

- lations: Patterns and theory. *Theoret. Popul. Biol.* 13:121-177.
- ROGERS, J. S. 1984. Deriving phylogenetic trees from allele frequencies. *Syst. Zool.* 33:52-63.
- . 1986. Deriving phylogenetic trees from allele frequencies: A comparison of nine genetic distances. *Syst. Zool.* 35:297-310.
- ROHLF, F. J. 1982. Consensus indices for comparing classifications. *Mathemat. Biosci.* 59:131-144.
- . 1986. NTSYS-pc. Numerical Taxonomy and Multivariate Analysis System for the IBM PC Microcomputer (and Compatibles). Applied Biostatistics, Setauket, NY.
- SCIENCE CITATION INDEX. 1980-1985. Institute for Scientific Research, Philadelphia, PA.
- SIMON, C. 1979. Evolution of periodical cicadas: Phylogenetic inferences based on allozymic data. *Syst. Zool.* 28:22-39.
- SLATKIN, M. 1980. The distribution of mutant alleles in a subdivided population. *Genetics* 95:503-524.
- . 1981. Estimating levels of gene flow in natural populations. *Genetics* 99:323-335.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. *Numerical Taxonomy*. Freeman, San Francisco, CA.
- SWOFFORD, D. L. 1985. PAUP—Phylogenetic Analysis Using Parsimony. Illinois Natural History Survey, Champaign.
- SWOFFORD, D. L., AND S. H. BERLOCHER. 1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. *Syst. Zool.* 36:293-325.
- YANG, S. Y., M. SOULÉ, AND G. C. GORMAN. 1974. *Anolis* lizards of the eastern Caribbean: A case study in evolution. I. Genetic relationships, phylogeny, and colonization sequence of the *roquet* group. *Syst. Zool.* 23:387-399.

Corresponding Editor: D. L. Swofford

*Evolution*, 43(3), 1989, pp. 683-688

## DENTAL DEVELOPMENT AS A MEASURE OF LIFE HISTORY IN PRIMATES

B. HOLLY SMITH

*Museum of Anthropology, University of Michigan, Ann Arbor, MI 48109*

Received March 11, 1988. Accepted December 16, 1988

G. A. Sacher's comparative studies of the lifespan of living mammals led him to conclude that longevity is controlled by relative brain size and, further, that brain metabolism and energetics comprise the pace-maker of vertebrate growth and aging (Sacher, 1959, 1975, 1978; Sacher and Staffeldt, 1974; see also Hofman [1983] and Armstrong [1983]). Mechanisms linking brain size and maturation may include direct physiological ones, as in the demands of fetal brain growth on gestation length and maternal metabolic turnover (Sacher and Staffeldt, 1974; Martin, 1983). Other links may involve ecological strategy, in which the benefits of large brains require delayed maturation and long life to be realized. The occurrence of large brains and long life in *K*-selected mammals that make relatively great investment in few young exemplify this (Martin, 1983). Primates become a critical case in any investigation of the relationship of brain size and maturation, as they are at extremes in mammals for both parameters. Humans take on particular importance as the most encephalized and the longest lived mammal (Sacher, 1975).

Recently Harvey and Clutton-Brock (1985) assembled extensive life-history data on 135 primate species, investigating the interrelationship of body size, brain size, and maturation. Although Sacher's hypothesis is usually phrased as a relationship between longevity and brain size, other life-history variables performed equally well or better as correlates of brain size in these data. Investigation of the longevity hypothesis is hampered

by the great difficulty of obtaining accurate figures for maximum lifespan in species. Sacher (1978) managed to explain 85% of the variance in mammalian lifespan (with the variables body weight, brain weight, metabolic rate, and body temperature), a figure he regarded as the maximum achievable due to error inherent in lifespan data. This problem extends in part to life-history measures in general. Many are reproductive parameters that are known to be relatively plastic and (excepting gestation length) subject to substantial modification by the environment (see Eveleth and Tanner, 1976). In comparison, maturation of dental and skeletal hard tissues has a smaller component of environmental variance (see Tanner, 1955). The dentition is arguably the most stable marker of maturation: dental development is highly heritable, is relatively resistant to nutritional extremes and even fairly severe developmental insults, and has a lower coefficient of variation than skeletal maturation (Lewis and Garn, 1960; Garn et al., 1965a, 1965b). Since the masticatory system processes the food that fuels the system in general, the dentition remains an important growth marker. Thus, tooth development must be completely integrated into the plan of growth and development, timed to growth of the skull, maturation of muscles of mastication, and somatic growth in general. Therefore, data on age of maturity of the dentition are here added to other measures of primate life history.

