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Brain evolution in cichlids of the African Great Lakes: brain and body size, general patterns, and evolutionary trends

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Summary

The cichlid fish communities of the East African Great Lakes are amongst the richest concentrations of vertebrate species on earth. These "explosive" radiations represent an unequaled system to address central questions in evolutionary biology, and have therefore figured prominently in studies of speciation, ecological plasticity, and molecular evolution. Cichlid radiations in the three major lakes (Victoria, Tanganyika, and Malawi) are generally similar in terms of trophic diversity, species richness, and rates of endemism. However, being largely independent of each other, they offer a true evolutionary experiment with treatment groups and replicates. Using computer-based morphometric methods, we compared brain morphology among 189 cichlid species from the East African Lakes and Madagascar. The Madagascan taxa were included as phylogenetically primitive representatives of the family Cichlidae. In this first paper we report data on the relationship between brain and body size, and address patterns of brain form variation among individuals, lakes, and sexes. Cichlid faunas of the three lakes, encompassing three putative subfamilies, exhibit surprisingly similar variation in the form of brain structures concerned with vision, olfaction, and the lateral line. However, across the African lakes, the greatest variation was observed in the development of association centres, in particular of the telencephalon. The lack of negative associations among brain regions across lakes indicated that enhanced development of one brain structure for a particular function is not compensated for by reduction of other modalities.

Introduction

The parallel, endemic radiations of cichlid fishes in the Great Lakes of East Africa are among the most remarkable known examples of rapid evolution and speciation among vertebrates. Each of the lakes, Victoria, Tanganyika, and Malawi, contains a unique assemblage of several hundred distinct species of cichlids exhibiting enormous behavioral and morphological diversity (Fryer and Iles 1972). Most species occur nowhere else in the world other than within a single type of habitat in a single lake, often being restricted to a geographical region of the lake. The three lakes are generally comparable in terms of species richness, rates of endemism, and degree of ecological differentiation (Lowe-McConnell 1993).

These species assemblages are the result of largely independent "explosive speciation" events and may serve as a unique, and in essence replicated, natural experiment that permits the isolation of certain treatment effects. We have investigated the way in which the brain has responded to natural selection in these systems. Although previous authors have reported contradicting results concerning the presence of parallel changes in brain morphology and ecological parameters, a relationship between ecological/behavioral variables and the development of the brain and its parts has been demonstrated for a variety of teleosts (Kotrschal and Junger 1988; Bauchot et al. 1989; Huber and Rylander 1992; Kotrschal and Palzenberger 1992), as well as other vertebrates (Pirlot and Pottier 1977; Healy and Guilford 1990; Bernard and Nurton 1993). Such relationships were particularly strong in those circumstances where closely related, monophyletic taxa with similarly-sized individuals were compared. Species of North American cy-

prinids inhabiting clear versus turbid water rely on different sensory modalities, and the importance of a particular modality is reflected in the size of the corresponding neural structures (Huber and Rylander 1992). Species adapted to clear water environments are characterized by large structures dealing with vision, and relatively smaller brain parts associated with taste and olfaction.

The functional spectrum of teleost olfaction which is routed to the olfactory bulb encompasses several aspects, including social communication (Finger 1988; Dulka 1993), feeding (Hara et al. 1993), and predator avoidance (Chivers and Smith 1993). Olfactory fibers comprise the most widespread set of sensory projections to the telencephalon (Davis et al. 1981; Becerra et al. 1994) which receives additional input from visual and gustatory (Davis and Kassel 1983; Friedlander 1983) as well as lateral line centers (Finger 1980). Telencephalon and hypothalamus also play a central role in more complex tasks such as learning, agonistic and social behaviors (Demski 1983). Eyes and optic lobes are intimately related to vision, the latter being the primary target of retinal fibers. The cerebellum plays a central role in proprioception, motor coordination, and eye movement (Demski 1983). Taste in fish is used both in locating food and in evaluating it once found, and is relayed primarily to visceral sensory structures in the medulla oblongata. Cerebellar crest and the octavolateralis area process mechanosensory lateral line stimuli and form a prominent ridge on the dorsal brain stem.

This study investigates the relative size of seven major divisions of the brain in 189 species of cichlids deriving from the three major East African lakes to assess the effects of selective pressures on gross brain structure. Here we address the following specific questions: What is the relationship between body size and brain size? What are the correlations between the various brain measures? How much does brain morphology differ within species, among lakes, and between the sexes? What are the overall patterns in cichlid brain evolution and how similar are these among the three lakes?

Methods

We examined a total of 216 specimens, representing 82 genera and 189 species from Lakes Malawi (N = 100), Tanganyika (N = 58) and Victoria (N = 55), and the island of Madagascar (N = 3). All appeared sexually mature in size and coloration except for those from Madagascar. Procedures for the preservation of specimens, such as fixation in formalin and storage in ethanol, result in tissue shrinkage. Since the age and provenance of the specimens varied and a number of the species are now extinct or nearly so (Witte et al. 1992) shrinkage was assumed to be equal across specimens and brain areas. Most specimens were in good to excellent condition however, and had been properly dehydrated following fixation so as to hold gross shrinkage and deformation to a minimum.

Standard length (tip of the snout to base of caudal fin), head length (tip of the snout to the posterior edge of the opercular slit), maximum body depth and maximum body width were measured to the nearest 0.01 mm using dial or digital calipers. The diameter of the eye was measured along the nasal-temporal axis to the nearest 0.01 mm. The skull was opened dorsally under a dissecting microscope and the entire brain removed from olfactory bulbs to the rostral end of the spinal cord. Dorsal, ventral and lateral views of the brains (Fig. 1) were videotaped and the images captured using video digitizers (Data Translation DT2255-60Hz or MacVision). Thirty five different measurements were taken from each brain using morphometric software (Microquant, Huber unpubl.). Linear measurements were maximum lengths of the respective structures. Shape was estimated as the deviation from roundness, ranging from one for a perfect circle to zero for a straight line. In the case of paired structures, measurements were made on the right side except in a few cases where this side was damaged. From the lateral view we measured brain length, olfactory nerve diameter, length and height of hypothalamus and hypophysis, and length, height and shape of olfactory bulb, telencephalon, optic tectum, cerebellum, and dor-

