cells tested, decreased external pH produced hyperpolarization, as would be predicted from the increased chloride conductance. In seven other cells, a^i_{Cl} was 40.7 ± 1.5 mM, with a range of 37 to 47 mM. Calculated E_{Cl} values were −53.3 ± 0.9 mv and ranged from −56 to −49 mv. For this group E_m was − 58 ± 0.8 mv, and, in two cells, decreased external pH evoked depolarization. This was also predictable from the increased chloride conductance and the relative values of E_{Cl} and E_m.

A somewhat parallel situation exists in the D (depolarizing) or H (hyperpolarizing) responses to acetylcholine shown by neurons of *Aplysia depilans* or *Helix pomatia*. In both species Cl conductance is increased, and the directional change of E_m is determined by E_{Cl} (*16*). In D cells of *Helix aspera*, $(Cl)_i$ was 27.5 mM, and in H cells it was 8.7 mM (*17*).

The reason for the two different levels of a^i_{Cl} is unknown. The giant cells showed hyperpolarizing responses (low a^i_{Cl}) throughout the year, whereas depolarizing responses (high a^i_{Cl}) were registered mainly in February and September. Strumwasser *et al.* (*18*) have reported a similar seasonal rhythm in the neural extract induction of behavioral egg-laying in *Aplysia*.

These experiments demonstrate that the effect of CO_2 depends upon the attendant fall in extracellular pH and not upon molecular CO_2 per se, decreased intracellular pH, or changes in bicarbonate ion concentration. Thus the addition of CO_2 at constant extracellular pH to the perfusate, a procedure which adds molecular CO_2 and bicarbonate ion and reduces intracellular pH, was without effect, whereas the addition of hydrogen ion in the form of a nonvolatile acid evoked the same effect as CO_2 and an equivalent fall in pH.

The increased chloride conductance elicited by a fall in pH has been reported (*19*). Such results are consistent with the classical idea of an amphoteric membrane whose selective permeability is due to the presence of fixed charges which allow passage of counter-ions and exclude co-ions. The dissociation of weakly ionizable groups will be altered by changes in external hydrogen ion, and this should result in a change of ionic permeabilities. At pH less than 7.5, the dissociation constants of the fixed charge groups are such that positive groups predominate and anion conductance increases. At higher pH, negative groups supervene and the passage of cations is facilitated.

The giant cells fell into two groups with respect to intracellular chloride activity. Those with low activities had $E_{Cl} > E_m$ and were hyperpolarized by CO_2; those with high activities had $E_{Cl} < E_m$ and were depolarized by CO_2. We propose, therefore, that the hyperpolarizing effect of CO_2 on cortical neurons and on phrenic and lumbar motoneurons, and the depolarizing effect on arterial chemoreceptors and respiratory center neurons, as well as the differences between several types of *Aplysia* neurons, can be explained by the same mechanism that produced hyperpolarization in some giant cells and depolarization in others. Thus, CO_2 causes a fall in extracellular pH which increases chloride conductance. If E_{Cl} for a given cell is greater than E_m, hyperpolarization ensues; if E_{Cl} is less than E_m, the cell is depolarized and an increased rate of discharge may follow.

J. L. WALKER, JR.
A. M. BROWN

Departments of Physiology and Medicine, University of Utah Medical Center, Salt Lake City 84112

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Line and Grade in the Extinct Medius Species Group of Sigmodon

Abstract. *Remains of* Sigmodon minor *and* Sigmodon medius, *extinct cotton rats comprising the* medius *species group, have been recovered from both Kansas and Arizona.* Sigmodon minor *evolved from* Sigmodon medius, *and the available evidence suggests that Kansas populations of* Sigmodon minor *were derived from Kansas populations of* Sigmodon medius, *while Arizona populations of* Sigmodon minor *were derived from Arizona populations of* Sigmodon medius. *This multiple origin of a single mammalian species is similar to the origin proposed by Carleton Coon for the races (subspecies) of* Homo sapiens.