Age of tooth eruption is available in the literature for 21 of the primate species listed in Harvey and Clut-

TABLE 1. Ages of eruption of mandibular first molar and of completed dentition (last permanent-tooth eruption) for 21 primate species.

Taxon	Age of eruption (yr)		Source
	Mandibular M <sub>1</sub>	Completed dentition	
<b>PROSIMII</b>			
<b>Lemuridae</b>			
<i>Lemur catta</i>	0.33	1.33	Eaglen, 1985
<i>Lemur fulvus</i>	0.50	1.33	Eaglen, 1985
<i>Lemur macaco</i>	0.50	—	Eaglen, 1985
<i>Varecia variegatus</i>	0.50	—	Eaglen, 1985
<i>Cheirogaleus medius</i>	0.12	—	Eaglen, 1985
<b>Indriidae</b>			
<i>Propithecus verreauxi</i>	0.33	—	Eaglen, 1985
<b>ANTHROPOIDEA</b>			
<b>Callitrichidae</b>			
<i>Callithrix jacchus</i>	0.31	0.96	Johnston et al., 1970
<i>Saguinus fuscicollis</i>	0.37	0.81	Glassman, 1983
<i>Saguinus nigricollis</i>	0.31	0.77	Chase and Cooper, 1969
<b>Cebidae</b>			
<i>Cebus albifrons</i>	1.06	—	Fleagle and Schaffler, 1982
<i>Cebus apella</i>	1.15	—	Galliari, 1985
<i>Saimiri sciureus</i>	0.43	1.67	Long and Cooper, 1968
<i>Aotus trivirgatus</i>	0.36	1.03	Hall et al., 1979
<b>Cercopithecidae</b>			
<i>Cercopithecus aethiops</i>	0.84	3.75	Hurme and van Wagenen, 1961
<i>Macaca fascicularis</i> (= <i>irus</i> )	1.34	6.76	Spiegel, 1934; Bowen and Koch, 1970
<i>Macaca mulatta</i>	1.36	5.54	Hurme and van Wagenen, 1961
<i>Macaca nemestrina</i>	1.37	5.92	Swindler, 1985
<i>Papio cynocephalus</i>	1.54	6.17	Reed, 1973
<b>Pongidae</b>			
<i>Pan troglodytes</i>	3.30	11.50	Nissen and Riesen, 1964
<i>Gorilla gorilla</i>	3.50	11.40	Willoughby, 1978
<b>Hominidae</b>			
<i>Homo sapiens</i>	6.00	20.00	Hurme, 1949; Fanning, 1962

ton-Brock (1985). Age of eruption of the mandibular first molar was available for all species (see Table 1). This is the first permanent tooth to erupt in primates (Schultz, 1935) as it is in generalized mammals as a group (see Slaughter et al., 1974). A second measure, age of completed dentition (age of last tooth eruption), is also included. Completion of the adult dentition has an orderly relationship with epiphyseal closure in a wide range of mammals (Shigehara, 1980) and, thus, can serve as a somatic (vs. sexual) marker of the beginning of adulthood (as in Schultz [1960]). It might be noted that ages of tooth eruption for prosimians are based on many fewer observations than are those for anthropoids.

The following life-history and size variables were taken from Harvey and Clutton-Brock (1985): 1) female body weight, 2) birth weight, 3) gestation length, 4) age of weaning, 5) interbirth interval, 6) age of attainment of sexual maturity in females, 7) age of first breeding for females, 8) lifespan, 9) neonatal brain weight, and 10) adult brain weight. A few variables are omitted here for reasons involving redundancy of results (male body weight), small sample size relative to dental data (age of male sexual maturity), and discrete

distribution (litter size); one variable shown to be unrelated to other variables by Harvey and Clutton-Brock (length of estrous cycle) is not included here. Although they represent only 15 primate genera, the 21 species considered are well distributed across the size range of the order and represent seven of the 11 traditionally recognized primate families. For a fair comparison of the effect of adding the dental variables, the entire data set is here restricted to species with dental data. In accordance with Harvey and Clutton-Brock (1985) and standard practice, logarithms of values are used in all correlation analyses.

