

(Marler and Hamilton, 1). That local dialects have not been demonstrated in other mammals except man may be due to the extensive gradation and acoustic complexity of most mammalian vocalizations, especially those of higher primates.

It is unlikely that variations in dialect are primarily genetic in origin. Año Nuevo Island was first reestablished as a breeding colony in 1961 by a few adults (8). The 50 full-grown bulls living there in 1968 and 1969 could not have been born there because (i) it takes 10 years or more for males to attain full size (9), and (ii) none of these males bore tags like those attached to most of the pups born on the island each year since 1961 (10). Clearly, most of these adult males must have immigrated from other rookeries, like the original settlers in 1961. These data, the uniformity of calls in the Año Nuevo population, and the minimal drift from one year to the next, suggest that immigrants adopted the vocal peculiarities or dialect of the breeding males already in residence. Indeed, one adult male first seen at Año Nuevo in 1969, consistently threatened other males by first emitting a burst of pulses at the rate of 4.7 pulse/sec immediately followed by another series at 1.0 pulse/sec (like other Año Nuevo males) (11). We know from tagging studies that interchange of animals occurs between colonies, particularly during the first year of life (12).

Young male elephant seals may copy some of the threat call characteristics of adult males in the colony where they find themselves. Such a mode of transmission would account for the rapid development of dialects in separated geographic areas and their apparent perpetuation from one generation to the next. Thus, it is also possible that man is not the only mammal in which normal vocalizations are learned from other species members.

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#### References and Notes

1. W. H. Thorpe, *Ibis* 100, 535 (1958); J. C. Bremond, in *Acoustic Behaviour of Animals*, R. G. Busnel, Ed. (Elsevier, Amsterdam, 1963), p. 709; P. Marler and W. J. Hamilton III, *Mechanisms of Animal Behavior* (Wiley, New York, 1966).
2. There is some evidence that pikas *Ochotona princeps*, pothead whales *Globicephala melana* and *G. macrorhyncha*, and squirrel mon-

- keys *Saimiri sciureus* show geographical variation in their calls [see H. E. Broadbrooks, *Amer. Midland Natur.* 73, 299 (1965); H. R. Krear, thesis, Univ. of Colorado (1965); W. E. Schevill, in *Marine Bio-Acoustics*, W. N. Tavolga, Ed. (Pergamon, Oxford, 1964), p. 311; P. Winter, *Folia Primatol.* 10, 216 (1969)]. However, taxonomic disputes need to be resolved and more data must be collected to determine whether these local variations can be most accurately described as dialects.
3. G. A. Bartholomew, *Univ. Calif. Publ. Zool.* 47, 369 (1952); B. J. Le Boeuf and R. S. Peterson, *Science* 163, 91 (1969).
4. G. A. Bartholomew and N. E. Collias, *Anim. Behav.* 10, 7 (1962).
5. In addition to the rookeries shown in Fig. 1, a few pups may be born each year on Santa Rosa Island, San Clemente Island, Isla San Martín, and Isla San Gerónimo.
6. P. Marler and M. Tamura, *Condor* 64, 368 (1962).
7. G. Thielcke, *Z. Tierpsychol.* 22, 542 (1965).
8. K. W. Radford, R. T. Orr, C. L. Hubbs, *Proc. Calif. Acad. Sci.* 31, 601 (1965). This colonization represents part of the reestablishment of this species on its former breeding range, after near extinction in the last century due to overexploitation by sealers. The present population was apparently reconstituted from a remnant herd of less than 100 individuals that inhabited Isla de Guadalupe at the turn of the century. Since then, the animals have been protected, and their population and range have been increasing. San Miguel and San Nicolas were reestablished in 1938 and 1949, respectively.
9. C. A. Repenning, personal communication.

The canine teeth of elephant seals provide a simple and reliable indication of age; the rate of deposition of calcified dentine and cementum varies seasonally, resulting in concentric layers. See R. Carrick, S. E. Csor-das, S. E. Ingham, *Commonw. Sci. Ind. Res. Organ. Wildlife Res.* 7, 161 (1962).

