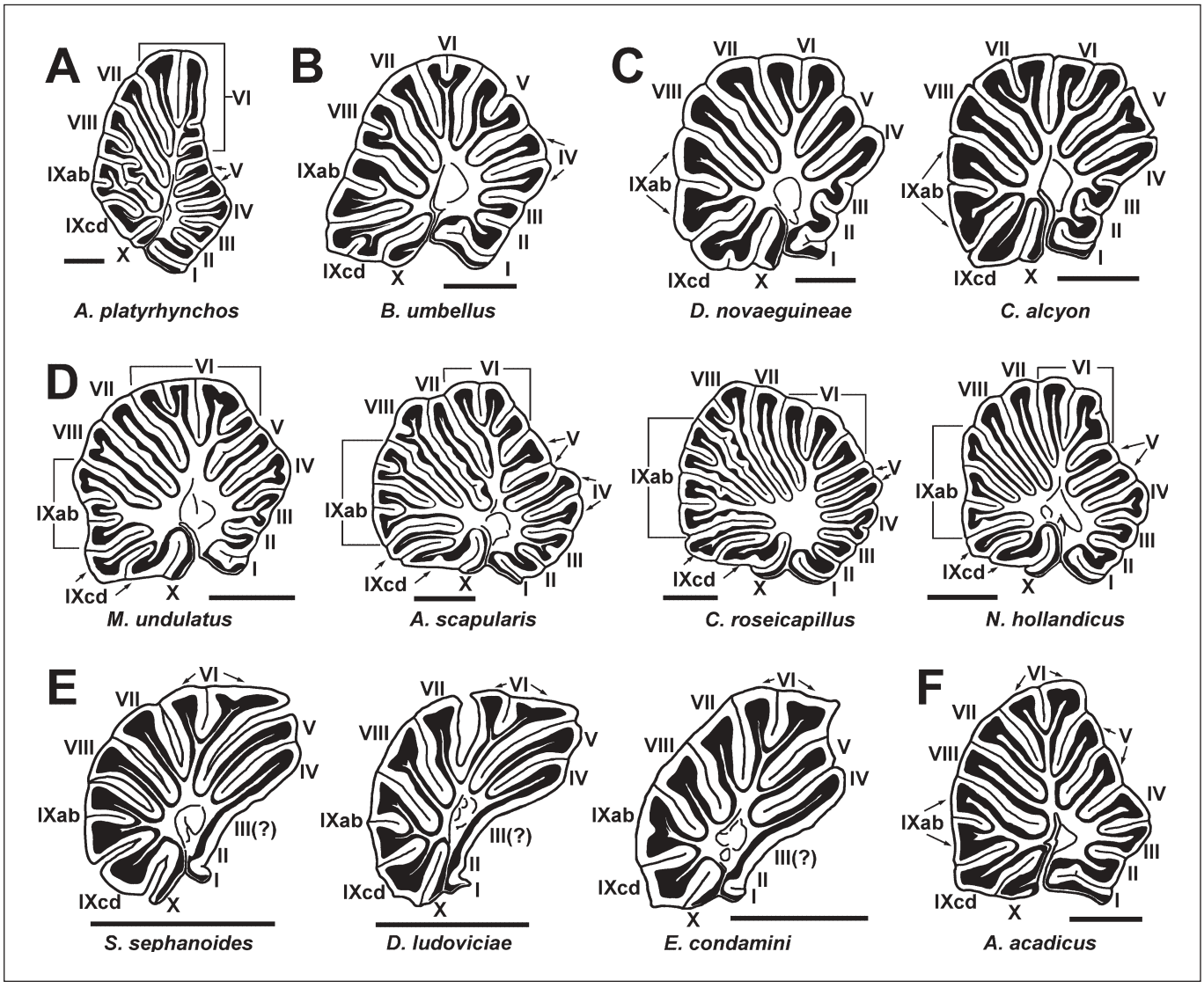
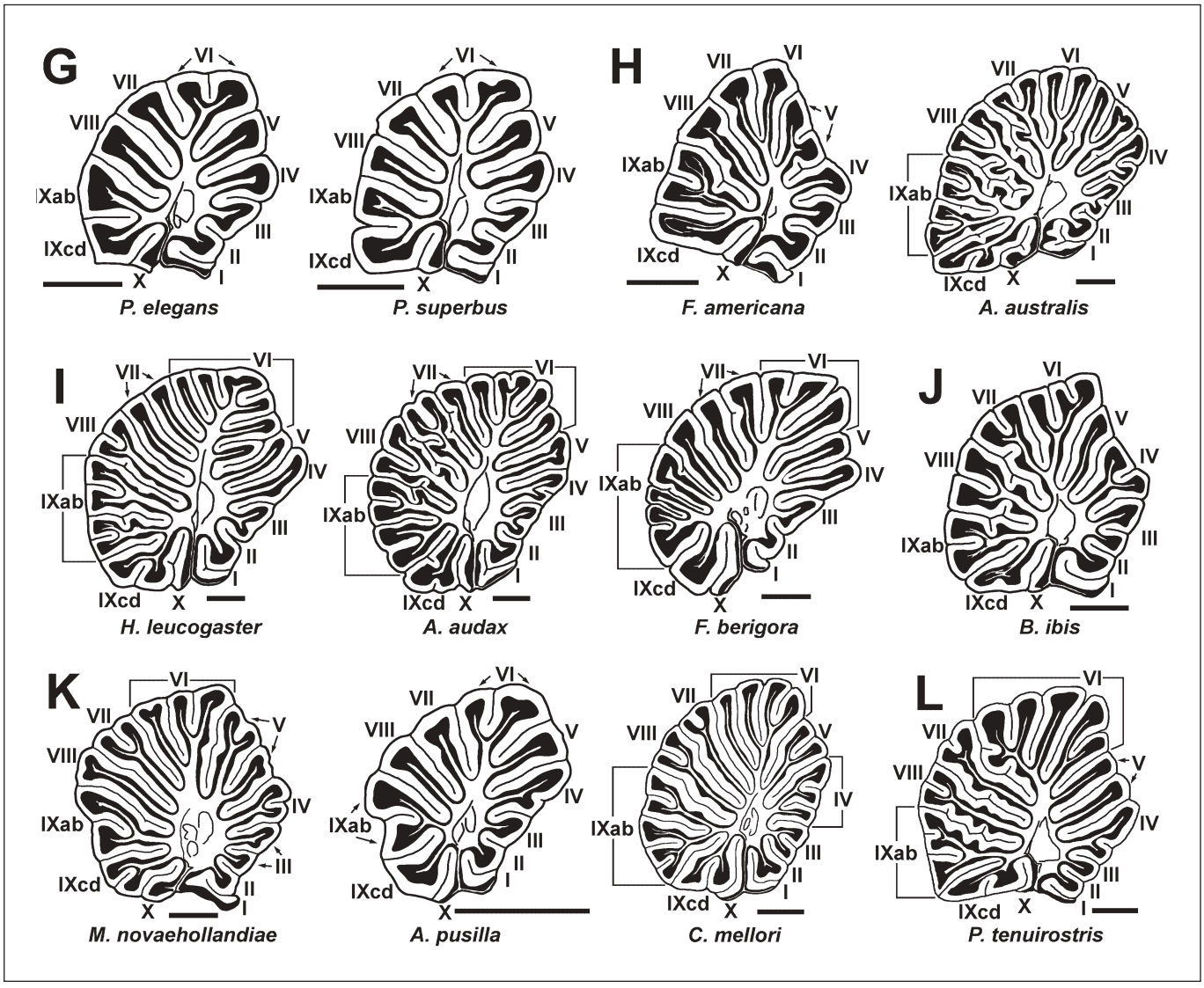