Table 2 shows the entire correlation matrix of reproductive variables, body weight, brain weight, and tooth maturation. In general, correlations involving the dental variables are increased over others in this array. Correlations of age of M<sub>1</sub> eruption with brain weight are among the highest attained:  $r = 0.98$  with adult brain weight, and  $r = 0.99$  with neonatal brain weight. The only other correlations to reach these levels are those of the partly autocorrelated neonatal brain weight and birth weight ( $r = 0.99$ ) and the nearly redundant variables neonatal and adult brain weight ( $r = 0.99$ ). The two dental variables are also highly correlated

TABLE 2. Correlation matrix for logarithms of life-history variables. Body weight and ages of sexual maturity and first breeding were for females only. Sample sizes are given in parentheses.

Variable	Variable												
	1	2	3	4	5	6	7	8	9	10	11	12	
1) Body weight	—												
2) Birth weight	0.93 (21)	—											
3) Gestation length	0.69 (18)	0.84 (18)	—										
4) Age at weaning	0.92 (14)	0.95 (14)	0.86 (12)	—									
5) Interbirth interval	0.89 (16)	0.85 (16)	0.73 (16)	0.88 (12)	—								
6) Age at sexual maturity	0.77 (13)	0.87 (13)	0.94 (12)	0.88 (9)	0.77 (11)	—							
7) Age at first breeding	0.87 (15)	0.95 (15)	0.89 (15)	0.92 (10)	0.89 (14)	0.95 (10)	—						
8) Lifespan	0.84 (14)	0.82 (14)	0.64 (13)	0.81 (8)	0.91 (11)	0.81 (9)	0.84 (11)	—					
9) Neonate brain weight	0.93 (11)	0.99 (11)	0.89 (11)	0.94 (9)	0.82 (11)	0.93 (9)	0.96 (10)	0.82 (9)	—				
10) Adult brain weight	0.94 (21)	0.98 (21)	0.82 (18)	0.93 (14)	0.88 (16)	0.87 (13)	0.95 (15)	0.88 (14)	0.99 (11)	—			
11) Age at complete dentition	0.93 (14)	0.97 (14)	0.86 (13)	0.95 (11)	0.81 (13)	0.97 (8)	0.93 (12)	0.86 (10)	0.99 (9)	0.97 (14)	—		
12) Age at M <sub>1</sub> eruption	0.89 (21)	0.96 (21)	0.85 (18)	0.93 (14)	0.82 (16)	0.86 (13)	0.93 (15)	0.85 (14)	0.99 (11)	0.98 (21)	0.98 (14)	—	

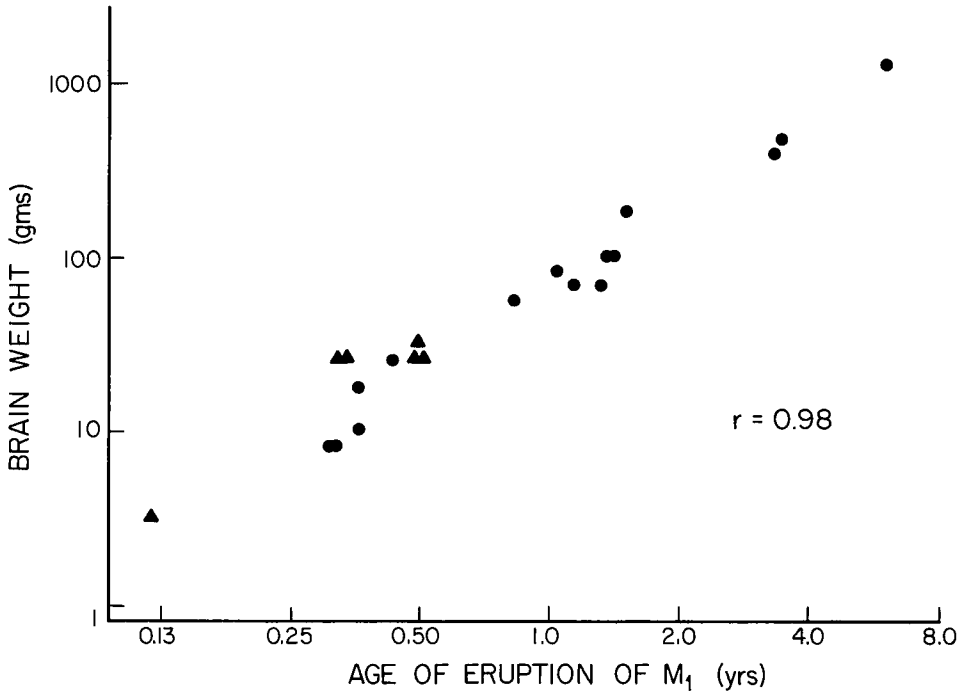


FIG. 1. Adult brain weights for 21 primate species plotted against age of eruption of the mandibular first molar; circles = anthropoids; triangles = prosimians. Note the logarithmic scale on both axes. From the rapid-maturing *Cheirogaleus* (far left) to the slow-maturing *Homo* (far right), dental maturation has a strong relationship with brain weight.