10. T. C. Poulter, *Annual Reports of Operations of Stanford Research Institute on Año Nuevo Island*, Menlo Park, California, 1961-66.
11. Because this male had two distinct pulse rates, he was excluded from other analyses reported in this paper.
12. Numerous marked pups born on one island land on another (as far away as 944 km) 3 to 4 months after birth. Although we have tagged only pups extensively, we have observed subadult males on Isla de Guadalupe that were tagged on San Miguel Island and vice versa. We do not yet know whether these are temporary movements or permanent relocations.
13. Studies in Año Nuevo State Reserve authorized by California Department of Parks and Recreation, W. P. Mott, Jr., Director; in Mexico by Dirección General de Pesca e Industrias Conexas, J. L. Cifuentes, Subdirector; and on the Channel Islands by the U.S. Navy Pacific Missile Range. We thank C. L. Hubbs, J. B. Stoddard, R. F. Dwyer, and D. M. Robinson for assistance in getting to the seal rookeries, L. J. Bidinlan, D. H. Ramsey, and T. A. Babb for field assistance, and T. C. Poulter, G. W. Boudreau, and L. J. Underkoffler for help in data analysis.
- \* Deceased 28 September 1969.

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## Climate and Evolutionary Rate

Stehli, Douglas, and Newell (1) present the thesis, previously advocated by Darlington (2) in a slightly different form, that evolutionary rates tend to be greater in tropical areas than in temperate ones. While this thesis may be correct, the evidence given needs examination. My competence is greatest for mammals and so I will emphasize this group.

Stehli *et al.* compare the earliest records of all extant mammalian families in central west Africa with those of northern Eurasia. There is an important bias here. The fossil record is very much poorer in the former area than in the latter, and this is generally true for comparisons between tropical and temperate regions. Therefore families which have been endemic to the present-day tropics throughout their existence will have a poorer chance of being found at a time near their origin than will families which have occurred in areas that are now temperate. The high proportion of tropical families not known earlier than the Pleistocene (Fig. 1) and the complete absence of such families in the cooler north temperate region illustrate this point. Bats, which have an unusually poor fossil record, are disproportionately numerous in the tropics. It is invalid to infer that families unknown before the Pleistocene origi-

nated relatively recently. For example, the Tupaiidae had no known fossil record at all until 1965, when a genus probably referable to that family was reported from the Middle Paleocene (3).

With the above-mentioned point of view, I have therefore analyzed the major tropical and north temperate faunas of recent mammals (4). Data on distribution are from Darlington (2), with a few modifications from standard regional checklists. Data on ages are from Romer (5) unless specifically noted otherwise. I have subjectively distinguished between families for which there is reason to believe the origin was appreciably earlier than the first record, and the remainder. I have included, in a distinguishable form, families regionally extinct after the last glaciation, because of the possibility that man contributed to their extinction (6, 7). Only the marine whales are excluded. The list of families (8) permits modification of my results by others using different criteria or data. Absence of such data and of geographic boundaries precludes detailed comparison with the results of Stehli *et al.* (1).

It is obvious from comparison of parts A to D in Fig. 1 with parts E and F that there is no tendency for tropical

families of mammals to be older than temperate families. In fact the reverse is ostensibly true, a probably fortuitous agreement with an idea of Matthew (9). Figure 2 shows the extent of this reversal when families present in both climates have been removed. Even inclusion of all doubtful ages leads to an identical mean of about  $24 \times 10^6$  years for both climates, whether or not the postglacial extinctions are considered. Other reasonable conventions can remove this reversal (10), proving its biological unimportance.

I follow Stehli *et al.* (1) and Simpson (11) in regarding the modified survivorship distributions as estimating, inversely, rates of origination of taxa. This is a form of taxonomic rate of evolution (11).

Some noise is present in the method used here in addition to the reasons given by Stehli *et al.*, because some families now endemic to one climate formerly occurred in the other and may have originated in either. It is the rate of origination in each climate that is relevant, and our knowledge of the area of origin of most families is too poor to study this rate directly. It follows that the correlation between places of origin and present distribution cannot be usefully estimated and although it is undoubtedly positive it may be much less than 1. Therefore positive results should be less suspect than negative ones.

The climate zones I use, as did Stehli *et al.*, are those which now exist and which therefore are the ones most relevant to current distributions. Earlier in the Cenozoic, however, when most mammalian families originated, the tropical and subtropical zones extended farther north to include parts of my North Eurasian and North American regions (12). This creates the further complication that effects of regional endemism and effects of climate will not coincide. With consideration of many more taxa when more evidence is available, however, this difference should itself permit a distinction between the two effects.