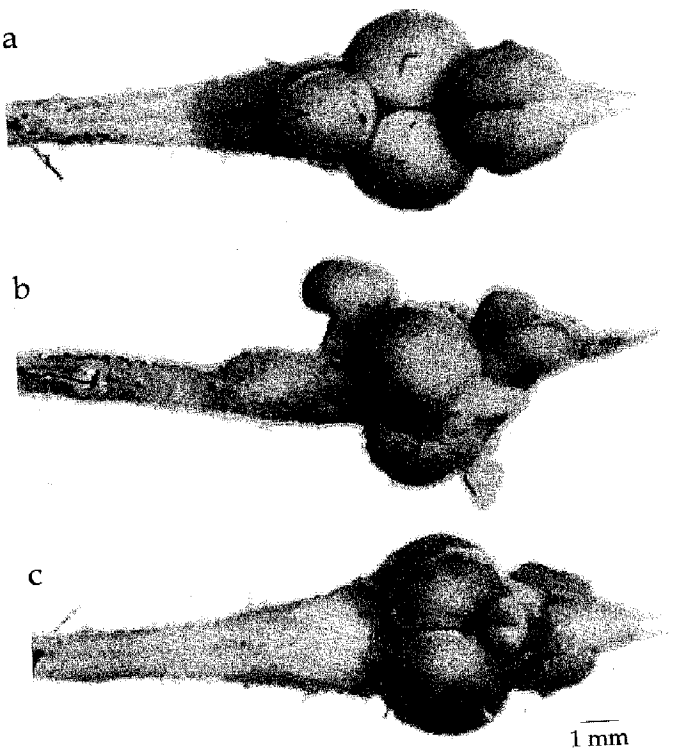

Fig. 1. Digitized image of *Hemitilapia oxyrhynchus* (MCZ 49495) brain, showing (a) dorsal, (b) lateral, and (c) ventral views, from which the 35 length and shape measurements detailed in the text were made.

sal medulla. Width and shape of telencephalon, optic tectum, cerebellum, and dorsal medulla were measured from the dorsal view, and width and shape of olfactory bulb, hypothalamus, and hypophysis from the ventral view (Fig. 2). Measurement error was quantified by repeating the 35 measures for a specimen 10 times. The coefficient of variation with respect to linear measurements averaged 5.5% and that for shape 5.8%.

The relationship between brain and body size was described using a logarithmic model ($y = \beta \times x^{\alpha}$) with x representing body length and y the length of the brain. The coefficient of encephalization (α) and the coefficient of allometry (β) were estimated from the data. To determine whether the shape of the head is related to the shape of the brain, we examined the association of the length/width ratio of the head to the length/width ratio of the brain.

Due to the severe environmental threats recently brought upon many of these species in the wild, a large proportion of our specimens were rare and often part of small collections. During brain removal considerable damage is done to these specimens and it was therefore not possible to use multiple individuals for every species. Cluster analysis was used to assess the degree of intraspecific variation present in five species for which multiple specimens were available.

To determine if brain morphology differs among the lakes, between sexes, or due to a possible interaction between the two: (1) a complete model two-way multivariate analysis of variance (MANOVA) of all brain measures was performed; (2) although not independent of the last analysis, MANOVAs were also performed for specific brain areas separately, namely for measures of the olfactory structures, optic structures, telencephalon, cerebellum, hypothalamus, and dorsal medulla.

In our attempts to investigate size relationships among neural structures, we (1) constructed a matrix of Pearson's correlation coefficients between all brain measures and (2) performed principal components analyses (PCA). With PCA, a form a factor analysis, we summarized the different brain measures with a smaller set of "derived" variables to identify underlying sources of variation in brain evolution (Sokal and Rohlf 1981; SPSS Inc. 1988). Separate PCAs were also constructed for each lake and compared in order to evaluate the similarity in patterns of brain evolution across lakes.

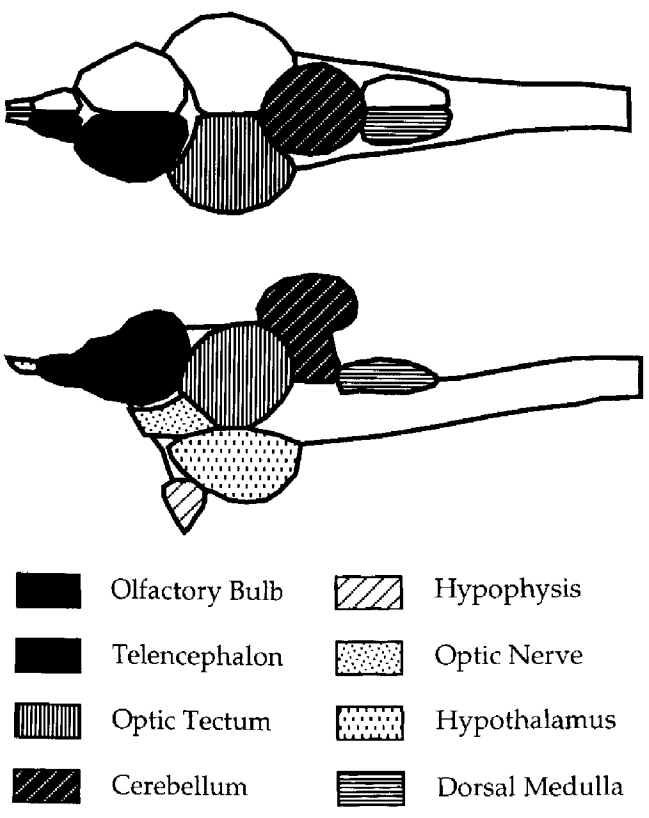

Fig. 2. Schematic drawing of a cichlid brain (dorsal and lateral views) illustrating the major brain divisions.

Material

For each lake and Madagascar, specimens are listed alphabetically within genera followed by the museum acronym, number, sex (M – male, F – female), and number of individuals in parentheses. Institutional acronyms are: Museum of Comparative Zoology, Harvard (MCZ); United States National Museum (USNM); American Museum of Natural History (AMNH); New England Aquarium (NEA). "X" indicates uncatalogued material.

Lake Victoria

The nomenclature of Lake Victoria haplochromines is in flux; here we follow the conventions established in Greenwood (1981) and Lippitsch (1993). When the genus *Haplochromis* is enclosed in quotes, the taxon in question has not yet received a generic diagnosis. When the specific name is enclosed in quotes, the taxon is undescribed and the cheironym devised by field investigators is given.