Fig. 3. Line drawings of mid-sagittal sections through the cerebellum for 24 of the species included in our analyses. The species are grouped according to order membership as follows: **A** Anseriformes – Mallard *(Anas platyrhynchos)*; **B** Galliformes – Ruffed Grouse *(Bonasa umbellus)*; **C** Coraciiformes – Laughing Kookaburra *(Dacelo novaeguineae)*, Belted Kingfisher (*Ceryle alcyon*, USNM 430744); **D** Psittaciformes – Budgerigar *(Melopsittacus undulatus)*, Australian King Parrot *(Alisterus scapularis)*, Galah *(Cacatua roseicapillus)*, Cockatiel *(Nymphicus hollandicus)*; **E** Trochiliformes – Green-backed Firecrown (*Sephanoides sephanoides*, FMNH 316784), Green-fronted Lancebill (*Doryfera ludoviciae*, FMNH 320498), Buff-tailed Sicklebill (*Eutoxeres condamini*, FMNH 315304); **F** Strigiformes – Northern Saw-whet Owl *(Aegolius acadicus)*; **G** Columbiformes – Brush Bronzewing *(Phaps elegans)*, Superb Fruit-dove (*Ptilinopus superbus*); **H** Gruiformes – American Coot *(Fulica americana)*, Australian Bustard (*Ardeotis australis*); **I** Falconiformes – White-bellied Sea Eagle *(Haliaeetus leucogaster)*, Wedge-tailed Eagle *(Aquila audax)*, Brown Falcon *(Falco berigora)*; **J** Cattle Egret *(Bubulcus ibis)*; **K** Passeriformes – Superb Lyrebird *(Menura novaehollandiae)*, Brown Thornbill *(Acanthiza pusilla)*, Little Raven *(Corvus mellori)*; and **L** Procellariiformes – Short-tailed Shearwater *(Puffinus tenuirostris)*. With this figure, illustrations of midsagittal sections of the cerebellum of all but one of the 96 species we studied have been shown in the literature [Senglaub, 1963; Larsell, 1967; Matochik et al., 1991; Iwaniuk et al., 2006b, c]. The exception is the Crimson Rosella *(Platycerus elegans)*, which is similar to the Australian King Parrot. The primary folia are indicated using the numerical taxonomy of Larsell [1967], which enumerates folia from I to X in a rostro-caudal direction. All scale bars = 3 mm.



tent, with the kingfishers (fig. 3C) and raptors [fig. 3I; Senglaub, 1963; Larsell, 1967], both of which have reduced anterior lobes and relatively small folia II and III.

Significant differences in the size of each folium were detected among orders (table 4). In fact, order membership accounted for more than half of the variation ($r^2 > 0.50$) in the size of folia V–VII among species. Plots of the relative size of each folium grouped according to order corroborate these findings; for most folia there are several orders that are well above or below the mean (fig. 4, 5).

It is also worth noting that there can be substantial variation within orders. For example, the two gruiforms, the American Coot and the Australian Bustard, differ considerably in the relative size of folia II and IXab. There are also large differences in the size of folia IXab and IXcd between the two pelecaniforms, Brandt's Cormorant and the Australian Pelican *(Pelecanus conspicillatus)*. Other examples include differences in folia II and III within the shorebirds (Laridae vs. Scolopacidae), folia II and IXab within the songbirds (Corvida vs. Passerida) and variation among families within the Caprimulgiformes, which we discussed in a previous study [Iwaniuk et al., 2006b]. Thus, although phylogeny, and in particular order membership, explain a significant amount of interspecific variation in folium size, some variation persists within orders.

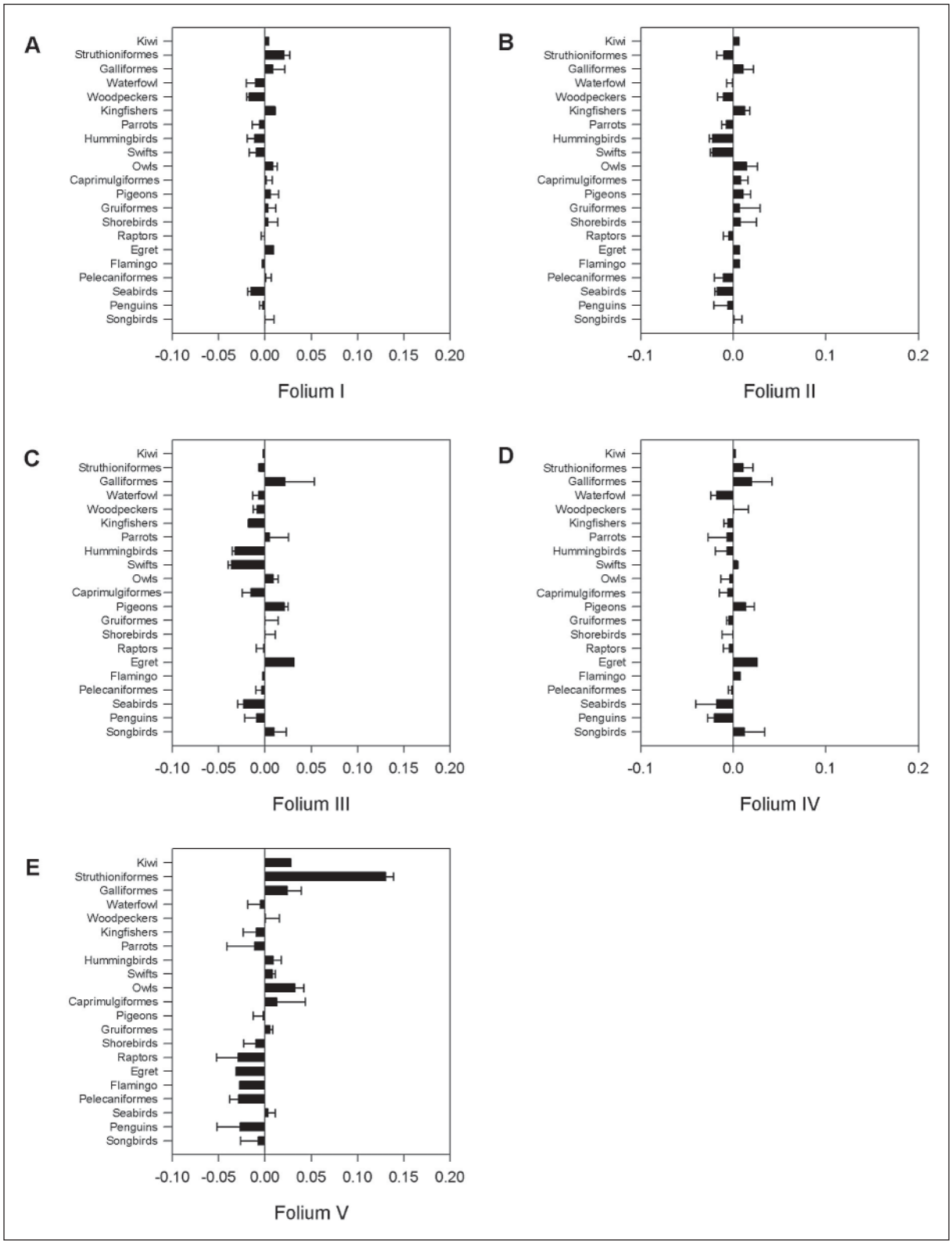


Fig. 4. Bar graphs indicating the variation in relative size of cerebellar folia within the anterior lobe: **A** folium I; **B** folium II; **C** folium III; **D** folium IV; and **E** folium V. The bars represent the average value of each order normalized to the average among all species and the error bars indicate their standard deviations.