The pelecypod data of Stehli *et al.* also do not seem to support the thesis of greater evolutionary rates in the tropics. The individual data are not yet published and I have had to estimate from the graphs. While it is true that families of apparently Neogene origin are relatively commoner among tropical endemics than among cosmo-

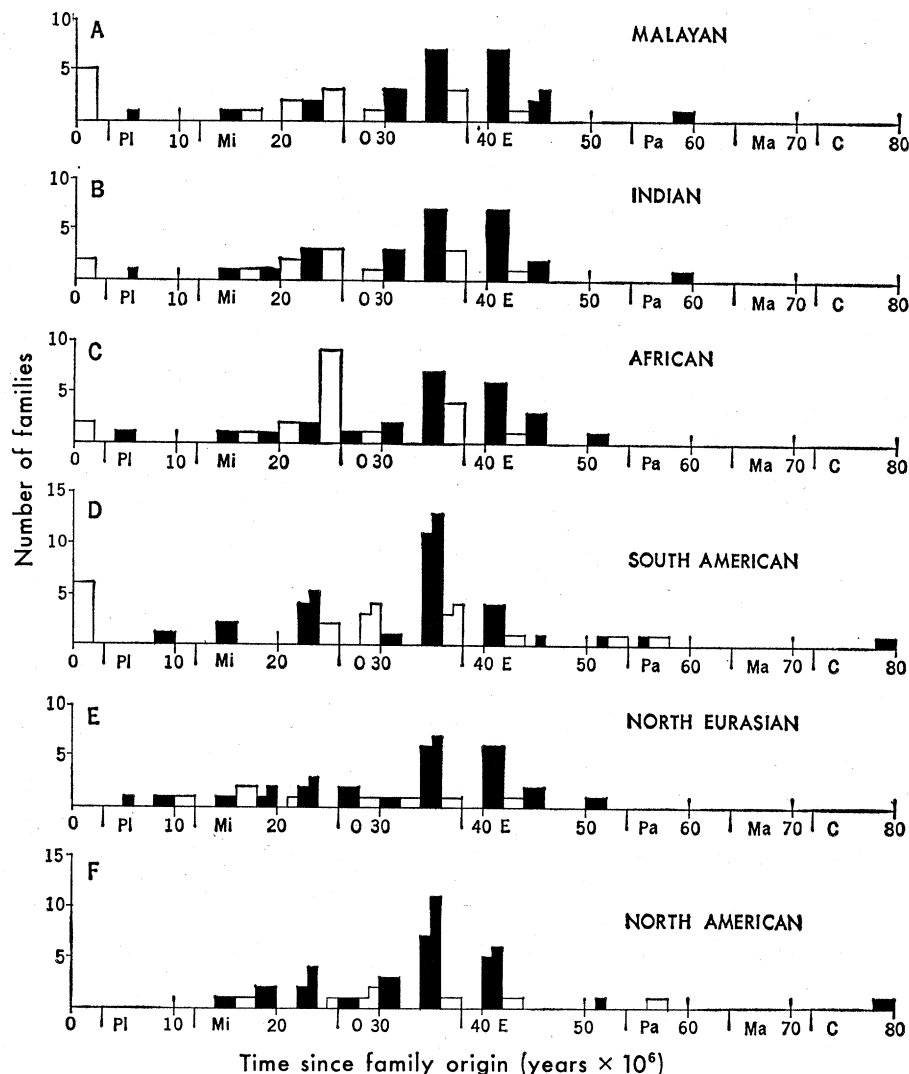


Fig. 1. Known ages of living mammal families in main temperate and tropical faunas (4, 26). Solid bars are ages believed nearly correct; open bars are probably seriously underestimated. Half-width bars are families regionally extinct in postglacial time. Each epoch or age except the Pliocene is divided into three parts; the Pliocene has two. Each white bar is to the right of its solid bar. Epochs and ages, from left to right: Pleistocene (unlabeled and including Recent), Pliocene, Miocene, Oligocene, Eocene, Paleocene, Maestrichtian, Campanian. One open unit from the Middle Miocene should be transferred to the Pleistocene in (A), (B), and (C).

