

Comments on the Manhattan Stratigraphic Measure

Diego Pol and Mark A. Norell

Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024

Accepted May 20, 2001

The Manhattan stratigraphic measure was proposed as a measure of congruence between temporal information retrieved from the fossil record and a phylogenetic hypothesis. This index is based on the fit of a Sankoff character representing the stratigraphic ages of terminal taxa and is calculated in a way analogous to the consistency index. Sample cases are analyzed in which this measure is insensitive to increasing amounts of conflict between stratigraphic and topological temporal information. A simple modification of the step matrix upon which the measure is based is proposed. The modified index, MSM*, overcomes the observed problem and is based on the measurement of the number and extent of ghost lineages. © 2001 The Willi Hennig Society

INTRODUCTION

Phylogenetic interpretation of cladistic hypotheses contains some temporal information in the relative ordering of the ages of inter-nested splitting events among lineages (i.e., nodes), according to the hierarchy implied in the cladogram. Fossil taxa also possess another kind of temporal information derived from the stratigraphic record that provides an absolute age for the first recognized appearance of a taxon. These two independent sources of temporal information on the

evolution of a group can be compared. Several measures that compare stratigraphic fit with cladistic topology have been proposed (Norell and Novacek, 1992; Huelsenbeck, 1994; Benton and Hitchin, 1996), but as noted before (Huelsenbeck, 1994; Siddall, 1996, 1998) all have inconsistencies and biases.

Recently, a new measure, the Manhattan stratigraphic measure (MSM), was proposed to circumvent some of the problems inherent in previous proposals. It is measurable across entire trees irrespective of shape or balance and is sensitive to the magnitude of time involved (Siddall, 1998).

However, we show here that MSM can be insensitive to the addition of new taxa that show increasing amounts of conflict between stratigraphy and phylogeny. A simple modification of the MSM and its implementation are introduced here.

THE MSM

The MSM is based on the optimization of a Sankoff character on a tree. This character is set assigning a different character state to each taxon and the costs of transformation between character states are defined in a symmetrical step matrix, based on the absolute

difference in first appearance ages between each pairwise comparison of taxa. Then, the character is optimized using Sankoff parsimony on the phylogenetic hypothesis and its length (L_o) is compared to the minimum length (L_m) that the age character can have in any phylogenetic hypothesis ($MSM = L_m/L_o$). By using first stratigraphic appearances as Sankoff character states, the MSM measures the fit of the age character in a straightforward and novel way that is analogous to the consistency index (Kluge and Farris, 1969).

Because MSM, as well as other measures, is still influenced by the number of taxa and the oldest age assignment, Siddall (1998) proposed a significance test for the MSM value. This test consists of permuting the age assignments across taxa to see how the fit (MSM) significantly differs from the fit of a random distribution of ages across all taxa.

PROBLEMS AND MODIFICATION OF MSM

A problem found in MSM occurs when several successive sister groups of equal age are bracketed by older taxa. In this case the MSM becomes insensitive to the number of stratigraphically incongruent taxa present in the group (Fig. 1). This performance is undesirable since each of these taxa implies a mismatch between the fossil record and the phylogenetic hypothesis, the so-called ghost lineages (Norell, 1992).

This kind of problem arises because the age character step matrix allows for reversal. According to the settings, the Sankoff optimization assigns the young age

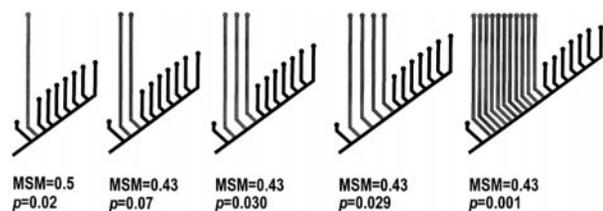


FIG. 1. Original MSM values and their significance are depicted in a case in which an increasing amount of conflict between stratigraphy and topology does not affect MSM values. When more than two late appearing basal taxa are recorded, the MSM is insensitive because the length of the age character does not increase when more stratigraphically incongruent taxa are recovered. Its significance increases as long as the conflict increases.

state observed in the late appearing basal taxon (2 Mya in Fig. 2) to each of the internal nodes leading to adjacent and equal-aged taxa. Thus, the addition of more basal and late appearing taxa does not change the age character length (i.e., would not change MSM values). In the next node leading to an older taxon (30 Mya in Fig. 2), a reversal in the age character optimization is postulated in the most parsimonious reconstruction according to the step matrix, going back from a young age to an older age (from 2 to 30 Mya) (Fig. 2). In these cases the Sankoff character is optimized according to the “first doublet rule” (Maddison *et al.*, 1984) and is not affected by the addition of more terminals with conflicting age data.