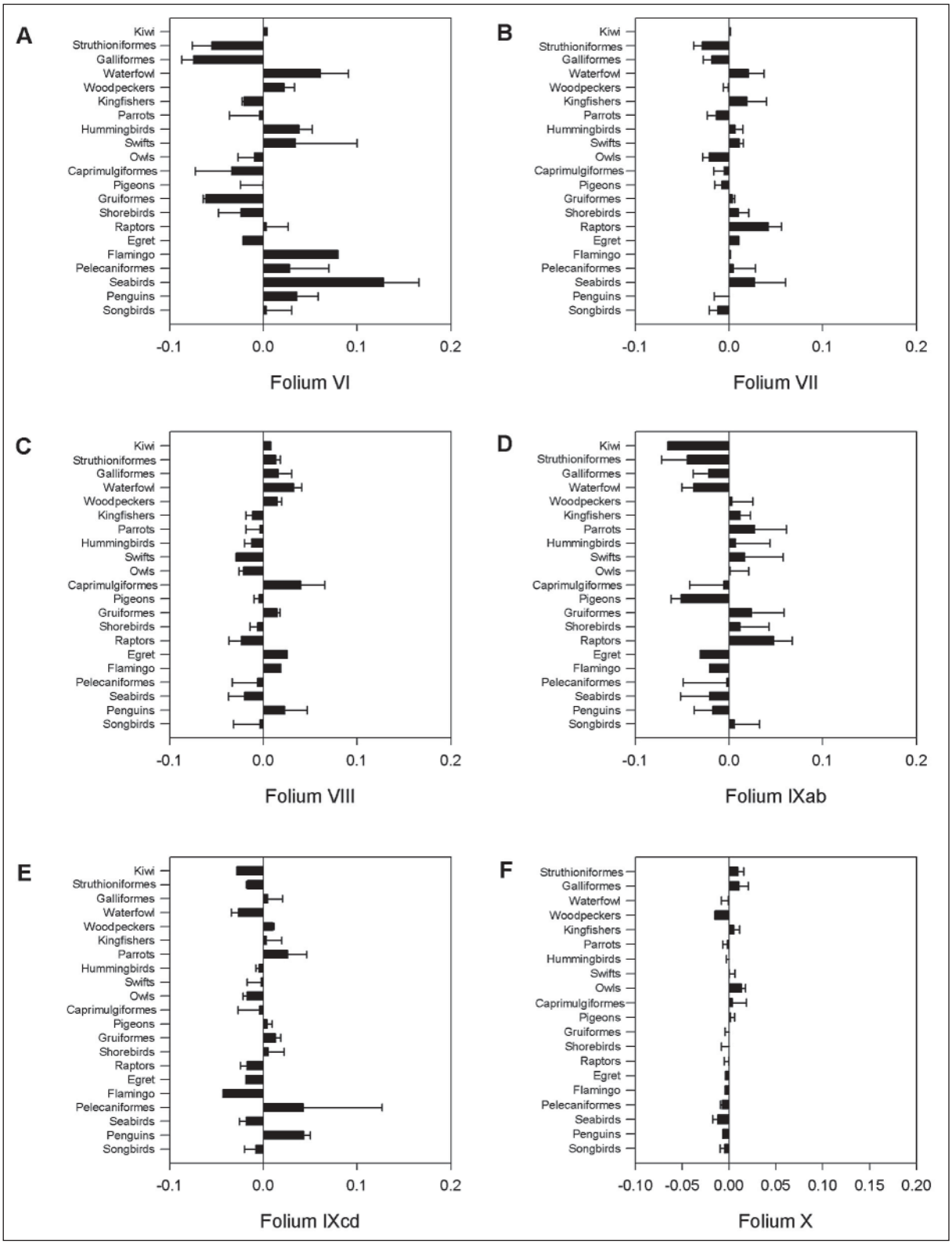


Fig. 5. Bar graphs indicating the variation in relative size of cerebellar folia within the posterior lobe: **A** folium VI; **B** folium VII; **C** folium VIII; **D** folium IXab; **E** folium IXcd; and **F** folium X. The bars represent the average value of each order normalized to the average among all species and the error bars indicate their standard deviations.

Table 5. Correlation matrix of the relative size of all eleven folia (I–X). The correlation coefficients (Pearson r) are shown where significant

	I	II	III	IV	V	VI	VII	VIII	IXab	IXcd	X
I											0.23
II	0.50		0.23						–0.35		
III	0.29	0.49								–0.32	
IV			0.25				–0.26		–0.34		
V	0.23					–0.27			–0.27		
VI	–0.45	–0.44	–0.37	–0.30	–0.31			–0.29	–0.34	–0.25	–0.25
VII	–0.25	–0.24	–0.33	–0.26	–0.40	0.30				–0.26	
VIII						–0.27					–0.28
IXab	–0.24	–0.34	–0.22		–0.36		0.23	–0.24			
IXcd							–0.25				
X	0.43	0.31			0.34	–0.35	–0.26		0.26		

The values below the shaded boxes used species as independent data points whereas the values above the shaded boxes used independent contrasts.

Correlations among Folia

Significant correlations occurred among many, but not all, of the folia examined (table 5). Although not shown, the correlations were the same using the residuals of folia IV and X from the allometric analysis discussed above (see Methods). In general, there was a trend for folia of the anterior lobe (I–V) to be negatively correlated with folia of the posterior lobe (VI–IXcd). Within the anterior lobe, however, folia tend to be positively correlated with one another. For example, folia I–III are all positively correlated with one another. Negative correlations among folia were also present within the posterior lobe. Overall, there were twice as many negative correlations (18) than positive correlations (12). Most of these correlations were supported by independent contrasts analysis and again, most of the correlations were negative (11/13). Taken together, these results indicate that the expansion of one folium is generally correlated with decreases in other folia whereas coordinated increases in size of folia are relatively rare.

Trigeminal Reliant Species

Out of our entire sample, we categorized 10 species as heavily reliant upon the trigeminal system: all four waterfowl, the Brown Kiwi *(Apteryx australis)*, all four shorebirds (Scolopacidae) and the Greater Flamingo. These 10 species did not have a significantly different anterior lobe ($F = 0.09$, d.f. = 1, 94, $p = 0.77$; fig. 6A) and posterior lobe ($F = 0.02$, d.f. = 1, 94, $p = 0.90$; fig. 6B) from other birds, but did have a smaller VbC ($F = 5.49$, d.f. = 1, 94, $p = 0.02$; fig. 6C).

With respect to individual folia, the trigeminal reliant species did have a moderately larger VI (mean = 0.1939) compared to the other species (mean = 0.1667), but this did not achieve significance ($F = 3.16$, d.f. = 1, 94, $p = 0.08$; fig. 7A). Comparisons among other individual folia were largely non-significant; no significant difference between trigeminal reliant and other species was detected for folia I, III, IV, V, VII, VIII or X (all p's > 0.06; fig. 7A). We did, however, detect significant differences in folia II ($F = 6.04$, d.f. = 1, 94, $p = 0.02$), IXab ($F = 6.66$, d.f. = 1, 94, $p = 0.01$) and IXcd ($F = 8.69$, d.f. = 1, 94, $p = 0.004$). Specifically, trigeminal reliant species have a significantly larger folium II and smaller folia IXab and IXcd (fig. 7A). Collapsing the folia into the two proposed trigeminal modules of the cerebellum yielded mixed results; trigeminal species did not have a significantly larger VIII and IXab than other species ($F = 1.46$, d.f. = 1, 94, $p = 0.23$), but did have a significantly larger V–VII ($F = 4.28$, d.f. = 1, 94, $p = 0.04$).

When compared with phylogeny-corrected F's, none of these tests were significant (all p's > 0.10). Thus, once phylogeny is taken into account, there are no detectable differences in the size of individual folia or combinations of folia between trigeminally reliant and other species. Given this lack of corroboration, we therefore conclude that folium size is not correlated with a reliance on trigeminal input.

Strong Fliers

Twenty-seven (27) species were classified as strong fliers: all of the waterfowl, swifts, hummingbirds, raptors, Arctic tern, seabirds, penguins and the barn swallow. These strong fliers had significantly smaller anterior lobes ($F = 49.35$, d.f. = 1, 94, $p < 0.0001$) and larger posterior lobes ($F = 44.59$, d.f. = 1, 94, $p < 0.0001$) than other species (fig. 8). No significant difference in VbC was detected ($F = 3.50$, d.f. = 1, 94, $p = 0.06$), but it did appear to be slightly smaller in strong fliers (fig. 8C). The differences in the anterior and posterior lobes were supported by comparisons with phylogeny-corrected critical F's (anterior = 11.91; posterior = 11.63). Thus, strong fliers have significantly smaller anterior lobes and larger posterior lobes than other species.

When broken down into individual folia, the strong fliers had significantly smaller folia I, II, III, IV and V and larger folia VI and VII (all F's > 5.00, p's < 0.03; fig. 7B). No significant differences were detected in any of the remaining folia (all p's > 0.10; fig. 7B). With the exception of folia IV and V (phylogeny-corrected $F = 18.62$, 20.20, respectively), these significant differences were also supported by comparisons with our phylogeny-corrected F's (I – 14.19, II – 12.60, III – 18.20, VI – 21.68, VII – 21.20). Although not shown, these results were the same when we analyzed the residuals of IV and X from the allometric analyses discussed above (see Materials and Methods). Thus, strong fliers have significantly larger folia VI and VII and smaller folia I–III than other birds even when phylogeny is taken into account.