"Haplochromis" "spot bar" sp. nov. NEA X, M
Astatoreochromis alluaudi MCZ X, M
Astatotilapia "greenback" NEA X, M
A. "red little mouth sp." nov. NEA X, M
A. "thickskin" MCZ X, M
A. 2-striped yellow green MCZ 25019, F
A. barbarae MCZ 25253, F
A. nubila NEA X, M
A. piceatus NEA X, M
A. two stripe whitelip NEA X, F
Enterochromis "nigrofasciatus" MCZ X, M
Haplochromis pseudonigricans MCZ 25352, M
Haplochromis I kribensis MCZ 25017, M
Haplochromis II diplotenia MCZ 25020, F
Haplochromis III nyereri NEA X, M
Haplotilapia retrodens MCZ 60308, M
Harpagochromis "grey pygmy" MCZ X, M
H. guiarti MCZ 60294, M
H. red-eye guiarti NEA X, M
Labrochromis "rock kribensis" MCZ X, M
L. "rock kribensis" MCZ 25864, F
L. "rock kribensis" Kenya MCZ 2426, F
L. ishmaeli MCZ 25821, F
L. rock kribensis molariform MCZ X, F
Lipochromis maxillaris NEA X, M

L. obesus MCZ 60300, F
Macropleurodus bicolor MCZ 25261, M
Neochromis "velvet black" MCZ X, M
N. madonna sp. nov. NEA X, M
N. nigricans MCZ 25310, M
Oreochromis esculentus MCZ K1073, F
Paralabidochromis chilotes MCZ 25913, M
P. plagiodon NEA X, M
Platytaeniodus degeni MCZ X, M;
Prognathochromis sp. MCZ 60315, F
Psammochromis riponianus MCZ 25152, M
Ptyochromis Russinga oral sheller NEA X, M
P. deep xenognathus NEA X, M
P. prodromus MCZ 32580, F
P. sauvagei MCZ 25146, M
P. sauvagei USOMA 001, M (5)
P. xenognathus MCZ X, M
Pyxichromis orthostoma NEA X, F
Xystichromis phytophagus MCZ 2002, M
Yssichromis argens MCZ X, M
Y. argens MCZ 89993, F
Y. coop MCZ 25015, M
Y. heusinkfeldi MCZ 25027, M
Y. laparogramma NEA X, M
Y. pyrrhocephalus MCZ 25026, M
Y. cf. *doublestripe* NEA X, M

Lake Tanganyika
Aulonocranus dewindti NEA X, M
Bathybates fasciatus MCZ 32552, F
B. ferox MCZ 32551, F
B. graueri MCZ 50825, M
B. leo MCZ 49287, M
B. minor MCZ 50822, F
Benthochromis tricoti MCZ 50834, M
Boulengerochromis microlepis MCZ 49303, M
Callochromis macrops MCZ 32628, F
C. pleurospilus MCZ 32592, M
Cardiopharynx schoutedini AMNH 58463, F
Ctenochromis horii MCZ 32635, M
Cyphotilapia frontosa MCZ 50837, F
Cyprichromis leptosoma NEA X, M
Ectodus descampsii MCZ 35345, F, M (5)
Eretmodus cyanostictus MCZ 50700, M
Julidochromis marlieri NEA X, M
Lamprologus attenuatus NEA X, M
L. brichardi MCZ 49225, F
L. callipterus MCZ 49274, M
L. compressiceps MCZ 50833, F
L. hecqui NEA X, M
L. pleuromaculatus MCZ 49265, M
Lestredea perspicax AMNH 58489, M
L. stappersia MCZ 32593, F
Limnochromis auritus MCZ 50835, M
Limnotilapia dardenii MCZ 32584, M
Lobochilotes labiatus NEA X, M
Neolamprologus calliurus MCZ 49260, F
N. furcifer MCZ 50831, M
N. modestus MCZ 49203, M
N. mondabu AMNH 11746, M
N. savoryi MCZ 49218, M
N. sexfasciatus NEA X, M
N. werneri MCZ 50308, F
Ophthalmotilapia sp. MCZ 49232, M
Paracyprichromis nigripinnis NEA X, M
Petrochromis polyodon MCZ 49233, M
Plecodus paradoxus MCZ 49330, F
Simochromis diagramma MCZ 50844, F
Telmatochromis dhonti MCZ 50693, M
Trematocara stigmaticum MCZ 50701, M
T. unimaculata AMNH 58475, F
T. variabile MCZ 50697, M
Triglichromis otostigma MCZ 49275, M
Tropheus moorii MCZ 50847, M
Tylochromis polylepis MCZ 32630, F
Xenochromis hecqui MCZ 49334, F
Xenotilapia longispinis MCZ 49267, M
X. melanogenys MCZ 49259, M
X. ochrogenys MCZ 49263, M
X. ornatipinnis MCZ 49266, M
X. sima MCZ 49269, M

Lake Malawi
Aulonocara ethylwynnae USNM 265468, M
A. jacobfreibergi USNM 261900, M
Buccochromis atritaeniatus MCZ 49460, F
Champsochromis caeruleus AMNH 31847, M
Chilotilapia euchilus NEA X, F
C. rhodesii AMNH 31860, F
Copadichromis chrysonotus MCZ 1979-010, F
C. flavimanus AMNH 31819, F
C. mloto MCZ X, M
C. mloto MCZ 49513, F, M (4)
C. mloto USNM 280304, M
C. quadrimaculatus MCZ 1979-010, M
C. trimaculatus MCZ 1979-010, F
C. virginalis MCZ 1979-010, M
C. virginalis NEA X, M
Cyathochromis obliquidens AMNH 31887, M
Cynotilapia afra NEA X, M
Dimidiochromis compressiceps AMNH 37362, F
D. dimidiatus AMNH 11714, F
D. strigatus AMNH 31768, M
Diplotaxodon argenteus MCZ 1979-010, F
Fossorochromis rostratus AMNH 37363, F
Genyochromis mento USNM 261811, M
Hemitilapia oxyrhynchus MCZ 49495, M
Labeotropheus fuelleborni USNM 261886, M
L. trewavasae USNM 261913, M
Labidochromis chisumulu NEA X, M
L. textilis AMNH 32413, M
L. vellicans AMNH 31902, M
Lethrinops altus MCZ 49501, F, M (5)
L. auritus MCZ 60429, M
L. christyi USNM 308850, M
L. furcifer USNM 265490, F
L. lethrinus MCZ 49505, F
L. parvidens MCZ 1979-010, F
L. polli USNM 280056, M
L. sp. MCZ 1979-010, F
Maravichromis guentheri AMNH 31808, F
M. lateristriga AMNH 31842, M
M. orthognathus AMNH 31767, F
M. sphaerodon MCZ 49516, M
M. spilostichus USNM 308854, F
Melanochromis auratus USNM 261835, M
M. johanni USNM 280087, M
M. vermivorus FMNH 76087, F