Contrary to the performance of the original MSM (Siddall, 1998), an index that measures incongruence between stratigraphic and phylogenetic temporal information should be sensitive to increasing amounts of conflict. Counterintuitively, with additional information of incongruence (i.e., additional taxa at the young age), not only does the MSM not change, it becomes more significant (Fig. 1). In order to solve this problem, a modification can be introduced in the character step matrix of the age character, prohibiting reversals (in effect making the optimization conform to Camin–Sokal parsimony rules) in the age character in the following way:

State A = 60 Mya
 State B = 30 Mya
 State C = 10 Mya
 State D = 2 Mya

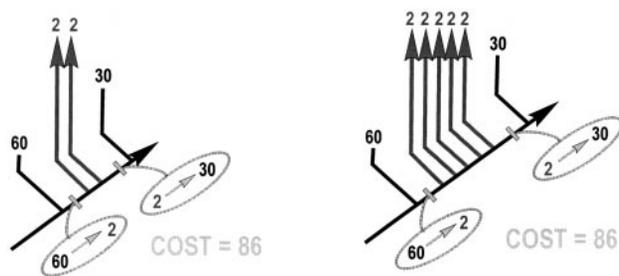


FIG. 2. Optimization of the Sankoff character based on the original formulation of the MSM. A forward transformation and a reversal transformation are postulated in the MPR of the age character in the basal nodes of the trees. As shown here, increasing the number of stratigraphically incongruent basal taxa does not affect the optimization of the Sankoff character, thus producing constant MSM values.

	A	B	C	D
A	0	30	50	58
B	∞	0	20	28
C	∞	∞	0	8
D	∞	∞	∞	0

This is consistent with Siddall's (1998) addition of artificial ROOT taxa for the most basal node, but now generalizes this principle across all internal nodes and relative to their respective phylogenetic positions. With this modified measure (MSM*), in the above-mentioned case, the internal nodes leading to the late appearing basal taxa would be reconstructed as having character state B. This implies that for each of the late appearing basal taxa, the age character length increases by 28 steps (Fig. 3). This is desirable, because the addition of each of these taxa represents an increase in the conflict between stratigraphy and topology. Consequently, the MSM*, calculated upon the modified step matrix, will decrease with increasing amounts of conflict (Fig. 3).

This modification makes the MSM* sensitive to amounts and extensions of ghost lineages, which are the basic and primary measures of mismatch between the fossil record and a phylogenetic hypothesis (Norrell, 1992).

SIGNIFICANCE

Sample cases exist where MSM is nearly invariant; however, significance increases dramatically (Fig. 1).

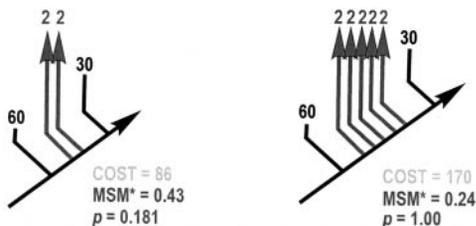


FIG. 3. MSM* values and their significance are shown for the cases in which the original MSM is insensitive to the conflict between stratigraphy and topology. The character optimization among basal nodes is modified as more late recovered basal taxa are present, increasing the length of the age character on the tree (L_m) and, thus, decreasing the MSM* values.

Misleading performance occurs because the test measures deviation of the age character length (L_o) from a random distribution of age character lengths across all taxa. According to the original step matrix parameters every single permutation that locates the age of one of the stratigraphically younger basal taxa in a more derived position will result in a longer length. This leads to the high significance levels of the MSM value as more and more young basal taxa are included.

The results of our modification of the step matrix show a consequent decrease in significance with increasing amounts of temporal conflict. This is because the age character length is based on the measurement of ghost lineages that are the signature of mismatch between the fossil record and a phylogenetic hypothesis (Fig. 3).