( $r = 0.98$ ). Other life-history variables (gestation length, age of weaning, interbirth interval, age of sexual maturity in females, age of first breeding in females, and lifespan) are correlated with brain weight with an average  $r$  of 0.90 (range: 0.82–0.95).

As shown in Figure 1, no species appear to be particularly aberrant in the relationship between dental maturation and brain weight. Even the large-brained *Homo sapiens* fits easily with other primates. The increase in correlations obtained when tooth eruption is substituted as the measure of maturation is probably due at least in part to a relative lack of error in these data. This is suggested because dental variables correlate as well or better with reproductive variables (mean of 12 correlations:  $r = 0.92$ ) as reproductive variables correlate with each other (mean of 15 correlations:  $r = 0.89$ ).

Dental measures of maturation make a stronger case that the correspondence of brain size and maturation rises above that expected due to the effect of body size alone. Table 3 shows a representative sample of partial correlations of life-history variables with brain size, with the effect of body weight held constant in multiple regression. The partial correlation of  $M_1$  eruption and adult brain weight remains  $r = 0.90$ , an extremely high value for a weight-corrected correlation. Other partial correlations of brain weight with life-history measures are substantially lower:  $r = 0.68$  with gestation length,  $r = 0.65$  with age of female sexual maturity, and  $r = 0.48$  with lifespan.

Why is eruption of the first molar more highly correlated with brain weight than are other life-history variables? One could argue that it is because brain size and tooth eruption have the closest and most direct causal link. However, the dentition has advantages over other markers of maturation in that it is robust to environmental perturbations and has relatively low variance. Thus, the dentition provides a growth marker that is reliable. Of some interest, the correlation between brain size and dental maturation is not just higher than those with other explanatory variables; it approaches  $r = 1.0$  in these data (based on a small, but representative sample of 21 species). This very high correlation suggests that age at tooth eruption is more than simply a better measure of lifespan, but that the factor related to brain size is maturation rate as a whole, rather than any one of its aspects (see also Sacher [1978] and Hofman [1983]). Age at tooth eruption serves as a good general measure of this rate.

Data on age at maturation of hard tissues may be difficult to obtain for a truly large sample of mammalian species, because collecting this information requires capture and possibly anesthesia or radiography of subjects. However, use of dental growth markers offers the compensation that tests of hypotheses can be extended to species in the fossil record. Incremental lines in teeth can provide ages of tooth formation or eruption events for fossil mammals (Fisher, 1984; Bromage and Dean, 1985; Beynon and Wood, 1987). Fossilized skeletal remains provide estimates of brain

TABLE 3. Representative sample of partial correlations of maturation and brain weight with the effect of body weight held constant. Sample sizes are given in parentheses.

Variable	Variable				
	1	2	3	4	5
1) Age at M <sub>1</sub> eruption	—				
2 Gestation length	0.69 (18)	—			
3) Age at sexual maturity	0.61 (13)	0.81 (12)	—		
4) Lifespan	0.36 (14)	-0.01 (13)	0.24 (9)	—	
5) Adult brain weight	0.90 (21)	0.68 (18)	0.65 (13)	0.48 (14)	—

and body weight. Earliest hominids, for example, are now known to show short maturation times and early eruption of M<sub>1</sub> (Bromage and Dean, 1985; Smith, 1986) in line with their low estimated encephalization, as predicted by Sacher (1975).

As Harvey and Clutton-Brock (1985 p. 561) point out, ubiquitous positive correlation of size and life history makes identification of causal networks difficult: "... large bodied mammals tend to have large brains, long gestation times, give birth to large young, wean later, reach sexual maturity later, have longer interbirth intervals, and live longer than smaller mammals." Still, hypothesized direct causal links require strong correlations for support, and low correlations may give grounds for hypothesis rejection. Across-the-board increase in correlation with the addition of dental measures of maturation indicates that dental growth markers are important for investigating mammalian life history.