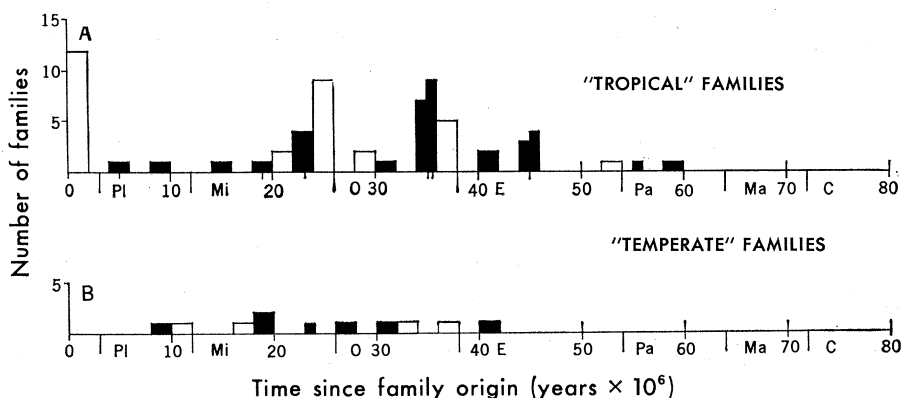


Fig. 2. Known ages of living mammal families occurring in either temperature or tropical regions of Fig. 1, but not in both. Symbols as in Fig. 1. The lines below certain "tropical" bars are the number of families to be deleted if late Pleistocene extinctions are considered; these families also occurred in the temperate areas then. One open unit from the Middle Miocene should be transferred to the Pleistocene in (A).

politans, the mean age is the same ( $129 \times 10^6$  compared with  $133 \times 10^6$ , respectively) (13). However, if one uses mean known ages of families for each of the pelecypod stations (14), the regression of age (millions of years) on unsigned latitude has a slope of 0.39, which differs from 0 with a probability of more than 0.99. The source of the remaining data, for Cretaceous planktonic foraminiferans, is not given, although the graphs as presented do support the thesis.

The ratio used to show that Permian brachiopods decrease in diversity poleward, does so merely analytically. The ratio is of Tethyan (tropical) endemics to cosmopolitans. Obviously the proportion of tropical endemics is greatest in tropical regions, since the class is defined by its distribution. It is merely surprising that some "Tethyan endemics" occur more than 70°N. The problem of variable sample size, which the ratio was meant to offset, is best controlled directly even if new samples must be collected.

Explanation and application of climatic differences in evolutionary rates must depend on the existence of such differences and these have not yet been adequately shown. Stehli (10) has unpublished results for recent foraminiferans that seem best interpretable by this hypothesis, however.

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#### References and Notes

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2. P. J. Darlington, Jr., *Zoogeography* (Wiley, New York, 1957).
3. L. Van Valen, *Evolution* **19**, 137 (1955).
4. I exclude Australia and New Guinea because of their isolation and poor known fossil record, and the south temperate faunas of South America and Africa because of their dominance by tropical families and because of the major climatic differences from the north temperate region [P. J. Darlington, Jr., *Biogeography of the Southern End of the World* (Harvard Univ. Press, Cambridge, Massachusetts, 1965)].
5. A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, ed. 3, 1966). This is the latest mainly reliable source and includes a few data even now unpublished by their own authors.
6. P. S. Martin and H. E. Wright, Jr., Eds. *Pleistocene Extinctions: The Search for a Cause* (Yale Univ. Press, New Haven, 1957).
7. Distributional data for regionally extinct families are from primary sources or recent reviews by regional or systematic specialists. I may have overlooked a few records, especially for tropical Asia and Africa.
8. The families in parentheses are those I regard as probably considerably older than their first records. The numbers i-vi refer to faunas: (i) Malayan, (ii) Indian, (iii) African, (iv) South American, (v) North Eurasian, (vi) North American. When preceded by "p" these are postglacial records of regionally extinct families. The references below document earliest records other than those in Romer