M. vermivorus USNM 280090, M
M. vermivorus USNM 261830, F
Nimbochromis linni AMNH 37360, M
N. livingstoni USNM 280744, F
N. polystigma USNM 261869, M
N. venustus MCZ 49494, F
Nyassachromis eucinostomus AMNH 31855, F
N. leuciscus MCZ 49517, F
Oreochromis shiranus AMNH 31871, F
Otopharynx argyrosoma MCZ 1979-010, M
O. decorus MCZ 49514, M
O. heterodon AMNH 31886, F
O. intermedius USNM 266834, F
O. intermedius AMNH 31834, M
O. nitidus MCZ 49515, F
O. pictus AMNH 31788, F
O. speciosus MCZ 49508, F
O. tetraspilus AMNH 31802, F
O. tetrastigma AMNH 43219, M
Petrotilapia genelutea USNM 270435, F
P. sp. MCZ 60446, M
P. sp. USNM 261800, M
P. tridentiger USNM 265572, M
Placidochromis electra AMNH 39103, M
P. johnstoni gold AMNH 37361, M
P. longimanus MCZ 49491, M
Protomelas fenestratus USNM 285234, M
P. kirki AMNH 11713, F
P. similis AMNH 32433, F
P. spilopterus AMNH 31761, M
P. taeniolatus AMNH 31841, F
P. triaenodon AMNH 43214, M
P. virgatus USNM 265561, M
Pseudotropheus aurora USNM 280092, M
P. elegans MCZ 49479, M
P. elongatus USNM 261816, M
P. livingstoni MCZ 49485, M
P. lombardi AMNH 35973, M
P. zebra MCZ 1979-010, M
Rhamphochromis esox/leptosoma NEA X, M
R. sp. USNM 280070, F
Stigmatochromis woodi USNM 308853, F
Taeniochromis holotaenia USNM 266822, M
Tramitochromis brevis MCZ 49452, F
T. variabilis complex MCZ 60423, M
Trematocranus placodon MCZ 49500, F

Madagascar
Paratilapia polleni AMNH 88101, –
Paretroplis polyactis AMNH 88180, F
Ptychochromis oligacanthus AMNH 88018, F

Results

The present study included adult individuals of both sexes with standard lengths ranging from 40 to 274 mm. Brain and body length were closely related, with an interspecific allometric coefficient (AC) of 0.490 (R^2 = 0.73, N = 172). AC values were similar for Victoria (AC = 0.535, R^2 = 0.76, N = 43), Tanganyika (AC = 0.507, R^2 = 0.71, N = 52), and

Table 1. Linear regression analysis of $\log_{10}$ brain measures on $\log_{10}$ standard length. The slope (allometric coefficient, AC), coefficient of determination (R^2) and sample size (N) are reported for all measures. In addition, the slopes for all measures are also reported for Victoria (AC_V), Tanganyika (AC_T), and Malawi (AC_M) separately.

	AC	R^2	N	AC_V	AC_T	AC_M
olfactory nerve diameter	0.578	0.204	162	0.357	0.660	0.440
olfactory bulb length	0.418	0.223	173	0.372	0.501	0.368
olfactory bulb width	0.478	0.268	169	0.404	0.527	0.402
olfactory bulb height	0.405	0.200	170	0.510	0.356	0.325
telencephalon length	0.392	0.370	185	0.582	0.403	0.244
telencephalon width	0.322	0.268	185	0.464	0.301	0.233
telencephalon height	0.416	0.450	185	0.505	0.420	0.297
eye diameter	0.764	0.762	185	0.707	0.837	0.716
optic tectum length	0.439	0.583	184	0.406	0.545	0.395
optic tectum width	0.378	0.499	185	0.329	0.464	0.312
optic tectum height	0.397	0.434	184	0.492	0.424	0.290
hypothalamus length	0.366	0.372	183	0.428	0.396	0.355
hypothalamus width	0.413	0.471	173	0.442	0.449	0.322
hypothalamus height	0.389	0.341	183	0.418	0.408	0.360
hypophysis length	0.553	0.330	55	0.513	0.585	1.030
hypophysis width	0.651	0.330	50	1.052	0.233	0.728
hypophysis height	0.736	0.449	55	0.878	0.742	0.591
cerebellum length	0.497	0.466	185	0.475	0.555	0.382
cerebellum width	0.365	0.318	183	0.338	0.527	0.241
cerebellum height	0.540	0.452	185	0.524	0.653	0.396
dorsal medulla length	0.593	0.372	182	0.629	0.484	0.656
dorsal medulla width	0.398	0.225	165	0.422	0.524	0.352
dorsal medulla height	0.465	0.154	182	0.211	0.686	0.323

Table 2. Descriptive statistics (mean ± standard deviation) of size measures (mm) for 189 cichlid species from Madagascar, and Lakes Victoria, Tanganyika, and Malawi. N – sample size.

	N	standard length	body depth	body width
Madagascar	3	84.64 ± 54.28	44.30 ± 29.65	14.35 ± 9.08
Victoria	55	76.83 ± 22.31	26.71 ± 9.29	13.35 ± 4.58
Tanganyika	58	84.94 ± 36.42	24.57 ± 8.43	13.53 ± 4.59
Malawi	100	95.05 ± 25.11	33.72 ± 9.36	14.80 ± 4.33

Malawi (AC = 0.442, R^2 = 0.70, N = 77). No significant differences were detected among lakes ($F_{2,166}$ = 1.228 *ns*) nor due to an interaction between standard length and lake ($F_{2,166}$ = 1.171 *ns*). In comparison, the three species of cichlids from Madagascar, which lie closer phylogenetically to the cichlid stem stock (Stiassny 1991) rendered an allometric coefficient of 0.489. Results of linear regressions between log-transformed standard length and all log-transformed brain measures are included in Table 1. No significant association between the shape of the head and that of the brain was evident across the three lakes ($F_{1,72}$ = 2.395 *ns*), Malawi alone ($F_{1,72}$ = 0.165 *ns*) and Tanganyika alone ($F_{1,50}$ = 0.488 *ns*). Only species of Victoria demonstrated a significant negative relationship between the two measures ($F_{1,41}$ = 8.145***).

