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James S. Farris; Mari Kallersjo; Arnold G. Kluge; Carol Bult

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APPENDIX

The following 10 characters were used for reanalysis of great ape/human relationships.

1. Pericentric inversion of chromosome 2p, found in *Homo, Pan troglodytes,* and *Pan paniscus,* ordered.
2. Pericentric inversion of chromosome 4 in *Pan troglodytes* and *Pan paniscus* and a linked pericentric inversion in *Gorilla,* unordered.
3. Pericentric inversion of chromosome 5 in *Pan troglodytes* and *Pan paniscus,* ordered.
4. Pericentric inversion of chromosome 7 in *Gorilla,* a subsequent paracentric inversion of chromosome 7 in *Pan troglodytes* and *Homo,* and subsequent paracentric inversion of chromosome 7 in *Pan paniscus,* ordered.
5. Pericentric inversion of chromosome 9 in *Homo* and subsequent pericentric inversion of chromosome 9 in *Pan troglodytes* and *Pan paniscus,* ordered.
6. Paracentric inversion of chromosome 10 in *Homo, Pan troglodytes,* and *Pan paniscus* and a linked pericentric inversion of chromosome 10 in *Gorilla,* unordered.
7. Pericentric inversion of chromosome 12 in *Pan troglodytes* and *Pan paniscus,* ordered.
8. Pericentric inversion of chromosome 15 in *Pan troglodytes* and *Pan paniscus,* ordered.
9. Pericentric inversion of chromosome 3 in *Homo, Pan troglodytes, Pan paniscus,* and *Gorilla,* ordered.
10. Pericentric inversion of chromosome 2p in *Homo, Pan troglodytes,* and *Gorilla* and subsequent pericentric inversion in *Pan paniscus,* ordered.

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JAMES S. FARRIS,[1,2] MARI KÄLLERSJÖ,[1] ARNOLD G. KLUGE,[3,5] AND CAROL BULT[4]

[1]*Naturhistoriska riksmuseet, Molekylärsystematiska laboratoriet, Box 50007, S-104 05, Stockholm, Sweden*
[2]*Department of Entomology, American Museum of Natural History, New York, New York 10024, USA*
[3]*Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, Michigan 48109, USA*
[4]*The Institute for Genomic Research, 932 Clopper Road, Gaithersburg, Maryland 20878, USA*

Wiens and Chippindale (1994) mentioned that the incongruence measure of Mickevich and Farris (1981) might be used in a test of heterogeneity, but they did not say how such a test could be performed. In fact, J.S.F. developed a test of this type and introduced it in his prototype arn program at the 1991 meeting of the Willi Hennig Society and later at the 1993 Nordic Phylogenetic Systematics Network meeting. C.B. presented papers using this test at the 1991 Willi Hennig Society meeting and at the Smithsonian Institution's Laboratory of Molecular Systematics in 1992 (the latter presentation included a demonstration of arn). The procedure was also

[5] E-mail: akluge@umich.edu.

described by J. M. Carpenter at the 1991 and 1994 meetings of the Entomological Society of America, by A. Tehler at the Fifth International Mycological Congress, and by A. Bruneau at the 1994 ESF Workshop on Molecular and Classical Taxonomy. A second program, kon, differing only in output format, was demonstrated by J.S.F. and used in a workshop at the 1993 meeting of the Nordic Phylogenetic Systematics Network. K. Nixon has also included this test in his program DADA. Further, Bremer and Struwe (1992) used Farris's arn program to contrast morphological and chemical characters. Bruneau et al. (1995) performed a three-matrix congruence test with isozyme, morphological, and restriction site data. Smith and Sytsma (1994) compared morphological and nucleotide sequence data, as did Tehler (1994, 1995a, 1995b). Herein, we briefly describe the motivation of that test.