Strong Hindlimbs

Twenty-six (26) species were classified as having strong hindlimbs based on locomotor and prey capture behaviors: two diving ducks, Brown Kiwi, all seven raptors, all six galliforms, Australian Bustard, Superb Lyrebird, all six owls, Greater Rhea *(Rhea americana)* and Ostrich *(Struthio camelus)*. Species with strong hindlimbs had significantly larger anterior lobes ($F = 11.02$, d.f. = 1, 94, $p = 0.001$; fig. 9A) and smaller posterior lobes ($F = 13.91$, d.f. = 1, 94, $p = 0.0003$; fig. 9B) than other birds, but no difference in VbC was detected ($F = 1.82$, d.f. = 1, 94, p =

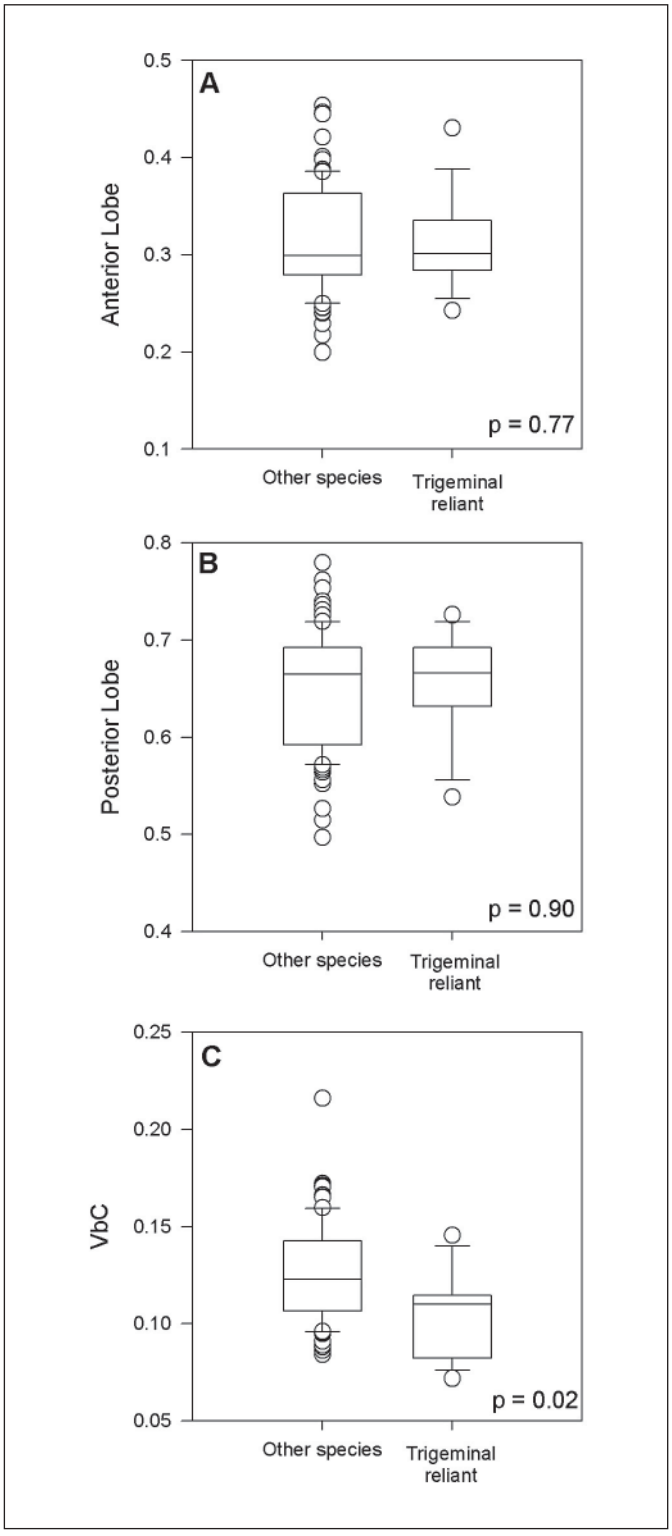
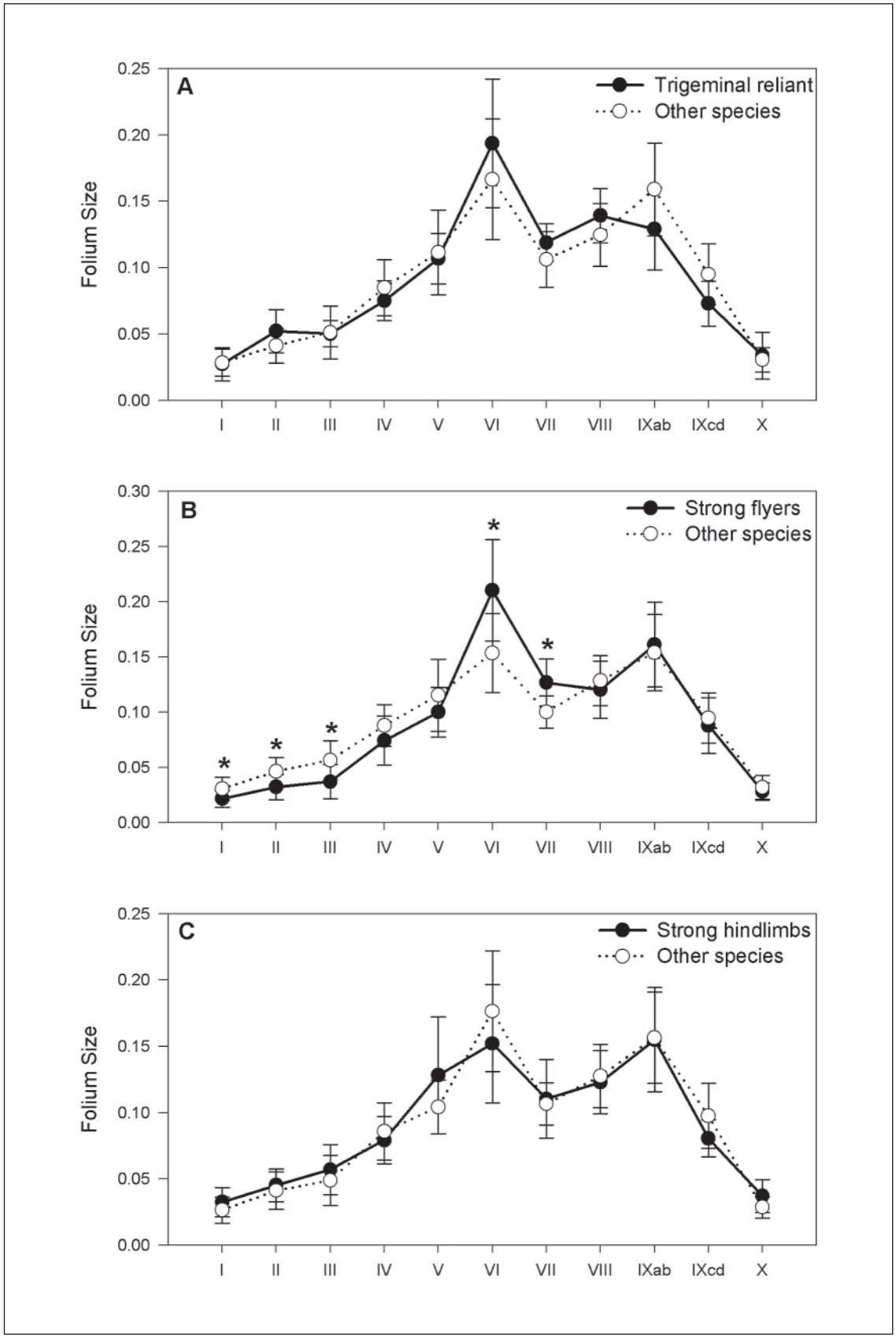


Fig. 6. Boxplots of the size of: **A** anterior lobe; **B** posterior lobe; and **C** vestibulocerebellum (VbC). Species are grouped according to whether they are reliant on the trigeminal system or not. Species were classified as reliant on the trigeminal system if they were listed as such by Larsell [1967] or engaged primarily in feeding behaviors likely to be reliant on trigeminal input, such as filter feeding (see Methods). p values indicating the significance of the difference between trigeminal reliant and other species are shown for each plot.