Removal of the effects of body size

To eliminate the effects of body size from the brain measurements we compared several methods, including regression analysis, factor analysis, and sheared PCA. All techniques produced very similar results when applied to this data set. A discriminant function analysis indicated that species from Victoria and Malawi are generally deep-

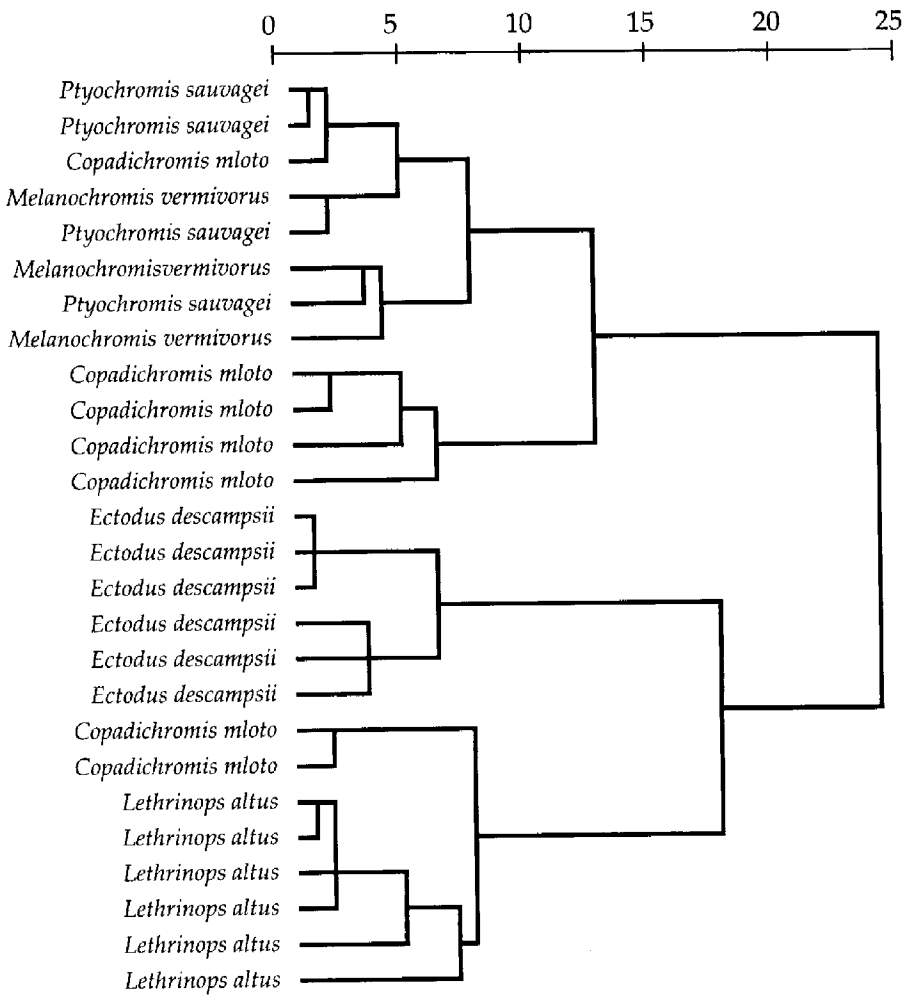

Fig. 3. Cluster analysis of five cichlid species (N = 26) to assess the extent of intraspecific variation in gross brain morphology. Scale represents measures of phenetic dissimilarity.

Table 3. Results of linear regression analyses of all brain measures onto body size. Abbreviations are sample size (N), squared correlation coefficient (R^2), significance *(P)*, $p < 0.001$ (***).

Variable	N	R^2	*P*
olfactory nerve diameter	187	0.1772	***
olfactory bulb length	201	0.2068	***
olfactory bulb width	196	0.2845	***
olfactory bulb height	198	0.1658	***
telencephalon length	213	0.3948	***
telencephalon width	213	0.2971	***
telencephalon height	213	0.4490	***
eye diameter	213	0.6188	***
optic tectum length	212	0.5680	***
optic tectum width	213	0.4441	***
optic tectum height	212	0.4034	***
hypothalamus length	211	0.3824	***
hypothalamus width	201	0.4392	***
hypothalamus height	211	0.3012	***
hypophysis length	62	0.4201	***
hypophysis width	59	0.3917	***
hypophysis height	62	0.4936	***
cerebellum length	213	0.4479	***
cerebellum width	211	0.2796	***
cerebellum height	213	0.4632	***
dorsal medulla length	210	0.3427	***
dorsal medulla width	192	0.2164	***
dorsal medulla height	210	0.1245	***

bodied and difficult to distinguish based on shape, while Tanganyika species are more elongated (descriptive statistics in Table 2). Thus species from Malawi and Victoria were treated separately from those of Tanganyika. The technique of our choice involved a two-step process. First an individual's "body size" was estimated from its standard length, body depth, and body width using factor analysis. PCA extracted one main axis explaining in excess of 92% of the variation contained in these size measures, and presumably representing body size. The models for Malawi/Victoria ($size = 0.023 \times length + 0.059 \times depth + 0.128 \times width - 5.667$) and Tanganyika ($size = 0.016 \times length + 0.068 \times depth + 0.128 \times width - 4.736$) proved similar. Second, linear regression analyses of all brain measures were performed onto this size/shape estimate (Table 3). These residuals, representing size-free neuroanatomical variation, were used for all subsequent analyses.

Intraspecific variation

To assess the partitioning of variation in brain morphology within and between species, a cluster analysis was performed on five species for which more than two individuals were available. A den-

Table 4. Results of two-way MANOVAs of (1) all brain measures, (2) olfactory structures only (olfactory bulb and olfactory nerve), (3) telencephalon, (4) visual structures (optic tectum, eye), (5) hypothalamus, (6) cerebellum, and (7) dorsal medulla with lake and sex as treatment effects. Abbreviations are degrees of freedom (df), Wilk's Lambda *(F)*, level of significance *(P)*, * $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $p < 0.001$.

	Source	df	*F*	*P*
(1) all brain measures	Lake	40,264	3.021	0.000***
	Sex	20,132	0.426	0.985
	Lake×Sex	40,264	1.199	0.204
(2) olfactory structures	Lake	8,342	3.105	0.002**
	Sex	4,171	0.589	0.671
	Lake×Sex	8,342	0.535	0.830
(3) telencephalon	Lake	6,412	3.375	0.003**
	Sex	3,206	0.232	0.874
	Lake×Sex	6,412	1.971	0.069
(4) visual structures	Lake	8,408	3.685	0.000***
	Sex	4,204	0.886	0.473
	Lake×Sex	8,408	0.841	0.567
(5) hypothalamus	Lake	6,388	2.460	0.024*
	Sex	3,194	0.126	0.945
	Lake×Sex	6,388	0.852	0.531
(6) cerebellum	Lake	6,408	4.755	0.000***
	Sex	3,204	0.216	0.885
	Lake×Sex	6,408	1.027	0.407
(7) dorsal medulla	Lake	6,368	6.724	0.000***
	Sex	3,184	0.342	0.795
	Lake×Sex	6,368	1.221	0.295

Table 5. Results of (univariate) ANOVAs of all brain measures with lake as treatment effect. If any of these tests proved significant, *a posteriori* comparisons (Tukey-Kramer HSD) were performed. Abbreviations are Victoria (V), Tanganyika (T), Malawi (M), non-significant (ns), level of significance *(P)*, * $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $p < 0.001$.