IMPLEMENTATION OF MSM*

The PAUP* (Swofford, 1999) command file should be modified from the original one presented by Siddall (1998) in the following way to calculate the modified MSM*:

```
#NEXUS;
begin data;
dimensions ntax = 9 nchar = 1;
format symbols = "a~z 0~9";
matrix
root a
taxA a
taxB b
taxC c
taxD d
taxE e
taxF f
taxG g
taxH h
;
end;
begin assumptions;
usertype strat = 8
a b c d e f g h
. 0 4 4 8 8 8 8
i . 4 4 8 8 8 8
i i . 0 4 4 4 4
```

```

i i i . 4 4 4 4
i i i i . 0 0 0
i i i i i . 0 0
i i i i i i . 0
i i i i i i i .
;
end;
begin paup;
log file = huels.log;
set autoclose;
ctype strat: 1;
hsearch noenforce;
pscore; [ <--Lm]
constraints mytree = [NOTE: taxon #1 =
"root"]
(1, ((9, 8), 2), (3, (4, (5, (6,
7))))));
hsearch enforce constraints = mytree;
pscore; [ <-- Lo]
outgroup 1;
permute randomize = ingroup nreps =
1000;
[ <-- P - value]
log stop;
quit;
end;

```

Additionally, non-PAUP users can easily calculate this measure using SPA (Goloboff, 1996). Two files are necessary, the DATA file and the RUN file. The DATA file contains the age character and the step matrix of age differences and can be constructed as follows:

```

xread
1 9
root 0
taxA 0
taxB 0
taxC 1
taxD 1
taxE 2
taxF 2
taxG 2
taxH 2
;
cost
[. $ 3
0 1 2
- 4 8

```

```

i - 4
i i -
(;
poly-;
tread
`tree to measure the MSM*`
(0((1(7 8))(2(3(4(5 6))))));
p/;

```

The RUN file contains the commands to calculate the MSM* of the tree included in the DATA file and is written in the NONA-PIWE macro language (Goloboff, 1993). This file must be named with the RUN extension (e.g., MSM.RUN) and executed (i.e., *run[msm]*) after the DATA file is read. The results are saved in the file MSM.OUT if it is implemented as follows:

```

set 0 maxstate[0];
set 4 cost_of[0 0 1]
loop 2 0'
set 1 cost_of[0 0 #];
if (1' > 4')
set 4 1'; end;
stop;
set 5 4'*1000
set 2 fit_of[0 0];
set 3 5'/2';
out = MSM.OUT;
mes The modified MSM is 0.3' (MSM = Lm/Lo
= 4'/2');
out/;
p/;

```

CONCLUSIONS

Despite inherent flaws in the original formulation of the MSM in certain situations, the original MSM will perform similarly to the modified measure (MSM*) in most situations. The MSM is an important new tool in examining the relationship between stratigraphic fit and phylogenetic hypotheses. In that way it is a useful tool with which to examine several kinds of paleobiologic questions and to evaluate the relative qualities of discrete fossil records. The recommendations made here solve some inconsistencies found in the performance of Siddall's proposed solution to this problem,

making the method applicable to a more universal range of temporal disparity cases in paleontology.

ACKNOWLEDGMENTS

We thank Mark Siddall, Peter Makovicky, and Ward Wheeler for discussion and for reading a draft of this paper.

REFERENCES

- Benton, M. J., and Hitchin, R. (1996). Testing the quality of the fossil record by groups and by major habitats. *Hist. Biol.* **12**, 111–157.
- Goloboff, P. A. (1993). NONA, Version 1.9. Software and documentation available from the author. San Miguel de Tucumán, Argentina.
- Goloboff, P. A. (1996). SPA—Sankoff Parsimony Analysis, Version 1.8. Software and documentation available from the author. San Miguel de Tucumán, Argentina.
- Huelsenbeck, J. (1994). Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* **20**, 470–483.
- Kluge, A., and Farris, J. S. (1969). Quantitative phyletics and the evolution of anurans. *Syst. Zool.* **18**, 1–32.
- Maddison, W. P., Donoghue, M. J., and Maddison, W. P. (1984). Out-group analysis and parsimony. *Syst. Zool.* **33**, 83–103.
- Norell, M. A. (1992). Taxic origin and temporal diversity: The effect of phylogeny. In “Extinction and Phylogeny” (M. J. Novacek and Q. D. Wheeler, Eds.), pp. 89–118. Columbia Univ. Press, New York.
- Norell, M. A., and Novacek, M. J. (1992). The fossil record and evolution: Comparing cladistics and paleontological evidence for vertebrate history. *Science* **255**, 1690–1693.
- Siddall, M. (1996). Stratigraphic consistency and the shape of things. *Syst. Biol.* **45**, 111–115.
- Siddall, M. (1998). Stratigraphic fit to phylogenies: A proposed solution. *Cladistics* **14**, 201–208.
- Swofford, D. L. (1999). PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b3a. Sinauer, Sunderland, MA.