A
Trigeminal reliant
Other species
Folium Size
0.25
0.20
0.15
0.10
0.05
0.00
I
II
III
IV
V
VI
VII
VIII
IXab
IXcd
X
B
Strong flyers
Other species
Folium Size
0.30
0.25
0.20
0.15
0.10
0.05
0.00
*
*
*
*
I
II
III
IV
V
VI
VII
VIII
IXab
IXcd
X
C
Strong hindlimbs
Other species
Folium Size
0.25
0.20
0.15
0.10
0.05
0.00
I
II
III
IV
V
VI
VII
VIII
IXab
IXcd
X

7

0.18; fig. 9C). The significant differences in the anterior and posterior lobes were not, however, supported by phylogeny-corrected critical F's (18.51 and 18.16, respectively).

Significant differences were also detected at the level of individual folia (fig. 7C). Folia I ($F = 9.65$, d.f. = 1, 94, $p = 0.003$), V ($F = 15.03$, d.f. = 1, 94, $p = 0.0002$) and X ($F = 15.87$, d.f. = 1, 94, $p = 0.0001$) were significantly larger and folia VI ($F = 6.81$, d.f. = 1, 94, $p = 0.01$) and IXcd ($F = 10.24$, d.f. = 1, 94, $p = 0.002$) were significantly smaller in species with strong hindlimbs. No such differences were detected in the remaining folia (II–IV, VII, VIII, IXab; fig. 7C). Once phylogeny was taken into account, the significant differences in folia I, X, VI and IXcd were not supported (all phylogeny-corrected critical F's > 14.00). Thus, strong hindlimbs are not significantly correlated with the expansion or contraction of individual folia.

Cluster Analysis

The cluster analysis largely confirmed our previous observations concerning differences within and among orders (fig. 10). Some orders, such as owls, pigeons and raptors, were adjacent to one another in multivariate space, indicating that they are similar to one another in overall shape. Other orders, however, were distributed throughout the dendrogram. For example, the shorebirds and caprimulgiforms occurred in various terminal clusters. Thus, there is clearly a phylogenetic component to the grouping of species in multivariate space, but the strength of the phylogenetic effect varies among orders.

Overall, the clustering relationships reflected significant differences in the proportional size of the folia (as determined by ANOVAs and post-hoc Tukey-Kramer tests), which are indicated at the branching points of the six clusters apparent at a height of 0.4 on the dendrogram (fig. 10). Thus, clusters A and B have relatively large anterior folia and small posterior folia whereas the opposite is true of clusters C-F; although the combination of large and small individual folia is unique to each cluster.

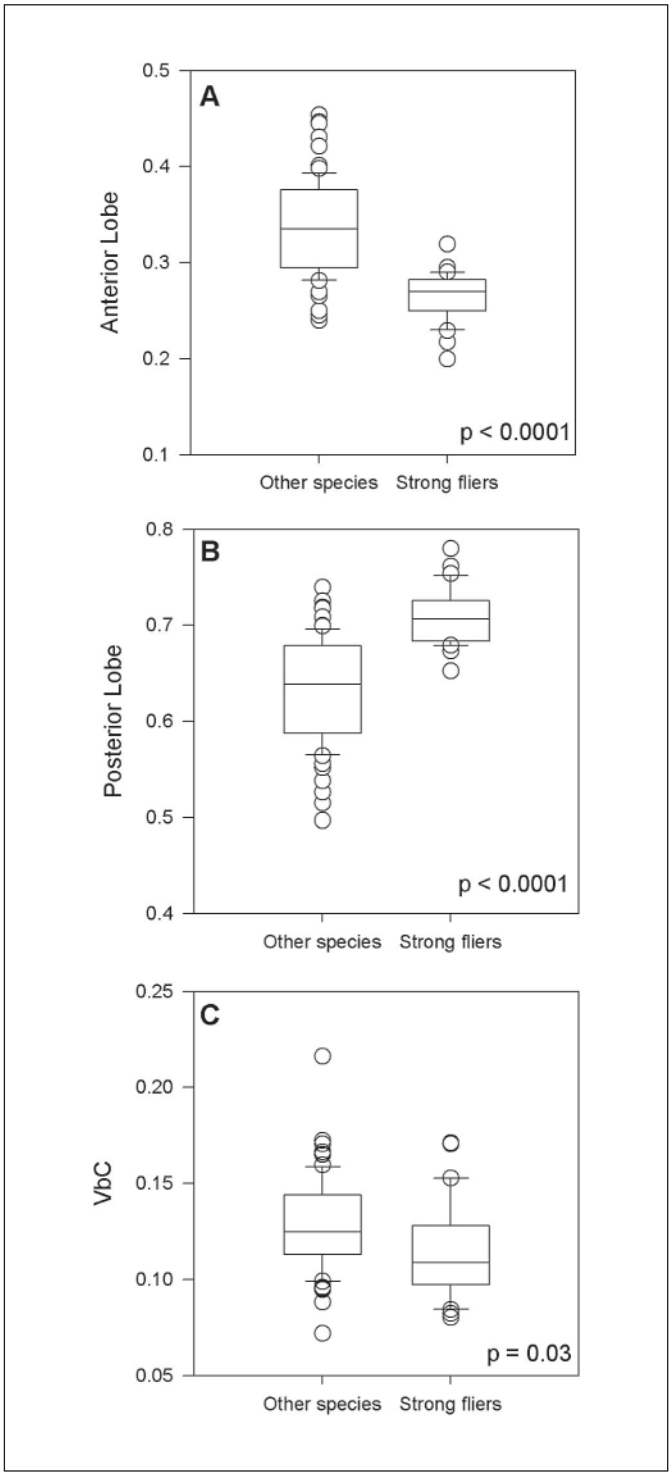
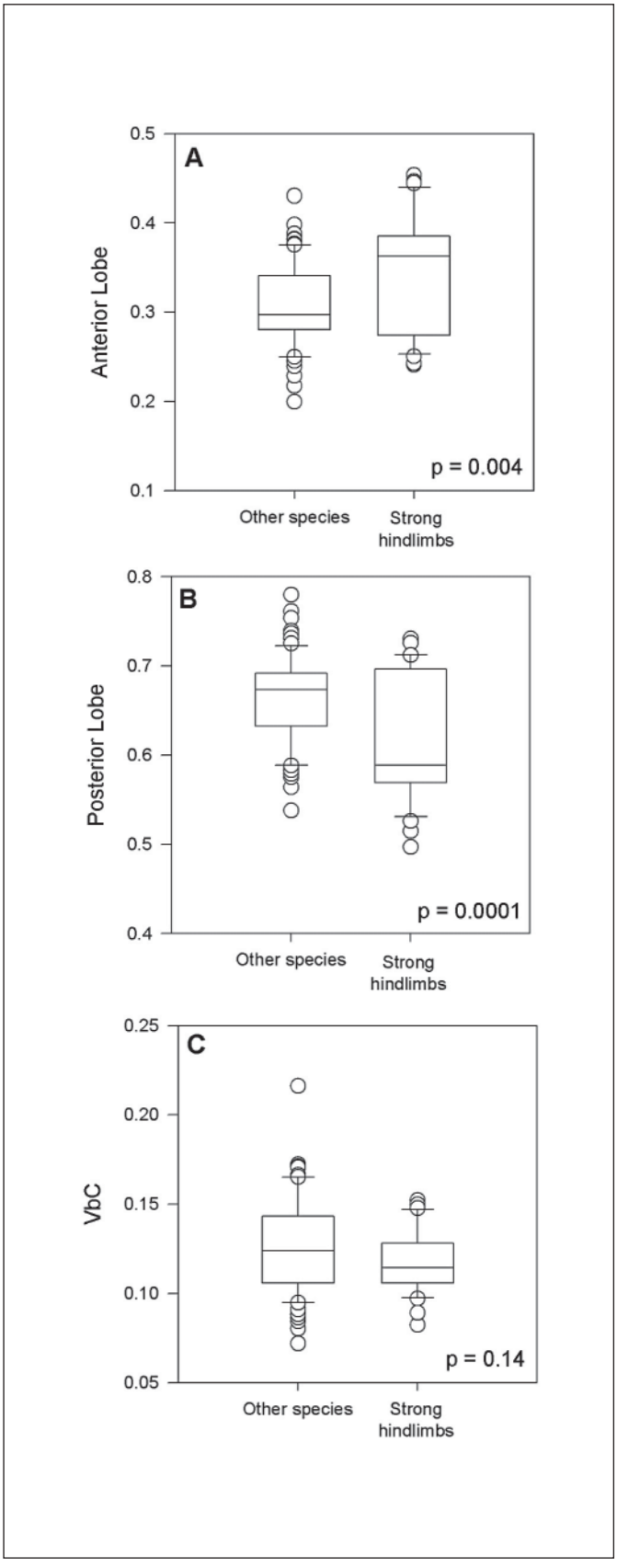


Fig. 7. Scatter-line plots are shown indicating the size of each of the eleven folia (I–X) for: **A** trigeminal reliant and other species; **B** strong fliers and other species; and **C** species with strong hindlimbs and other species. Each data point represents the mean for that group and the error bars indicate the standard deviations. Asterisks indicate significant differences that were detected using both conventional and phylogeny-corrected statistics.