#### ACKNOWLEDGMENTS

This research was supported by National Science Foundation Grant BNS-8717738. The Primate Information Center of Seattle, Washington, helped with the search for tooth-eruption data. I thank P. D. Gingerich and anonymous reviewers for comments on the manuscript.

#### LITERATURE CITED

- ARMSTRONG, E. 1983. Relative brain size and metabolism in mammals. *Science* 220:1302-1304.
- BEYNON, A. D., AND B. A. WOOD. 1987. Patterns and rates of enamel growth in the molar teeth of early hominids. *Nature* 326:493-496.
- BOWEN, W. H., AND G. KOCH. 1970. Determination of age in monkeys (*Macaca irus*) on the basis of dental development. *Lab. Anim.* 4:113-123.
- BROMAGE, T. G., AND M. C. DEAN. 1985. Re-evaluation of the age at death of immature fossil hominids. *Nature* 317:525-527.
- CHASE, J. E., AND R. W. COOPER. 1969. *Sanguinus nigricollis*—Physical growth and dental eruption in a small population of captive-born individuals. *Amer. J. Phys. Anthropol.* 30:111-116.
- EAGLEN, R. H. 1985. Behavioral correlates of tooth eruption in Madagascar lemurs. *Amer. J. Phys. Anthropol.* 66:307-315.
- EVELETH, P. B., AND J. M. TANNER. 1976. *Worldwide Variation in Human Growth*. Cambridge Univ. Press, Cambridge, U.K.
- FANNING, E. A. 1962. Third molar emergence in Bostonians. *Amer. J. Phys. Anthropol.* 20:339-346.
- FISHER, D. C. 1984. Taphonomic analysis of late Pleistocene mastodon occurrences: Evidence of butchery by North American Paleo-Indians. *Paleobiology* 10:338-357.
- FLEAGLE, J. G., AND M. B. SCHAFFLER. 1982. Development and eruption of the mandibular cheek teeth in *Cebus albifrons*. *Fol. Primatol.* 38:158-169.
- GALLIARI, C. A. 1985. Dental eruption in captive-born *Cebus apella*: From birth to 30 months old. *Primates* 26:506-510.
- GARN, S. M., A. B. LEWIS, AND R. M. BLIZZARD. 1965a. Endocrine factors in dental development. *J. Dent. Res.* 44:243-248.
- GARN, S. M., A. B. LEWIS, AND R. S. KERESKY. 1965b. Genetic, nutritional, and maturational correlates of dental development. *J. Dent. Res.* 44:228-242.
- GLASSMAN, D. M. 1983. Growth and development in the saddle-back tamarin: The sequence and timing of dental eruption and epiphyseal union. *Amer. J. Primatol.* 5:51-59.
- HALL, R. D., R. J. BEATTIE, AND G. H. WYCKOFF. 1979. Weight gains and sequence of dental eruptions in infant owl monkeys (*Aotus trivirgatus*), pp. 321-328. In G. C. Ruppenthal (ed.), *Nursery Care of Nonhuman Primates*. Plenum, N.Y.
- HARVEY, P. H., AND T. H. CLUTTON-BROCK. 1985. Life-history variation in primates. *Evolution* 39:559-581.
- HOFMAN, M. A. 1983. Energy metabolism, brain size and longevity in mammals. *Quart. Rev. Biol.* 58:495-512.
- HURME, V. O. 1949. Ranges of normalcy in the eruption of permanent teeth. *J. Dent. Child.* 16:11-15.
- HURME, V. O., AND G. VAN WAGENEN. 1961. Basic data on the emergence of permanent teeth in the rhesus monkey (*Macaca mulatta*). *Proc. Amer. Phil. Soc.* 105:105-140.
- JOHNSTON, G. W., S. DREIZEN, AND B. M. LEVY. 1970. Dental development in the cotton ear marmoset (*Callithrix jacchus*). *Amer. J. Phys. Anthropol.* 33:41-48.