Comparison	*P*	*a posteriori* comparisons
olfactory structures		
olfactory nerve diameter	ns	
olfactory bulb length	ns	
olfactory bulb width	***	V M T
olfactory bulb height	ns	
telencephalon		
telencephalon length	ns	
telencephalon width	**	V M T
telencephalon height	**	M V T
optic structures		
optic tectum length	ns	
optic tectum width	*	M V T
optic tectum height	ns	
eye diameter	**	V M T
hypothalamus		
hypothalamus length	*	V M T
hypothalamus width	ns	
hypothalamus height	ns	
cerebellum		
cerebellum length	***	M V T
cerebellum width	ns	
cerebellum height	ns	
dorsal medulla		
dorsal medulla length	*	M V T
dorsal medulla width	ns	
dorsal medulla height	*	V M T

drogram summarizing these results is presented in Fig. 3. Individuals of two species, the insectivores *Lethrinops altus* (Malawi) and *Ectodus descampsii* (Tanganyika), clustered as distinct but adjacent nearest neighbors, separate from other cichlids. The remaining specimens did not form unitary, species-specific clusters, confirming the existence of intraspecific variability in at least some species. The amount of variation within species was, however, considerably less than that between species.

Effects of lake and sex-specific differences in brain morphology

A two-way MANOVA with all brain measures as dependent variables and lake and sex as independent variables revealed significant differences in brain morphology among lakes, but none between sexes or due to an interaction of sex and lake (Table 4). Separate MANOVAs were also performed for measures of olfactory structures, telencephalon, visual structures, cerebellum, hypothalamus, and dorsal medulla (Table 4). The results obtained for the various structures mirrored the overall results, indicating that there are significant differences among the lakes in all structures but none that can be attributed to sex-specific differences or to interaction effects. Univariate tests including *a posteriori* comparisons were carried out for each measure (Table 5).

Relationships among brain measures

The matrix of Pearson's Correlation Coefficients between the brain measures is reported in Figure 4. The highest correlations were found among different measures of the dorsal medulla, and between measures of the telencephalon, optic tectum, and cerebellum. An alternative method for the investigation of size relationships among the brain measures is factor analysis. When all individuals are considered irrespective of lake, this analysis identified six PC-axes with an Eigenvalue ≥1 cumulatively accounting for 71.4% of the variation. The loadings of all measures on each PC-axis following varimax rotation are listed in Table 6. The major source of variation (PC1, 31%) concerned differences in telencephalon size, indicating that evolutionary changes in brain morphology of cichlids in the East African lakes relate primarily to the development of this complex association center. The remaining axes concern the development of various sensory modalities, with structures related to lateral line mechanosensation (PC2) accounting for an additional 13.8%, olfactory structures (PC3) for 9.9%, and visual structures (PC4) for 6.2%.

Similarity of evolutionary trends in brain morphology across lakes

Three separate factor analyses were performed, one for each lake, and the matrices of factor loadings are listed for Victoria, Tanganyika, and Malawi in Tables 7, 8, and 9 respectively. The lakes were characterized by virtually identical sets of six PC-Axes, with one axis representing telencephalic variation and one each representing olfactory, visual, and lateral line structures. The lakes, however, differed in the relative importance of these axes. Although in cichlids of all lakes combined, the main source of variation proved to be the development of the telencephalon, evolution of the visual system proved most important within the assemblages of Victoria (35.5%), Tanganyika (37.3%) and Malawi (35.2%) individually. Further sources of within-lake variation are, in order of im-

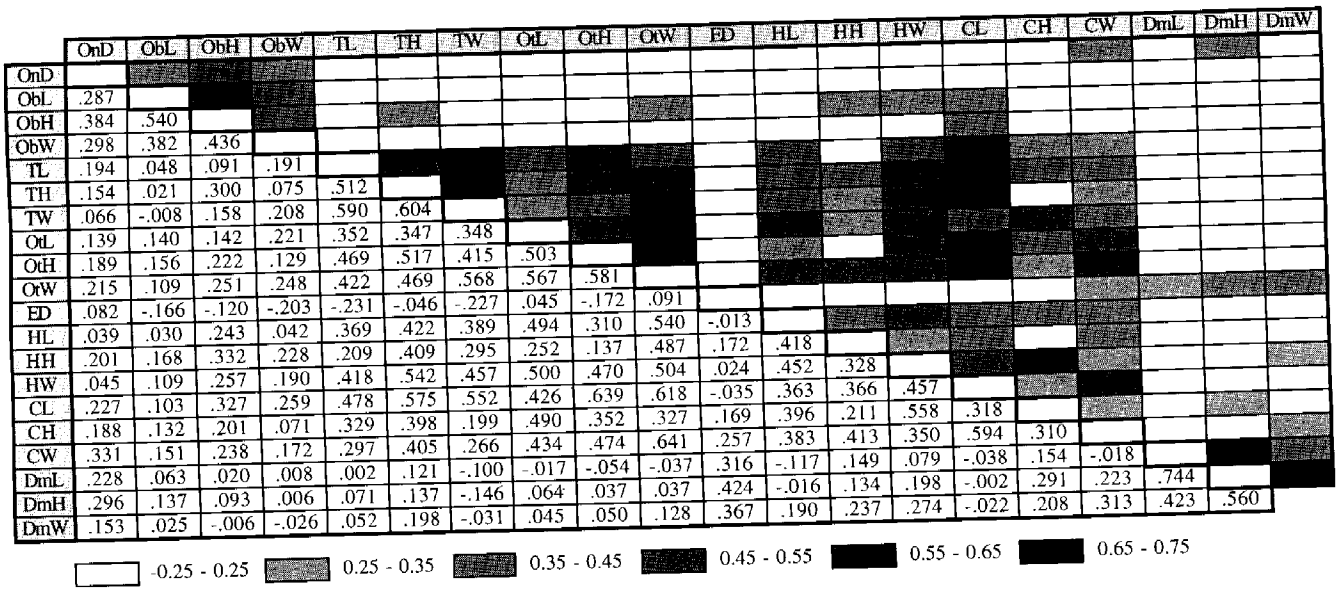

Fig. 4. Pearson's correlation coefficients for correlations between olfactory nerve diameter (OnD), olfactory bulb length (ObL), olfactory bulb height (ObH), olfactory bulb width (ObW), telencephalon length (TL), telencephalon height (TH), telencephalon width (TW), optic tectum length (OtL), optic tectum height (OtH), optic tectum width (OtW), eye diameter (ED), hypothalamus length (HL), hypothalamus height (HH), hypothalamus width (HW), cerebellum length (CL), cerebellum height (CH), cerebellum width (CW), dorsal medulla length (DmL), dorsal medulla height (DmH), and dorsal medulla width (DmW) are listed in the lower left triangle. The value of the correlation coefficient is also indicated graphically for the corresponding box in the upper right triangle.