Fig. 8. Boxplots of the size of: **A** anterior lobe; **B** posterior lobe; and **C** vestibulocerebellum (VbC). Species are grouped according to whether they are strong fliers or not. Species were classified as strong fliers if they were listed as such by Larsell [1967] or spend most of their lives on the wing. p values indicating the significance of the difference between trigeminal reliant and other species are shown for each plot.



It is also worth noting the distribution of our behavioral categories across the dendrogram. For example, the trigeminally-reliant species are distributed throughout the dendrogram and are not localized to any particular cluster. Most of the species with strong hindlimbs are found in clusters A and B. The strong fliers, however, are primarily found in clusters C and D, which are characterized by large folia VI and VII. The remaining strong fliers are found in cluster F, which also has a large VII. The raptors, which were classified as both strong fliers and having strong hindlimbs, were grouped together in cluster F.

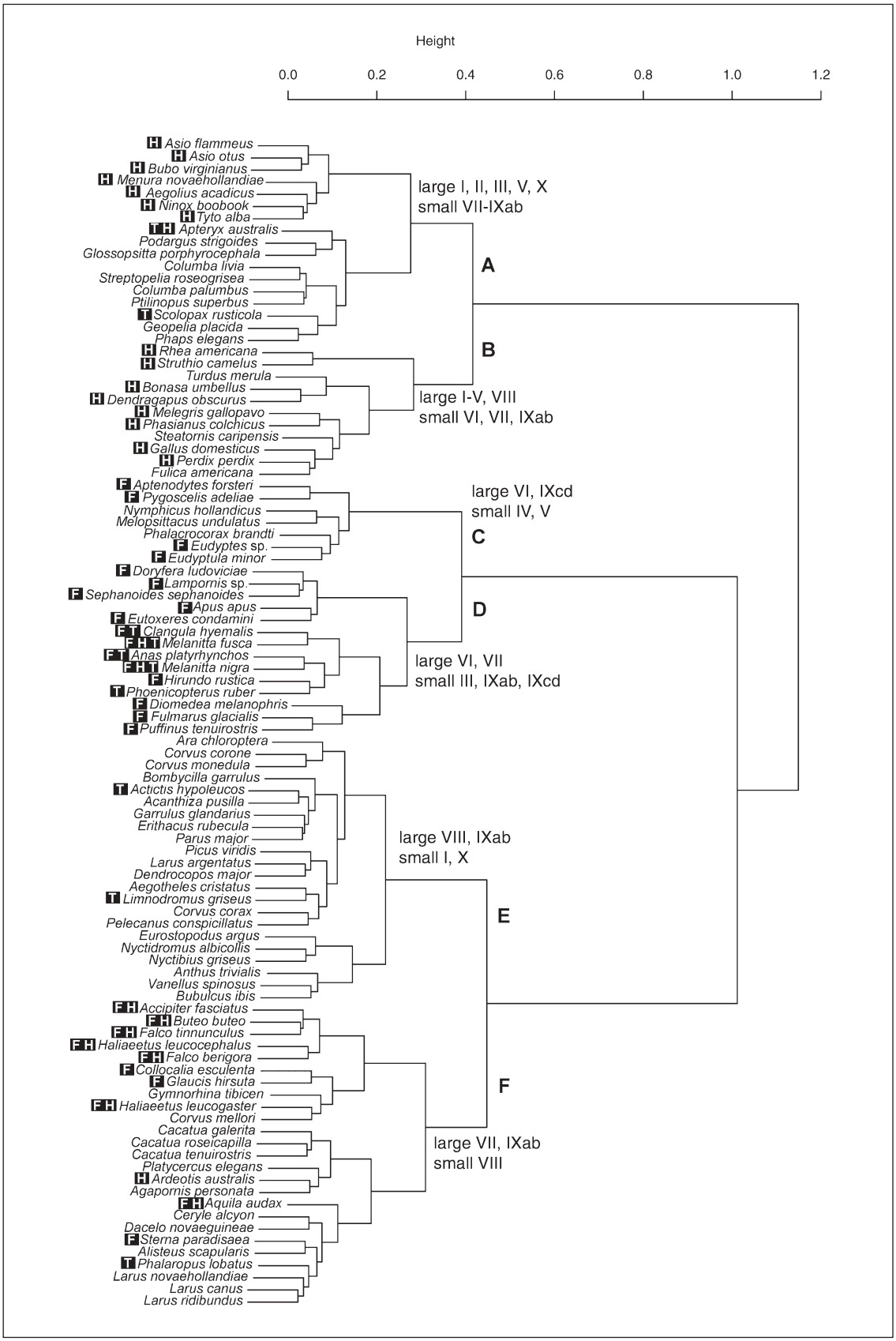
Discussion

Our analyses revealed that phylogenetic history, and in particular order membership, plays a significant role in the evolution of size differences among the cerebellar folia. Although our multivariate analyses indicated substantial variation in the proportional size of individual cerebellar folia, we found evidence of at least one significant correlation between the size of folia and a behavior. Specifically, folia VI and VII were significantly larger and folia I-III were significantly smaller in strong flying birds compared to other species. Evidence for a significant correlation between strong hindlimbs and the anterior lobe were mixed, and trigeminal reliance was not significantly correlated with the size of individual folia or groups of folia. Overall, our results provide a more accurate framework from which we will gain a better understanding of how the avian cerebellum has evolved and how cerebellar morphology reflects behavior.

Fig. 9. Boxplots of the size of: **A** anterior lobe; **B** posterior lobe; and **C** vestibulocerebellum (VbC). Species are grouped according to whether they have strong hindlimbs or not. Species were classified as having strong hindlimbs based on locomotor and prey capture behaviors (see Methods). p values indicating the significance of the difference between trigeminal reliant and other species are shown for each plot.

Fig. 10. A dendrogram resulting from a Ward's cluster analysis of the proportional size of each of the primary folia (I–X). The height of the dendrogram refers to the similarity index calculated across all folia. For six of the clusters (indicated by the bold letters A–F), significant differences in folia size resulting from ANOVAs are presented. The letters at the beginning of some of the species indicated that were classified in our analyses as: 'F' – strong fliers, 'H' – strong hindlimbs, and 'T' – trigeminal reliant.