The Mickevich and Farris (1981) index determines incongruence between two data matrices **X** and **Y** from the lengths L_X and L_Y of most-parsimonious trees for each matrix and $L_{(X+Y)}$, the length of a most-parsimonious tree for the matrix obtained by combining **X** and **Y**. Only the denominator $D = L_{(X+Y)} - (L_X + L_Y)$ of the original index is needed for the test described here.

As Mickevich and Farris (1981) observed, their measure avoids a difficulty common to most other measures, which are generally based on comparing trees as such, e.g., by counting groups on a consensus tree. A group has the same influence on such counts, regardless of the strength of evidence supporting the group. This fact has also been pointed out by other authors (notably Miyamoto [1985]) and to our knowledge is not seriously controversial. The main problem, then, is to arrive at an appropriate null distribution for the measure.

Any randomization method would yield a distribution that is "null" in some sense, but not all of these would be equally suitable. Data matrices might, for example, be randomly permuted, as in Archie's (1989) test (cf. Källersjö et al., 1992). But that procedure models complete independence of characters. Any kind of structure in data—not just incongruence between matrices in particular—might cause significant departure from that model. If that method were used, interpreting significance as indicative of incongruence could thus easily be misleading.

A more useful distribution is obtained by regarding the observed matrices of M and N characters (sites, etc.) as having been sampled at random from a single statistical population. On that premise, any division of the total $M + N$ characters into two matrices of the same two sizes should be equally likely. The null distribution of the incongruence measure D would be then determined by averaging over possible partitions of the $M + N$ characters into suites of sizes M and N.

Of course those partitions may be numerous, even for matrices of moderate size. Fortunately, to obtain a significance test it is only necessary to compute D for a relatively small number of partitions, these being chosen at random from among those possible.

To perform the test, the value of D is found for the observed data matrices and then for a number W of randomly selected partitions of the characters into matrices of the two original sizes. If a number S of the D values from randomly selected partitions is smaller than the observed D, then the Type I error rate (tail probability) of rejecting the null hypothesis is $1 - S/(W + 1)$. If $W = 99$ and $S = 95$, for example, this indicates significance at the 5% level.

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Ancestral Areas Revisited

FREDRIK RONQUIST

Department of Entomology, Swedish Museum of Natural History, Box 50007, S-104 05 Stockholm, Sweden[1]

Bremer (1992) recently proposed a method (ancestral area analysis) for reconstructing the ancestral distribution of a group of organisms assuming no vicariance, only dispersal among areas. I have argued (Ronquist, 1994) that ancestral area analysis is based on unreasonable process assumptions and that standard parsimony optimization allowing reversible change (Fitch optimization) is a more appropriate technique for reconstructing ancestral distribution areas under the constraint of no vicariance. Here, I address some of the points raised by Bremer (1995) in his reply to my criticisms.

PROCESS ASSUMPTIONS

Bremer (1995) did not like my justification of Fitch optimization by reference to underlying processes. In his ancestral area analysis, "nothing is assumed about process" (Bremer, 1992:438). Clearly, unwarranted assumptions should be avoided, but the assumption argument is a red herring. Any method of evolutionary inference can be described without reference to processes; Fitch optimization assumes no more about processes than does ancestral area analysis. The salient point is that the success of a method of evolutionary inference is linked to the properties of the process being studied. For instance, the relative success of tree-building methods is related to the nature of character evolution (Huelsenbeck and Hillis, 1993, and references cited therein). My argument is that ancestral area analysis, although constructed without reference to process, consistently results in correct inferences only when dispersal is irreversible. Because it is unlikely that dispersal is irreversible, ancestral area analysis is flawed.

MANY AND DEEP BRANCHES

Ancestral area analysis was proposed as "a method for establishing relative probabilities that areas were part of the ancestral area, given the information on their presence on deep and numerous branches in a cladogram" (Bremer, 1995:256). Bremer introduced the gain/loss quotient under irreversible parsimony as an index to this probability. However, the gain/loss quotient is not consistent with the stated ob-

E-mail: fredrik.ronquist@nrm.se.