- (5). The earliest ages I use are coded as follows: A, Pleistocene (including Recent); B, late Pliocene; C, early Pliocene; D, late Miocene; E, Middle Miocene; F, early Miocene; G, late Oligocene; H, Middle Oligocene; J, early Oligocene; K, late Eocene; L, Middle Eocene; N, late Paleocene; P, Middle Paleocene; Q, early Campanian. Didelphidae (iv, vi) Q (15), (Caenolestidae) (iv) M, Tupaiidae (i, ii) P (3), (Macroscelididae) (iii) J, (Galeopithecidae) (i) A, Erinaceidae (i-iii, v) K, Talpidae (i, ii, v, vi) K, Soricidae (i-vi) K (16), Tenrecidae (iii) L (17), (Chrysochloridae) (iii) F, (Pteropodidae) (i-iii) A (18), (Rhinopomatidae) (i-iii) A, (Emballonuridae) (i-iv) J, (Noctilionidae) (iv) A, (Nycteridae) (i-iii) A, (Megadermatidae) (i-iii) J, (Rhynchophidae) (i-iii) K, (Hipposideridae) (i-iii) L, (Phyllostomatidae) (iv) J, (Desmodontidae) (iv) A, (Natalidae) (iv) A, (Furipteridae) (iv) A, (Thryopteridae) (iv) A, (Vespertilionidae) (i-vi) J, (Molossidae) (i-vi) G, (Loriidae) (i-iii) F, (Tarsiidae) (i) A (19), (Callithricidae) (iv) G, (Cebidae) (iv) G, (Cercopithecidae) (i-iii) F, (Pongidae) (i-iii) J, (Hominae) (i-vi) D, (Aplodontidae) (vi) K, (Sciuridae) (i-vi) J, (Echimyidae) (iv) J, (Chinchillidae) (iv) J, (Dasyproctidae) (iv) J, (Dinomysidae) (iv) F, (Caviidae) (iv) D, (Hydrochoeridae) (iv) C, (Erethizontidae) (iv, vi) J, (Cricetidae) (ii-vi) J, (Muridae) (i-iii, v) D, (Dipodidae) (iii, v) G, (Zapodidae) (v, vi) G, (Geomyidae) (vi) H, (Heteromyidae) (iv, vi) J, (Gliridae) (iii, v) L (20), (Placanthomyidae) (i, ii) A, (Seleviniidae) (v) C, (Spalacidae) (v) C, (Rhizomyidae) (iii) H, (Castoridae) (v, vi) J, (Thryonomidae) (iii) A (21), (Bathyergidae) (iii) F (22), (Hystricidae) (i-iii, p-v) E, (Anomaluridae) (iii) F (22), (Pedetidae) (iii) F, (Dasyrodidae) (v, vi) N (23), (Glyptodontidae) (p-iv) L, (Megalonychiidae) (p-iv, p-vi) F (24), (Megatheriidae) (p-iv, p-vi) G, (Bradypodidae) (iv) A, (Mylodontidae) (p-iv, p-vi) J, (Myrmecophagidae) (iv) F, (Manidae) (i-iii) J, (Ochtonidae) (v, vi) H, (Leporidae) (i-vi) K, (Canidae) (i-vi) K, (Ursidae) (i, ii, iv-vi) H, (Otariidae) (iv-vi) F, (Odobenidae) (v, vi) D, (Procyonidae) (iv, vi) J, (Mustelidae) (i-vi) J, (Phocidae) (v, vi) E, (Viverridae) (i-iii) K, (Hyaenidae) (ii, iii, p-v) E, (Felidae) (i-vi) K, (Orycteropodidae) (iii) F, (Platanistidae) (ii, iv) F, (Procaviidae) (iii) J, (Gomphotheriidae) (p-iv, p-vi) J, (Mastodontidae) (p-vi) F, (Elephantidae) (i-iii, p-v, p-vi) F, (Dugongidae) (i, ii, v) L, (Trichechidae) (iii, iv) F, (Macrauchenidae) (iv) N, (Toxodontidae) (p-iv) J, (Equidae) (iii, p-iv, v, p-vi) M, (Tapiridae) (i, iv, p-vi) J, (Rhinocerotidae) (i-iii, p-v) J (25), (Suidae) (i-iii, v) J, (Tayassuidae) (iv, p-vi) J, (Anthracotheriidae) (p-i) L, (Hippopotamidae) (p-i, p-ii, iii, p-v) B, (Camelidae) (iv, p-vi) K, (Tragulidae) (i-iii) F, (Giraffidae) (iii) F, (Cervidae) (i, ii, iv-vi) F, (Antilocapridae) (vi) E, (Bovidae) (i-iii, v, vi) H.
9. W. D. Matthew, *Ann. N.Y. Acad. Sci.* **24**, 171 (1915).
10. F. G. Stehli, personal communication.
11. G. G. Simpson, *Major Features of Evolution* (Columbia Univ. Press, New York, 1953).
12. M. Schwarzbach, *Climates of the Past* (Van Nostrand, London, 1963).
13. My total percentage for the cosmopolitans is only 91, which suggests an inaccuracy in the graph. Any real effect may be related to better sampling of cosmopolitans, as is true for temperate mammals.
14. Data given by F. G. Stehli, personal communication, as mean ages.
15. R. C. Fox, *Nature* **220**, 1046 (1968).
16. P. Rabinson, C. C. Black, M. R. Dawson, *Science* **145**, 809 (1964).
17. L. Van Valen, *Bull. Amer. Mus. Nat. Hist.* **135**, 217 (1967).
18. I provisionally exclude *Archaeopteropus* from the Pteropodidae. Like *Icaronycteris*, it has high-cusped teeth and an ungual phalanx on the second digit of the manus, and it may be referred to the Microchiroptera at least pending better knowledge of its shoulder. However, body size is large and the talonid of a cheek tooth is small. The Miocene record of *Roussettus* refers to the megadermatid microchiropteran *Miomegaderma* [C. Gaillard, *Bull. Soc. Linn. Lyon* **7**, 110 (1928)]; the earliest known record of the Pteropodidae is therefore Pleistocene.
19. There are no known fossil tarsoids unless the Microchoerinae are included.
20. L. Thaer, *Mem. Mus. Nat. Hist. Nat. (Paris) N.S. Ser. C* **17**, 1 (1966).
21. A. E. Wood, *Bull. Peabody Mus. Nat. Hist. Yale Univ.* **28**, 23 (1968).