9


Height
0.0
0.2
0.4
0.6
0.8
1.0
1.2
H Asio flammeus
H Asio otus
H Bubo virginianus
H Menura novaehollandiae
H Aegolius acadicus
H Ninox boobook
H Tyto alba
T H Apteryx australis
Podargus strigoides
Glossopsitta porphyrocephala
Columba livia
Streptopelia roseogrisea
Columba palumbus
Ptilinopus superbus
T Scolopax rusticola
Geopelia placida
Phaps elegans
H Rhea americana
H Struthio camelus
Turdus merula
H Bonasa umbellus
H Dendragapus obscurus
H Melegris gallopavo
H Phasianus colchicus
Steatornis caripensis
H Gallus domesticus
H Perdix perdix
Fulica americana
F Aptenodytes forsteri
F Pygoscelis adeliae
Nymphicus hollandicus
Melopsittacus undulatus
Phalacrocorax brandti
F Eudyptes sp.
F Eudyptula minor
F Doryfera ludoviciae
F Lampornis sp.
F Sephanoides sephanoides
F Apus apus
F Eutoxeres condamini
F T Clangula hyemalis
F H T Melanitta fusca
F T Anas platyrhynchos
F H T Melanitta nigra
F Hirundo rustica
T Phoenicopterus ruber
F Diomedea melanophris
F Fulmarus glacialis
F Puffinus tenuirostris
Ara chloroptera
Corvus corone
Corvus monedula
Bombycilla garrulus
T Actictis hypoleucos
Acanthiza pusilla
Garrulus glandarius
Erithacus rubecula
Parus major
Picus viridis
Larus argentatus
Dendrocopos major
Aegotheles cristatus
T Limnodromus griseus
Corvus corax
Pelecanus conspicillatus
Eurostopodus argus
Nyctidromus albicollis
Nyctibius griseus
Anthus trivialis
Vanellus spinosus
Bubulcus ibis
F H Accipiter fasciatus
F H Buteo buteo
F H Falco tinnunculus
F H Haliaeetus leucocephalus
F H Falco berigora
F Collocalia esculenta
F Glaucis hirsuta
Gymnorhina tibicen
F H Haliaeetus leucogaster
Corvus mellori
Cacatua galerita
Cacatua roseicapilla
Cacatua tenuirostris
Platycercus elegans
H Ardeotis australis
Agapornis personata
F H Aquila audax
Ceryle alcyon
Dacelo novaeguineae
F Sterna paradisaea
Alisteus scapularis
T Phalaropus lobatus
Larus novaehollandiae
Larus canus
Larus ridibundus
large I, II, III, V, X
small VII-IXab
A
B
large I-V, VIII
small VI, VII, IXab
large VI, IXcd
small IV, V
C
D
large VI, VII
small III, IXab, IXcd
large VIII, IXab
small I, X
E
F
large VII, IXab
small VIII

10

Variation within and among Orders

Phylogenetic history exerts a significant effect on many behavioral and neural traits [Harvey and Pagel, 1991; Blomberg et al., 2003; Striedter, 2005], so it was not surprising that we also detected significant phylogenetic signal in our data set for subdivisions of the cerebellum and most individual folia. As demonstrated by our nested ANOVAs, much of this phylogenetic signal reflected significant differences among orders; some orders have significantly larger and smaller cerebellar folia than others.

Our statistical analysis largely corroborates qualitative observations made in this study and by Larsell [1967]: raptors have a large VII, chicken-like birds (Galliformes), waterfowl and penguins have a larger than average VIII and hummingbirds and swifts have a reduced III (fig. 4, 5). Perhaps more interesting was the substantial variation within orders and between sister-groups. For example, despite being sister-taxa [Sibley and Ahlquist, 1990; Kennedy and Page, 2002], the penguins and seabirds exhibit considerable variation in cerebellar morphology. Penguins are characterized by a larger I, VIII and IXcd and smaller V, VI, VII than seabirds. Similarly, the two gruiforms measured, the American Coot and Australian Bustard, have some folia that are similar in size, but several others that are not (table 1). Lastly, there is some variation within the shorebirds, songbirds and caprimulgiforms. There are prominent behavioral differences among many of these taxa. For example, gulls and corvids have much higher tool use [Lefebvre et al., 2002] and feeding innovation rates [Lefebvre et al., 1997] than other shorebirds and passerines, respectively. Whether any of this intra-ordinal variation reflects behavioral differences is uncertain because relatively few species were surveyed within each order. Nevertheless, behavioral differences could be at least partially responsible for the significant variation among and within orders.

There are factors other than behavior that could also influence the proportional size of cerebellar folia. For example, braincase morphology could impose biomechanical constraints on how the cerebellum develops. The morphology of the jaw musculature, orbit orientation, eye shape and skull morphology are all highly conserved within many orders and families, which could then lead to significant phylogenetic effects and large differences in cerebellar morphology among orders. Alternatively, changes in the size of folia might reflect specific sensory and sensorimotor differences among orders, such as stereopsis in owls [Pettigrew and Konishi, 1976; van der Willigen et al., 1998] and some caprimulgiforms [Pettigrew, 1986], vocal learning [Jarvis, 2004] or even echolocation [Iwaniuk et al., 2006a]. Distinguishing among these alternatives is, however, complicated by a bewildering array of behavioral and cerebellar diversity among orders. Until such a time that these alternatives can be coded in a meaningful way or cerebellar morphology is examined in an even broader range of species, it will be difficult to assess the relative importance of these mitigating factors.

Variation among Folia

Not only does the proportional size of a folium vary among orders and with some sensory and cognitive abilities, it also varies with the size of other folia. As shown in our correlation matrix, increases in the size of one folium are correlated with decreases in the size of some, but not all, other folia. For example, using species as independent data points, VII is negatively correlated with I–V, IXcd and X, positively correlated with VI and IXab and not significantly correlated with VIII (table 5). Similarly, if the independent contrasts analyses are examined, II is positively correlated with III, negatively correlated with IXab and not significantly correlated with any of the remaining folia. This is remarkably similar to the mosaic pattern of evolution that characterizes the inter-relationships among brain regions in both mammals [Barton and Harvey, 2000; Finlay et al., 2001; Barton et al., 2003] and birds [Iwaniuk et al., 2004; Iwaniuk and Hurd, 2005] and might reflect trade-offs among folia due to behavioral differences (see below).

This mosaic pattern of foliar evolution is also apparent in the cluster analysis. The six clusters identified in the dendrogram (fig. 10) reflect differences in the proportional size of the cerebellar folia in both directions. That is, each group can be differentiated from the others by a unique combination of relatively small and large folia. A similar pattern was also found for the evolution of individual brain regions among birds; clusters were differentiated from one another by the presence of both large and small brain regions [Iwaniuk and Hurd, 2005]. Thus, it appears that expansion of a brain region is accompanied by decreases in other brain regions, regardless of whether the analyses are based on the composition of the entire brain or parts of an individual structure.

Behavioral Correlates of Folium Size

One of the main conclusions from Larsell's [1967] survey of the avian cerebellum was that the expansion of individual folia was correlated with behavioral differences among species. As mentioned previously, correlations are

frequently drawn between the size of cerebellar lobules or folia with behaviors [Larsell, 1967, 1970; Welker, 1990; Paulin, 1993]. As outlined above, we found evidence that strong fliers have enlarged folia, but no evidence to support the enlargement or shrinkage of folia in trigeminally-reliant species. With respect to birds with strong hindlimbs, the evidence was mixed.

Contrary to Larsell's [1967] conclusion that the expansion of folium VI reflects trigeminal input, we found no evidence to support such a claim. Even when we examined other folia and combinations of folia, no consistent significant differences were detected between trigeminally-reliant species and other species. Similarly, trigeminally-reliant species were distributed throughout our cluster analysis (fig. 10). This does not necessarily mean that an increase in trigeminal input is not accompanied by enlargement of particular folia. In fact, the difference in trigeminal projections to the cerebellum in the pigeon [Arends and Zeigler, 1989] and mallard [Arends et al., 1984] could mean that different folia are enlarged with respect to trigeminal input because of differences in projection patterns. In addition, our classification of which species most likely relied on trigeminal input was based primarily on broad differences in feeding style thought to be dependent on the trigeminal system. Perhaps with a more accurate measure of trigeminal input, such as mechanoreceptive sensitivity or the size of somatosensory structures [e.g., rostral wulst, Pettigrew and Frost, 1985; nucleus basalis, Wild and Farabaugh, 1996; Wild et al., 1997, 2001; nucleus sensorius principalis trigeminalis, Dubbeldam, 1990], we would detect a significant difference. Based on our categorization, however, we must conclude that foliar expansion/contraction is not correlated with trigeminal input.