- LEWIS, A. B., AND S. M. GARN. 1960. The relationship between tooth formation and other maturational factors. *Angle Orthod.* 30:70-77.
- LONG, J. O., AND R. W. COOPER. 1968. Physical growth and dental eruption in captive-bred squirrel monkeys *Saimiri sciureus* (Leticia, Columbia), pp. 193-205. In L. A. Rosenblum and R. W. Cooper (eds.), *The Squirrel Monkey*. Academic Press, N.Y.
- MARTIN, R. D. 1983. Human Brain Evolution in an Ecological Context. Fifty-second James Arthur Lecture on the Evolution of the Human Brain. American Museum of Natural History, N.Y.
- NISSEN, H. W., AND A. H. RIESEN. 1964. The eruption of the permanent dentition of chimpanzee. *Amer. J. Phys. Anthropol.* 22:285-294.
- REED, O. M. 1973. *Papio cynocephalus* age determination. *Amer. J. Phys. Anthropol.* 38:309-314.
- SACHER, G. A. 1959. Relationship of lifespan to brain weight and body weight in mammals, pp. 115-133. In G. E. W. Wolstenholme and M. O'Connor (eds.), *C.I.B.A. Foundation Colloquia on Aging Volume 5: The Lifespan of Animals*. Churchill, London, U.K.
- . 1975. Maturation and longevity in relation to cranial capacity in hominid evolution, pp. 417-441. In R. H. Tuttle (ed.), *Primate Functional Morphology and Evolution*. Mouton, The Hague, Neth.
- . 1978. Longevity, aging, and death: An evolutionary perspective. *Gerontology* 18:112-119.
- SACHER, G. A., AND E. F. STAFFELDT. 1974. Relation of gestation time to brain weight for placental mammals: Implications for the theory of vertebrate growth. *Amer. Natur.* 108:593-616.
- SCHULTZ, A. H. 1935. Eruption and decay of the permanent teeth in primates. *Amer. J. Phys. Anthropol.* 19:489-581.
- . 1960. Age changes in primates and their modification in man, pp. 1-20. In J. M. Tanner (ed.), *Human Growth*. Pergamon, Oxford, U.K.
- SHIGEHARA, N. 1980. Epiphyseal union, tooth eruption, and sexual maturation in the common tree shrew, with reference to its systematic problem. *Primates* 21:1-19.
- SLAUGHTER, B. H., R. H. PINE, AND N. E. PINE. 1974. Eruption of cheek teeth in Insectivora and Carnivora. *J. Mammal.* 55:115-125.
- SMITH, B. H. 1986. Dental development in *Australopithecus* and early *Homo*. *Nature* 323:327-330.
- SPIEGEL, A. 1934. Der zeitliche Ablauf der Bezahnung und des Zahnwechsels bei Javamakaken (*Macaca irus mordax* Th. & Wr.). *Z. Wiss. Zool.* 145:711-732.
- SWINDLER, D. R. 1985. Nonhuman primate dental development and its relationship to human dental development, pp. 67-94. In E. S. Watts (ed.), *Nonhuman Primate Models for Human Growth and Development*. Liss, N.Y.
- TANNER, J. M. 1955. *Growth at Adolescence*. Blackwell, Oxford, U.K.
- WILLOUGHBY, D. P. 1978. *All About Gorillas*. Barnes, South Brunswick, N.J.

Corresponding Editor: D. I. Rubenstein

*Evolution*, 43(3), 1989, pp. 688-693

EVIDENCE FOR SELECTION ON SENSORY STRUCTURES IN A CAVE POPULATION OF  
*GAMMARUS MINUS* (AMPHIPODA)

ROSS JONES<sup>1</sup>

*Department of Ecology and Evolutionary Biology, Northwestern University, Evanston, IL 60201*

AND

DAVID C. CULVER

*Department of Biology, The American University, Washington, DC 20016*

Received May 19, 1988. Accepted December 6, 1988

A long tradition in evolutionary biology has been to explain morphological differentiation as adaptation to different habitats. This adaptationist program has been criticized (Gould and Lewontin, 1979) because it ignores other mechanisms of evolution, such as developmental constraints or random processes which can cause nonadaptive changes. This has led to an in-

creased attempt to measure selection in natural populations in order to estimate its relative importance as an evolutionary mechanism (Endler, 1986).

The evolution of sensory structures in cave animals is an excellent model system for studying the role of selective and nonselective mechanisms of morphological evolution. Many animals limited to a cave environment show a drastic reduction in eye size compared to their closest surface relatives. Most of these species also show convergence of traits which Christiansen (1961) termed cave-dependent traits. Among these traits are increases in the size or complexity of the nonvisual

<sup>1</sup> Mailing address: Department of Biology, The American University, 4400 Massachusetts Ave., N.W., Washington, DC 20016.