Table 6. Factor loadings of each variable on PC-axes following varimax rotation and variance explained by each axis (V). Abbreviations are Eigenvalue (EV), length (L), height (H), and width (W). To increase readability of the table, all values between –0.35 and +0.35 have been omitted.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Olfactory nerve diameter	–	–	0.389	0.491	–	–
Olfactory bulb L.	–	–	0.810	–	–	–
Olfactory bulb H.	–	–	0.844	–	–	–
Olfactory bulb W.	–	–	–	–	–	–
Telencephalon L.	0.778	–	–	–	–	–
Telencephalon H.	0.717	–	–	–	–	–
Telencephalon W.	0.791	–	–	–	–	–
Eye diameter	–0.531	0.448	–	0.416	–	–
Optic tectum L.	–	–	–	–	0.746	–
Optic tectum H.	0.445	–	–	0.462	–	–
Optic tectum W.	–	–	–	0.509	0.363	0.379
Hypothalamus L.	–	–	–	–	0.500	0.509
Hypothalamus H.	–	–	–	–	–	0.778
Hypothalamus W.	–	–	–	–	0.616	–
Cerebellum L.	0.473	–	–	0.538	–	–
Cerebellum H.	–	–	–	–	0.793	–
Cerebellum W.	–	–	–	0.789	–	–
Dorsal medulla L.	–	0.896	–	–	–	–
Dorsal medulla H.	–	0.900	–	–	–	–
Dorsal medulla W.	–	0.678	–	–	–	–
EV	6.207	2.751	1.973	1.244	1.071	1.024
V%	31.0	13.8	9.9	6.2	5.4	5.1
Cumulative V%	31.0	44.8	54.7	60.9	66.3	71.4

Table 7. Lake Victoria cichlids: Factor loadings of each variable on PC-axes following varimax rotation and variance explained by each axis (V). Abbreviations are Eigenvalue (EV), length (L), height (H), and width (W). To increase readability of the table, all values between –0.35 and +0.35 have been omitted.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Olfactory nerve diameter	–	0.447	–	–	–	0.711
Olfactory bulb L.	–	0.546	0.609	–	–	–
Olfactory bulb H.	–	0.889	–	–	–	–
Olfactory bulb W.	–	0.694	–	–	–	–
Telencephalon L.	–	–	–	0.589	–	–
Telencephalon H.	–	–	–	0.821	–	–
Telencephalon W.	–	–	–	–	–	0.661
Eye diameter	–	–	–	–	0.930	–
Optic tectum L.	0.532	–	–	–	–	–
Optic tectum H.	0.782	–0.382	–	–	–	–
Optic tectum W.	0.466	–	–	0.374	–	–
Hypothalamus L.	–	–	–	0.828	–	–
Hypothalamus H.	–	–	–0.380	0.655	–	–
Hypothalamus W.	0.562	–	–	0.423	–	–
Cerebellum L.	0.838	–	–	–	–	–
Cerebellum H.	0.844	–	–	–	–	–
Cerebellum W.	–	–	–	0.418	0.439	–
Dorsal medulla L.	–	–	0.850	–	–	–
Dorsal medulla H.	–	–	0.872	–	–	–
Dorsal medulla W.	–	–	0.412	0.973	–	–
EV	7.036	2.829	2.130	1.337	1.138	0.981
V%	35.2	14.1	10.7	6.7	5.7	4.9
Cumulative V%	35.2	49.3	60.0	66.7	72.4	77.3

Table 8. Lake Tanganyika cichlids: Factor loadings of each variable on PC-axes following varimax rotation and variance explained by each axis (V). Abbreviations are Eigenvalue (EV), length (L), height (H), and width (W). To increase readability of the table, all values between –0.35 and +0.35 have been omitted.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Olfactory nerve diameter	–	–	–	–	0.679
Olfactory bulb L.	–	–	0.898	–	–
Olfactory bulb H.	–	–	0.919	–	–
Olfactory bulb W.	–	–	0.844	–	–
Telencephalon L.	–	–	–	0.834	–
Telencephalon H.	0.486	–	–	0.508	–
Telencephalon W.	–	–	–	0.866	–
Eye diameter	–	0.453	–	–0.635	0.455
Optic tectum L.	–	–	–	–	–
Optic tectum H.	0.781	–	–	–	–
Optic tectum W.	0.830	–	–	–	–
Hypothalamus L.	0.863	–	–	–	–
Hypothalamus H.	0.525	–	–	–	0.388
Hypothalamus W.	0.715	–	–	–	–0.409
Cerebellum L.	0.694	–	–	–	–
Cerebellum H.	0.889	–	–	–	–
Cerebellum W.	0.931	–	–	–0.429	–
Dorsal medulla L.	–0.366	0.935	–	–	–
Dorsal medulla H.	–	0.917	–	–	–
Dorsal medulla W.	–	0.721	–	–0.384	–
EV	7.450	3.064	2.262	1.329	1.028
V%	37.3	15.3	11.3	6.6	5.1
Cumulative V%	37.3	52.6	63.9	70.5	75.6

Table 9. Lake Malawi cichlids: Factor loadings of each variable on PC-axes following varimax rotation and variance explained by each axis (V). Abbreviations are Eigenvalue (EV), length (L), height (H), and width (W). To increase readability of the table, all values between –0.35 and +0.35 have been omitted.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Olfactory nerve diameter	0.467	–	0.488	–	–0.478	–
Olfactory bulb L.	–	–	0.838	–	–	–
Olfactory bulb H.	–	–	0.778	–	–	–
Olfactory bulb W.	–	–	–	–	–	–
Telencephalon L.	–	–	–	0.772	–	–
Telencephalon H.	–	–	–	0.687	–	–
Telencephalon W.	–	–	–	0.738	–	–
Eye diameter	0.512	0.449	–0.380	–0.355	–	–
Optic tectum L.	–	–	–	–	–	0.745
Optic tectum H.	0.478	–	–	0.478	–	–
Optic tectum W.	0.801	–	–	–	–	–
Hypothalamus L.	–	–	–	–	0.570	0.570
Hypothalamus H.	–	0.368	–	–	0.636	–
Hypothalamus W.	–	–	–	0.400	–	0.500
Cerebellum L.	0.719	–	–	0.404	–	–
Cerebellum H.	–	–	–	–	–	0.768
Cerebellum W.	0.815	–	–	–	–	–
Dorsal medulla L.	–	0.904	–	–	–	–
Dorsal medulla H.	–	0.902	–	–	–	–
Dorsal medulla W.	–	0.767	–	–	–	–
EV	5.447	3.066	2.056	1.554	1.270	1.028
V%	35.2	14.1	10.7	6.7	5.7	4.9
Cumulative V%	35.2	49.3	60.0	66.7	72.4	77.3

portance, the development of olfactory, lateral line, visual, and telencephalic structures for Victoria, and lateral line, olfaction, visual and telencephalon in Tanganyika and Malawi.