Some concern has developed (*1*) over the somewhat unorthodox theory of the origin of human races presented by Coon in his book *The Origin of Races* (*2*). This theory was explained by Coon and crystallized further by Van Valen (*3*). Coon suggested a separate origin for each of five basic racial (subspecific) stocks of *Homo sapiens* (*sapiens* grade) from the same number of stocks of *Homo erectus* (*erectus* grade) in five separate world areas. He further suggested that evolution from the *erectus* grade to the *sapiens* grade need not have occurred simultaneously within all the evolving stocks.

Van Valen considered the above mechanism ". . . eminently plausible genetically" (*3*), but Montagu (*1*) considered it genetically implausible. Neither presented any evidence for their respective positions, which occasioned Montagu's pertinent query (*1*), "Where in the whole of animated nature is there

			KANSAS	ARIZONA
PLEISTOCENE	Yarmouth	Irvingtonian	Borchers–*Sigmodon minor*	Curtis Ranch–*S. minor*
	Kansan		Cudahy	
	Aftonian	Late Blancan	Sanders–*S. medius* Deer Park	Tusker–*S. medius*
	Nebraskan		Dixon	
PLIOCENE	Early Blancan		Benders–*S.* cf. *medius* Rexroad–*S. medius* Fox Canyon Saw Rock Canyon	Benson Ranch–*S. medius*
	Hemphillian			

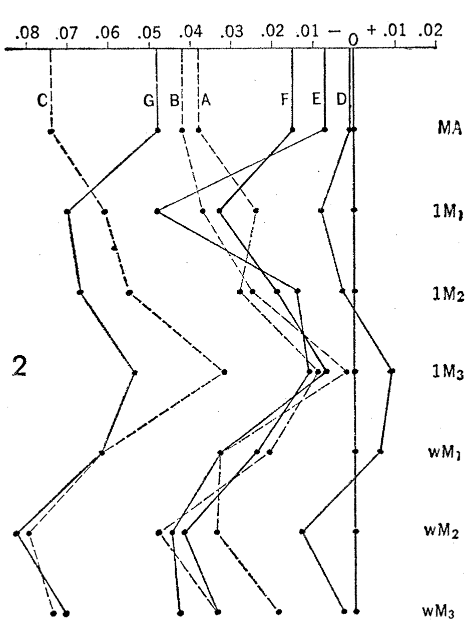
Fig. 1. Correlation of Kansas and Arizona deposits containing fossil *Sigmodon*.

a parallel to the kind of evolution that Coon suggests for *Homo sapiens*?" As Van Valen noted (*3*), "Our knowledge of the fossil history of nonhuman subspecies is almost negligible." An analogous situation, however, was recently presented by Freudenthal (*4*) for *Megacricetodon* evolution. He suggested a multiple origin of three subspecies of *Megacricetodon gregarius* from three subspecies of *M. crusafonti*. Evolution of the cotton rats, genus *Sigmodon*, may provide another situation similar to the racial evolution in *Homo sapiens* (*5*). Although the nature of the fossil record of these creatures does not allow conclusive proof of a multiple origin of a single *Sigmodon* species, the fossil material available is certainly suggestive of such a phenomenon.

Cotton rats have been recovered from stratigraphically superposed deposits of late Pliocene through middle Pleistocene age in Meade County, Kansas. These deposits have been correlated with glacial and interglacial events (*6*), and the sequence is outlined in Fig. 1. *Sigmodon medius* Gidley 1922 (= *S. intermedius* Hibbard 1938) is present in the Rexroad (*7*) and Sanders (*8*) Local Faunas. *Sigmodon minor* Gidley 1922 (= *S. hilli* Hibbard 1941) is present in the Borchers Local Fauna (*9*). *Sigmodon* cf. *medius* is also present in the Benders Local Fauna (*10*), but the sample (one individual) is inadequate for meaningful statistical treatment. *Sigmodon medius* is also found in the Benson Ranch (*11*) and Tusker Local Faunas (*12*) of Arizona. *Sigmodon minor* is present in the Curtis Ranch Local Fauna (*11*) of the same state. The stratigraphic relationships of the Arizona faunas are not now known. Another sample of fossil *Sigmodon* has been recovered from the Wendell Fox Pasture locality in the Meade Basin (*10*). This sample is compared here with the other Kansas *Sigmodon* samples, but its taxonomic position is now uncertain, as is the stratigraphic relationship of the locality to other deposits in the Meade Basin.

