

Version 2, the base composition at each of the three positions within codons was, as in Version 1, taken to be the 5-family average. However, in Version 2, the values of  $p_1$ ,  $p_2$  and  $p_3$  were not assumed a priori but were estimated along with the  $r$ ,  $p$ , and  $T_2$  by requiring the estimated parameters to fit the  $N_k$  as well as the  $M_k$ . Version 3 differed from Version 2 only in that the base compositions were not the 5-family averages, but the mean composition of rabbit alpha and beta hemoglobin mRNA at loci that have been observed to vary. The values of  $M_k$  and  $N_k$  calculated from REH theory in Versions 2 and 3 are in agreement (Table 22, bottom) with the experimentally determined values (Table 22, top). Nevertheless, the evolutionary parameters estimated (Table 22, middle) from these two versions differ from one another, and the difference arises from the different base compositions and nucleotide transition probabilities used in the two versions. The parameters estimated from Version 3 are likely the more accurate because the base compositions used in that version more closely approximate the conditions prevailing

during the divergence of rabbit alpha and beta hemoglobin. This demonstrates that for accurate evolutionary estimates each gene family must be considered separately. Tables of values averaged over several families, though desirable from the viewpoint of simplicity, can only lead to erroneous estimates.

Finally, we note the generality of these results. Using Version 3 of REH theory, we have calculated the evolutionary parameters of Table 22 for the VP1 and VP2 capsid protein genes for the three divergences between BKV, SV40 and polyoma tumor viruses; for the three divergences between human, mouse and rabbit beta hemoglobin mRNAs and genes; and for the yeast iso-1- and iso-2-cytochrome *c* genes. For each of these ten divergences REH theory gave a complete explanation of the  $M_k$  and  $N_k$ . These results were reported in Vancouver at the Second International Congress of Systematic and Evolutionary Biology in July (1980). The details for these calculations are in press (in: *Macromolecular Sequences in Systematics and Evolutionary Biology*, M Goodman, ed, Plenum Press, New York).

## Erratum

On page 214, the first three sentences of Section 2.3 should have read:

*2.3 Probability of Back Mutation.* At a given nucleotide position  $m$  (= 1 to 3) within the codon, the probability

$$m_{BB}^{(X)}$$

that a base initially B(= A,C,G or U) at that locus will after X-one step base replacements remain B is (Holmquist 1976b)

$$m_{ii}^{(X)} = \sum_{i,j=1}^4 m_{ij} \cdot m_{sj}^X \quad (1)$$

The index  $i$  identifies the base (A, C, G, or U) and the index  $j$  identifies the term (at most four if all the coefficients  $\rho_{ij}$  are nonzero and if all the arguments  $s_j$  are distinct). The coefficients and arguments of Eq. 1 are straightforwardly calculated (see Eq. 10 and 14 in Holmquist 1976b) from the nucleotide transition probabilities alone.

On page 215 the last paragraph of Section 2.3 should be deleted.

On page 219 the first sentence following Equation (9) should have read:

In Eq. 8,  $p^2$  is the probability of a replacement occurring at the second position within the codon;  $2p'_{GA}$  the conditional probability that is the second position within a codon is occupied by G, and it changes, it will change to A (rather than to C or T(U); and  $B_{im}$  is the mole fraction of the base  $i$  ( $i = 1, 2, 3, \text{ or } 4: 1 = A, 2 = C, 3 = G, 4 = T(U)$ ) at the  $m^{\text{th}}$  nucleotide position within the codon.

On page 225 the last sentence of second footnote in Table 6 should have read:

The relative frequencies with which the first, second and third position within the codon fixed mutations were taken to be 0.12, 0.12 and 0.76, respectively.

On page 239 the title of Table 13a should have read:

**Table 13a.**  $\beta$  Hemoglobin Genes or mRNA ( $p_1:p_2:p_3::0.12:0.12:0.76$ )

On page 240 the title of Table 14a should have read:

**Table 14a.** Myoglobin Genes or mRNA ( $p_1:p_2:p_3::0.12:0.12:0.76$ )

On page 257 The sentence beginning in line 15 should have read:

Nevertheless, the evolutionary parameters  $\mu_2$ ,  $T_2$  and  $REH_2$ , if estimated from the equations of REH theory are reasonably concordant whether the primary data are the amino acid sequences or the mRNAs.

On page 260: The "Note Added in Proof" referred to in the third line following Equation 29 is the note of the above corrigendum.

The last sentence of the second paragraph should have read:

This result indicates that it is the mechanism (a constrained stochastic process) of molecular divergence, and not the details (the exact mole fraction of A, for example) that dominates accurate estimates of genetic distance.

On page 262 the first sentence of the second paragraph should have read:

Michael Coates and Simon Stone, in the Departments of Zoology and Botany of the University of Adelaide have recently studied the effect of a limited set of functionally equivalent residues on estimates of the total mutations fixed (*J. Mol. Evol.*, in press) in isolation from some of the other nonrandom factors of the present paper.