Comparing species with strong hindlimbs versus other species, using conventional statistics, it appeared that there were differences in folia I, VI, IXcd and X, but once we incorporated phylogenetic information, no significant differences were detected. In the cluster analysis, however, most of the species with strong hindlimbs were clustered together in the top part of the dendrogram (fig.10). One possible reason for this lack of significant effect is the inclusion of both predatory and cursorial species as having strong hindlimbs. It should be noted that if we restricted our analyses to only cursorial species versus other birds, a significant difference was detected for the sum of IXab and IXcd ($F = 5.39$, d.f. = 1, 94, $p = 0.02$), but in the opposite direction to that expected based on Larsell [1967]. That is, cursorial birds have a smaller IX than other birds. Previous analyses suggested that the size of the anterior lobe, and in particular folia II and III, were correlated with hindlimb musculature and walking ability [Larsell, 1967; Iwaniuk et al., 2006b]. The study of Iwaniuk et al. [2006b] was, however, limited in its species coverage to the caprimulgiforms, swifts, hummingbirds, owls and a few outgroups. Considering the additional data in the present study, although some species with weak hindlimbs did have small anterior folia (e.g., swifts, hummingbirds), other groups such as seabirds and penguins also have small folia II and III, but much larger hindlimb musculature [Schreiweis, 1982]. The reduction in size of these folia in the hummingbirds and swifts is even more striking than that of the seabirds and penguins, but it does raise questions regarding the functional significance of anterior lobe reduction. Although the legs and feet were represented in the anterior folia (primarily in II and III) in Whitlock [1952], more recent studies have found that somatosensory input from the legs is distributed among folia II, VI, IXab and IXcd [Schulte and Necker 1998; Necker, 2001]. The marked reduction in swifts, hummingbirds and some caprimulgiforms thus might be indicative of shared ancestry [Sibley and Ahlquist, 1990; Cracraft et al., 2004] or a by-product of some biomechanical feature, such as the orientation of the optic lobes, and not hindlimb musculature. Further research into spinal projections to and from the cerebellum would aid in clarifying this matter.

The behavioral category in which we observed consistent significant differences in the size of the folia was strong flight; on average, strong fliers had significantly larger folia VI and VII and smaller folia I–III than the other species. In the cluster analysis, the strong fliers were found in the bottom two-thirds of the dendrogram and only in those groups identified as having a large VI and/or VII (see fig. 10). The reduction of folia I–III is unlikely to reflect a decrease in their importance in strong fliers, but rather the negative correlations described among folia (table 5). That is, for folia VI and VII to become proportionally larger, there must be a decrease in the proportional size of other folia and in this case, it is folia I–III of the anterior lobe. The enlargement of folia VI and VII is unlikely to reflect the wings themselves because proprioceptive stimulation of the wings and spinal projections from the cervical enlargement are concentrated in folia III–V [Whitlock, 1952; Schulte and Necker, 1998; Necker, 2001]. In mammals, lobules VI and VII are regarded as the oculomotor vermis, based on both anatomy and physiology [Voogd and Barmack, 2006]. Although these lobules also receive proprioceptive, vestibular and auditory inputs [Voogd and Barmack, 2006], they play a key role in the guidance and modification of eye

movements. A similar case can also be made for folia VI and VII in birds; they receive facial tactile, auditory and visual input [Whitlock, 1952; Gross, 1970; Clarke, 1974, 1977; Arends et al., 1984]. However, there is virtually no spinal proprioceptive input to VI or VII [Schulte and Necker, 1998]. Visual input, in particular, appears to be strong in the posterior part of VI (i.e., IVc) and VII [Clarke, 1974, 1977]. This visual input arises from not only the tectofugal system, via the pontine nuclei, but also the nucleus lentiformis mesencephali (LM) of the pretectum [Pakan et al., 2005; Pakan and Wylie, in press]. Although the tecto-pontine system is involved in processing local motion [e.g., Frost and Nakayama, 1983] for orientation and avoidance [Ewert, 1970; Ingle, 1970; Hellmann et al., 2004], the LM processes 'optic flow' and is important for generating optomotor responses [e.g., Gioanni et al., 1983; Winterson and Brauth, 1985; McKenna and Wallman, 1985; Wylie and Crowder, 2000]. It has been suggested that an integration of local motion analysis and optic flow analysis is important for 'steering behaviour' during locomotion in complex environments [Sherk and Fowler, 2001; Elder et al., 2005; Page and Duffy, 2005; Sato et al., 2005; Logan and Duffy, in press]. An increase in cerebellar-mediated visual processing might be of particular benefit to several of the species that were classified as strong fliers. For example, hummingbirds, swallows, swifts, terns, seabirds and raptors all execute rapid changes in direction and speed when flying and all of them rely heavily on visual cues to detect prey. This is equally true of penguins that can execute similarly rapid movements while 'flying' under water in the visually guided pursuit of prey [Ropert-Coudert et al., 2000]. An increase in the size of those cerebellar regions receiving visual input could aid in directing these visually guided rapid movements during prey capture. How waterfowl fit into this hypothesis is unclear, but re-classifying them as 'other' species had no effect on the significance of our results (i.e., VI and VII still larger and I–III still smaller in strong fliers). It therefore appears that the expansion of VI and VII reflect an increase in visual processing requirements of visually-guided prey capture.

Are the Folia Functionally Different?

The primary assumption of Larsell [1967], and many of the tests performed in the present study, is that the folia are functionally distinct regions of the avian cerebellum. Each of the folia represent either part of a somatotopic map (anterior lobe) or a particular sensory modality (posterior lobe). Welker [1990] also emphasized that cerebellar lobules in mammals represent relatively discrete structural, hodological and functional divisions. Furthermore, he suggested that interspecific variation in the number of folia and lobules reflected behavioral complexity such that: 'Larger, or perceptually-behaviorally more complex mammals have a larger and more elaborately foliated cerebellar cortex than do smaller or less complex mammals.' [page 99, Welker, 1990]. Given that several mammalian and avian taxa appear to have some folia enlarged and other reduced [Larsell, 1967, 1970; Paulin, 1993], the hypothesis that folium size reflects behavior seems reasonable and agrees with the general principle that the size of a neural structure is a reflection of the behavior subserved by that structure [Jerison, 1973].

In terms of the functional organization of the cerebellum, the emphasis has shifted from lobules and folia to zones in recent years. The cerebellum is functionally organized into parasagittal zones that can be identified both anatomically and physiologically [Hawkes, 1997; Herrup and Kuemerle, 1997; Voogd et al., 2003; Sugihara and Shinoda, 2004; Voogd and Ruigrok, 2004; Voogd and Wylie, 2004; Cicirata et al., 2005; Sillitoe et al., 2005]. These zones cut across foliar and lobular boundaries in a perpendicular direction. The functional significance of these zones remains unclear [Sillitoe et al., 2005], but given an overlap between physiologically and anatomically defined zones [e.g., Sugihara and Shinoda, 2004], it is at least possible that these zones are more functionally important than folia or lobules. If this is true, however, the question remains as to why folia size varies among species in somewhat predictable dimensions. One possibility is that increasing the breadth or number of zones somehow improves processing capacity. Such a case has been made for the addition of cortical areas in mammals [Krubitzer, 2000; Changizi, 2001; Kaas, 2005], but it is unknown whether this also applies to the cerebellum.

Conclusions

Although phylogenetic history and some behaviors are correlated with the relative size of individual cerebellar folia, there remains a considerable amount of variation to be explained. This large degree of variation might reflect the development of sensory and motor regions within the brain. Alternatively, there could simply be a large amount of variation in the size of folia because of factors unrelated to behavior and cognition. Developmental or biomechanical constraints (i.e., braincase architecture) might affect how each folium develops such

that some folia expand whereas other contract in size. Nevertheless, expansion/contraction of at least some folia appears to be correlated with flight behavior and could reflect increased visual processing demands on the cerebellum. The exploration of other behaviors that might also be correlated with folium size in birds will be dependent on determining specific behaviors that involve the cerebellum, adequate categorization of those behaviors and further studies into the hodological organization of the avian cerebellum among taxa.

Acknowledgements

We wish to thank the curatorial staff of the National Museum of Natural History (Washington), the Bishop Museum (Honolulu) and the Field Museum of Natural History (Chicago, Ill., USA) for kindly loaning us specimens for this study, the wildlife sanctuaries and veterinary clinics that collected specimens on our behalf and Barrie Frost, Gerard Gory and Dale Clayton for sending us additional specimens. This research was funded by fellowships and grants to ANI from the Alberta Ingenuity Fund and the Natural Sciences and Engineering Research Council of Canada (NSERC), to PLH from NSERC and to DRWW from NSERC, the Canada Research Chairs Program and the Canadian Institute of Health Research.

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