Sigmodon minor was clearly derived from *S. medius* (*5*). *Sigmodon medius* and *S. minor* from Kansas are con-

2



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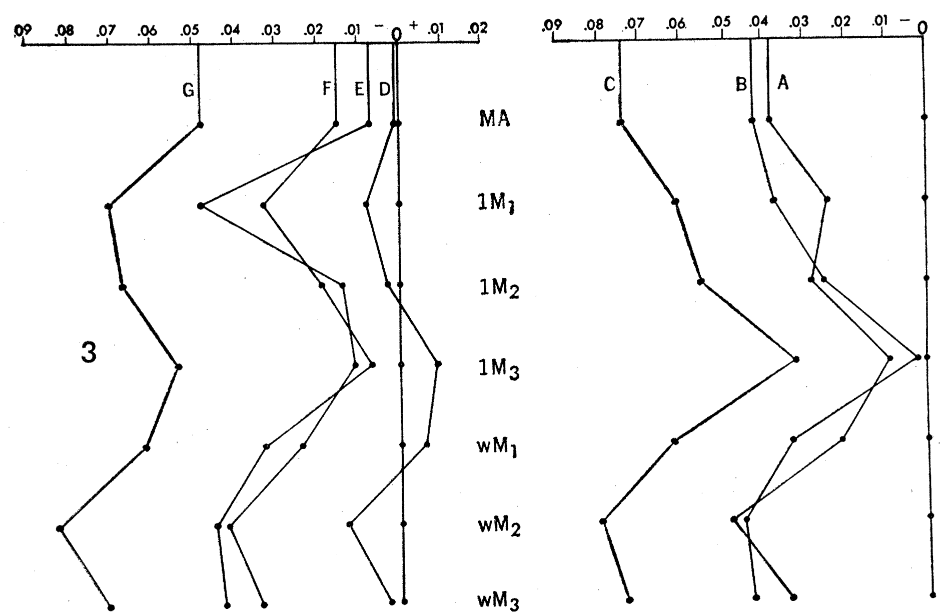

Fig. 2. Composite ratio diagram relating the Kansas and Arizona fossil *Sigmodon*. *A*, Benson Ranch *S. medius*; *B*, Tusker *S. medius*; *C*, Curtis Ranch *S. minor*; *D*, Wendell Fox Pasture *Sigmodon* sp.; *E*, Rexroad *S. medius*; *F*, Sanders *S. medius*; *G*, Borchers *S. minor*. MA, mandibular alveolar length; lM_1, lM_2, lM_3, length of the three lower molars; wM_1, wM_2, wM_3, width of the three lower molars. The standard is an extinct species of *Sigmodon* from Florida of another species group. Fig. 3. Ratio diagrams of Arizona (right) and Kansas (left) fossil *Sigmodon* plotted by state. Identifications are given in the legend of Fig. 2.

sidered subspecies K of their respective species. *Sigmodon medius* and *S. minor* from Arizona are considered subspecies A of their respective species.

Although there is not now any absolute method to allow exact correlation of the Kansas deposits with the Arizona deposits, published and unpublished records of fossil vertebrates from these localities, plus the morphological similarity of *Sigmodon medius* from Kansas to *S. medius* from Arizona, indicate a Blancan date (or dates; Benson Ranch is probably early Blancan, whereas the Tusker Local Fauna is possibly latest Blancan) for deposits in Arizona containing *S. medius*. The Curtis Ranch Local Fauna, containing *S. minor*, must be younger than Blancan, and I tentatively correlate it with the Borchers Local Fauna from Kansas, which also includes *S. minor* (Fig. 1).

The immediate questions that bear on Coon's theory of the origin of human races are these: (i) did *Sigmodon minor* evolve both in Arizona and in Kansas from populations of *S. medius* in each state, or (ii) did *S. minor* evolve in a single area (perhaps neither state) and disperse to Kansas and Arizona? If *S. minor* originated as in case i, then we must find characteristics shared in common by *S. medius* and *S. minor* in Kansas that are distinct from those in the same evolving lineage in Arizona.