Discussion

Numerous authors have remarked upon the strong convergence among ecological radiations of cichlid fishes in the African Great Lakes (Fryer and Iles 1972). Lakes Malawi, Tanganyika, and Victoria all exhibit species-rich trophic radiations with strikingly parallel adaptations in dental, cranial, and post-cranial features. Hidden beneath these similarities, however, are differences in both adaptive mode and form variance among the three cichlid faunas (Witte 1984). In many cases, these contrasts may be the result of ecological differences among the lakes, due ultimately to variation in lake morphometry (Bootsma and Hecky 1993). Thus, it is not surprising that analysis of brain morphology among representative cichlids from the three lakes should reveal significant variation, but the strong effect attributable to lake is of particular interest. The balance of similarities and differences in patterns of brain evolution in parallel radiations occupying distinct environmental milieus can contribute valuable insights into the way the nervous system functions under various environmental conditions and how it has responded to natural selection.

The brain structures that we measured did not differ randomly and independently of each other. Rather, factor analysis confirmed that brain measures covaried as stable sets of variables, suggesting the controlling effects of allometric, co-adaptive, or functional contingencies in brain development. It is likely, for example, that the relationship between olfactory nerve diameter and olfactory bulb size is the result of functional ties between the structures involved. A similar case may be argued with respect to correlations between the eye and optic tectum. The presence of an association in size between optic tectum and cerebellum closely matches patterns detected previously in the brain evolution of cyprinids (Huber and Rylander 1992). Conceivably the prominent accessory optic system, involving cell groups in the retina, optic tectum, pretectum and cerebellum (Braford and Northcutt 1983), is responsible for this association, and selection for visual function drives pretectal, tectal, and cerebellar size in similar ways.

In accordance with studies in other teleosts (Huber and Rylander 1992; Kotrschal and Palzenberger 1992), the brains of cichlids exhibit marked differences with respect to the relative develop-

ment of the primary sensory structures of vision, olfaction, and mechanosensation. If one assumes that comparable volumes provide comparable functional capabilities, then a particular position for each species in a coordinate system of sensory modalities may be suggested based on the size of the brain structures concerned with these modalities. One of the most interesting results, however, is that such variation in the size of brain structures is not only limited to structures of the primary senses. The telencephalon proved by far the most variable structure in cichlid brain morphology. Although various of its subdivisions receive prominent olfactory projections, the telencephalon appears also to contain multimodal association centers responsible for many localized behavioral functions relating to feeding, reproductive and aggressive behavior (Demski 1983).

Interpretation of structural variation in cichlid brains must proceed with a measure of caution for two main reasons. Firstly, multiple senses may contribute to the size of some brain structures and histological sectioning would be required to adequately partition the relative contributions of these centers. For example, both lateral line and taste projections may contribute to our measures of the size of the dorsal medulla, with dorsal components relating to acoustico-lateralis (ventromedial nucleus, crista cerebelli) and ventromedial aspects relating to taste. Secondly, considerable degrees of intraspecific variability are possible (Fig. 3). There are several possible sources for this variation. Phenotypic plasticity in the brain would hardly be surprising in organisms already infamous for their skeletal plasticity (e.g., Hoogerhoud 1984, 1986). Certainly this is worth further investigation. Moreover, some of the intraspecific variation observed could be due to taxonomic artifact. The species diversity in all three lakes has been consistently underestimated, and older field collections may well have contained mixtures of superficially similar taxa.

Most noteworthy among the patterns that we detected was a strong difference in brain form variation among the three lakes. Although factors with very similar structure appeared recurrently from lake to lake, they varied in order of importance. The first factor in all cases summarized information about the visual system. For Lakes Tanganyika and Malawi, the second factor was strongly correlated to olfactory structures. The difference in importance of olfactory development between Lake Victoria (where the olfactory factor accounted for >14% of total variance) and Lakes Tanganyika and Malawi (11.3% and 10.7% respectively), is likely to reflect biologically significant differences in selective environment. Lake Tanganyika and Lake Malawi are both highly transparent rift lakes with extremely steep basin morphometries. Water column productivity and turbidity are both lower in the rift lakes than in Lake Victoria. We postulate that the evolution of olfactory capabilities has therefore been proportionately favored in the evolution of Lake Victoria cichlids, and that this is reflected in the greater relative size of olfactory bulbs in these animals as compared to their counterparts in the rift lakes.

A. posteriori tests reveal evidence for a more subtle structure to interlake differences, which are more likely attributable to phylogeny than the environment. Although Lakes Malawi and Tanganyika are more similar ecologically, the cichlid faunas of Lake Malawi and Lake Victoria are more closely related to each other than either is to that of Lake Tanganyika, which is polyphyletic and rich in ancient lineages (Lowe-McConnell 1993). Contrasts that tend to link Malawi and Victoria may thus be the result of a closer common ancestry. This can be tested through more detailed analyses of the Lake Tanganyika species flocks, which include several haplochromine derivative lineages.

Measures of interspecific allometric coefficients for East African cichlids determined in this study are lower than those reported previously for lizards (0.66, Platel 1975), amphibians (0.60, Thireau 1973), and other teleosts (0.67, Ridet et al. 1975; Ridet and Bauchot 1990). This indicates that changes in brain size are proportionally less than predicted from evolutionary changes in body size.

Compensation, the simultaneous reduction in one structure due to the concomitant increase in another, has been considered a prominent factor in structuring brains, giving rise to the negative size relationships among structures dealing with different modalities (Kotrschal and Junger 1988; Kotrschal and Palzenberger 1992; Schellart 1992). However, few studies have distinguished between compensation and changes of the respective sensory lobes due to independent adaptive forces. As in previous studies (Gomahr et al. 1992; Huber and Rylander 1992), we found no evidence of compensation in cichlid brains; all significant correlations were positive and changes in the various structures appeared to be governed by their own independent forces. Although many species have evolved enhanced abilities in a particular sensory system of major importance to their life-style, few species have concurrently allowed other sensory systems to degenerate extensively (Blaxter 1988). This may, in part, be explained by the fact that in cichlids the brain does not appear to be significantly constrained by the space available within the skull. During dissections it was noted that the brain frequently occupied less than half of the space available within the brain case. The balance was filled with amorphous tissue; a trend which was

even more pronounced in larger specimens. It is suggested that the constructional morphology of the head is dominated by evolution of jaw characteristics with their own set of spatial constraints driving for maximum adaptive confines (Barel 1983).

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