22. R. Lavocat, *Notes Mem. Serv. Geol. Maroc* **155**, 1 (1951).
23. G. G. Simpson, *Bull. Amer. Mus. Nat. Hist.* **91**, 1 (1948).
24. S. E. Hirschfeld and S. D. Webb, *Bull. Fla. State Mus.* **12**, 213 (1958).
25. L. B. Radinsky, *Evolution* **23**, 308 (1959).
26. The regions are bounded as follows. Malayan: Asia south of China and east of Burma, plus Sumatra, Java, Borneo, and the Philippines; Indian: India, Pakistan, and Nepal; African: the region between the Rift Valley, the Atlantic, 10°S, and the Sahara; South American: the region north of 10°S; North Eurasian: the region north of 45°N; and North American: the region north of the mouth of the Ohio River.
27. Partly supported by a Research Career Development Award from NIH and by NSF grant GB-11741. I thank F. G. Stehli for helpful discussions.

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## Enzyme Nomenclature:

### New Edition Planned

The Joint IUPAC-IUB Commission on Biochemical Nomenclature (CBN) decided in 1968 to include enzyme nomenclature within its field of work. After considering the report *Enzyme Nomenclature: Recommendations (1964) of the International Union of Biochemistry on the nomenclature and classification of enzymes, together with their units and the symbols of enzyme kinetics* (Elsevier, New York, 1965), CBN decided, at its 1969 meeting, that the time was appropriate for a revision and an extension of this report. It has therefore set up a committee which has been asked to work toward a revision of *Enzyme Nomenclature*, including the addition of newly described enzymes, by 1971. The convener of the committee is Professor E. C. Webb, Department of Biochemistry, The University of Queensland, St. Lucia, Brisbane, 4067 Australia. It would be helpful to the committee if all biochemists who have suggestions concerning the addition of enzymes that are omitted from the existing report, concerning errors in the existing report, or concerning improvements in the existing names would send them directly to Professor E. C. Webb as soon as possible and preferably before 31 March 1970.

O. HOFFMANN-OSTENHOF  
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Commission on Biochemical  
Nomenclature

#### Note

1. Further information can be obtained from Dr. Waldo E. Cohn, Biology Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee. Dr. Cohn is secretary of CBN and director of the NAS-NRC Office of Biochemical Nomenclature.

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