Sigmodon medius from Arizona and *S. medius* from Kansas demonstrate almost the same dental pattern. The dental pattern of *S. minor* is different from that of *S. medius*, but the pattern in *S. minor* from Kansas is the same as that of *S. minor* from Arizona. The morphometric response of the lower dentition and mandible within each species from the two states is, however, characteristically different.

Measurements of the mandibles and lower dentitions are graphically portrayed (Figs. 2 and 3) by the method presented originally by Simpson (*13*). When I first made a composite graph (Fig. 2), it was apparent that three groups were represented, but the variation in certain portions of the plots, notably in the region of the mandibular alveolar (MA) length and the length of the M_1, was unusual. When the ratio diagrams for the species were plotted by state (Fig. 3), a state-specific pattern was evident. For the measurements plotted in Fig. 3, it is clear that within each state *Sigmodon minor* differs from *S. medius* solely in size; between states there is an obvious morphometric dichotomy. Subspecies K of *S. medius* differs from subspecies A of *S. medius* in having an absolutely greater average MA length. The same relationship holds true for subspecies K versus subspecies A of *S. minor*. The cause of this increased MA length in the Kansas subspecies has not yet been determined, but it must be related to thickening of mandibular bone, to increased anterior-posterior spacing of the teeth, or to both features.

These differences may be interpreted as in situ evolution (that is, in the same general area but not necessarily in the same square mile), subspecies K of *Sigmodon medius* giving rise to subspecies K of *S. minor*; subspecies A of *S. medius* giving rise to subspecies A of *S. minor*. This evolutionary pattern is analogous to the pattern proposed by Coon, in which the *medius* grade cotton rat equals the *erectus* grade hominid, the *minor* grade cotton rat equals the *sapiens* grade hominid, and subspecies A and K of both *Sigmodon* species are equatable to any two subspecies of *erectus* and their *sapiens* descendants.

Although the pattern demonstrated above fulfills the major criterion for evolution in case i, case ii evolution remains equally as probable. As shown in Fig. 1, *Sigmodon* is absent from the Cudahy Fauna of Kansas (*14*). This fauna contains an array of rootless-cheek-toothed microtine rodents, which apparently replaced *Sigmodon* in the Meade Basin during latest Kansan time. The Cudahy Fauna has also been recognized in northern Texas (*15*), and here too rootless-cheek-toothed microtines appear. When *Sigmodon* is seen again in the Meade Basin (in the Borchers Local Fauna) it is as the very microtine-like *S. minor*. It is clear then that *S. minor* evolved from *S. medius* in some geographical area other than the stratigraphic zone representing the Cudahy Local Fauna. As such, it is conceivable that *S. minor* was derived from a single population of *S. medius*, perhaps in northern Mexico, and that *S. minor* subsequently moved back to both Arizona and Kansas. Given this pattern, the resemblance between *S. minor* and *S. medius* from the same state would by definition be considered parallel evolution. It should be noted, however, that a *Sigmodon* species is absent also from the Dixon and Deer Park Local Faunas of Kansas and yet appears again unchanged from the Rexroad *S. medius* in the Sanders Local Fauna (Fig. 1). Thus it remains possible that *S. medius* was not displaced far south, or at any rate that the Kansas and Arizona *S. medius* populations retained their subspecific (racial) independence as that species in Kansas and Arizona passed the *minor* grade threshold.

ROBERT A. MARTIN
*Department of Biology,
South Dakota School of Mines
and Technology, Rapid City 57701*

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Carbon Dioxide Fixation by Mouse Embryos prior to Implantation

Abstract. *Mouse embryos in the stage of development prior to implantation were cultured in vitro in a medium that contained radioactive bicarbonate. The radioactivity was incorporated into the proteins and nucleic acids that were acid soluble. Uptake of radioactivity occurred into protein in the unfertilized ovum and was highest in all fractions in the early blastocyst stage. No incorporation was detected in the lipid fraction.*

The stages of mammalian embryos prior to implantation develop within the secretions of the oviduct and uterus. Moreover, there is evidence that these early stages are nutritionally dependent on maternal secretions (*1*). One component of secretions of the oviduct, present in considerable concentration, is bicarbonate (*2*); this substance is believed to be an essential component of culture mediums for mouse embryos (*1*). On the basis of these facts, Biggers *et al.* suggested that carbon dioxide fixation occurs during the cleavage stages