

Comparing Trees of Birds (Tip-Dating vs a posteriori Timescaling Methods)

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```
set.seed(1)

library(paleotree)

## Loading required package: ape

library(geiger)
library(paleoTS)
library(plyr)
library(phytools)

## Loading required package: maps

##
## # ATTENTION: maps v3.0 has an updated 'world' map. #
## # Many country borders and names have changed since 1990. #
## # Type '?world' or 'news(package="maps")'. See README_v3. #

##
## Attaching package: 'maps'

## The following object is masked from 'package:plyr':
##
## ozone

library(parallel)
library(beanplot)

# important control variables

# set birth-death-sampling rates from tip-dating analyses
# median rates from SABD model in BEAST2, 30% burnin (02-05-16)
brRate = 0.0464
extRate = 0.0050112
sampRate = 0.04

# set the age of Zanabazar_junior
zanaDate=66

# burn-in
burnIn<-0.3
```

Data Used

Phylogenetic Data and Time-scaling Methods

For this comparison, I used these sets of trees:

1. The 100 trees randomly subsampled from Nick's BEAST2 run with BDSS, where "Zanabazar_junior" was given a 0 tip-age, requiring the ages to be adjusted by 66 Ma.
2. The 100 trees randomly subsampled from Nick's BEAST2 run with SABD, with dating like above.
3. The 100 trees randomly subsampled from April's MrBayes run with FBD (note from April, using UNIX command `sort -R input | head -n 100 >output`)

Trees timescaled with post-hoc methods were created by combining the first 100 trees from Graeme's set of most parsimonious trees and the stratigraphic data collected by Graeme, with first appearance times used as the 'time of observation' for tip-taxa. Note that I'm using the 'bin_' timescaling functions in paleotree, which make use of the stratigraphic uncertainty data to put uniform priors for drawing appearance dates:

4. 'Basic' time-scaled trees, i.e. minimum age dating where each clade is as old as its oldest member.
5. Minimum-branch-length trees, where the 'basic' time-scaled tree is taken and then internal branching nodes are pulled backwards in time so that every internode branch is more than or equal a set minimum branch length (MBL). Here, MBL was set to 1 Ma, following Benson et al. 2014. Although it would be easy to criticize MBL and several related post-hoc methods as being very unrealistic, in this case I've included MBL as it was a time-scaling method used by Benson et al., so that we have a similar analytical baseline.
6. cal3 time-scaled trees, where the node ages are drawn stochastically from probability distributions determined by the first appearance time of daughter lineages and the instantaneous rates of branching (λ), extinction (μ) and sampling (ψ) in the fossil record (hence 'cal3', because the probability distributions are calibrated by three rates which need to be provided as input). These node ages are drawn sequentially, moving upwards from the root, such that the root tends to be poorly constrained as it lacks any earlier 'outgroups' to constrain its estimated date of divergence. It would be ideal to think of cal3 as a second-generation post-hoc time-scaling function. However, cal3 has two additional properties, both of which are also applied in this analysis: (1) the freedom to consider taxa as potentially ancestral (leading to the occasional inclusion of a terminal zero-length branch) and (2) an algorithm for resolving soft polytomies based on the likelihood of a given branching order under the birth-death-sampling model used to calibrate node ages. For this analysis, I used the median posterior birth, death and sampling rates from the BEAST2 SABD analysis: branching rate = $0.0464 (\text{lineages} * \text{Ma})^{-1}$, extinction rate = $0.0050112 (\text{lineages} * \text{Ma})^{-1}$, and sampling rate = $0.04 (\text{lineages} * \text{Ma})^{-1}$, with a 30% burn-in. It would be unusual to do this for a typical cal3 analysis (why tip-date if you're going to run cal3...?), but this is to maximize comparability of the cal3 and BEAST2 results.

After all, don't we want to know if cal3 and tip-dating give similar answers?

```
#####  
#getting phylogenetic data, time-scaling is below post-data-cleaning  
  
#get BEAST trees  
#sample 100 in post-burn-in  
  
# BDSS
```

```

treesB2BDSS<-read.nexus("B2BDSS_treeelog.nex")
treesB2BDSS<-treesB2BDSS[-(1:(length(treesB2BDSS)*burnIn))]
sampleB2BDSS<-sort(sample(1:length(treesB2BDSS),size=100,replace=FALSE))
treesB2BDSS<-treesB2BDSS[sampleB2BDSS]

# SABD

treesB2SABD<-read.nexus("B2SABD_treeelog.nex")
treesB2SABD<-treesB2SABD[-(1:(length(treesB2SABD)*burnIn))]
sampleB2SABD<-sort(sample(1:length(treesB2SABD),size=100,replace=FALSE))
treesB2SABD<-treesB2SABD[sampleB2SABD]

class(treesB2BDSS)<-class(treesB2SABD)<-"multiPhylo"

#get MrBayes trees
#load 4 files containing 25 trees each

treesMrB<-read.nexus(file="MrBayesFBD_100treeSample_burn03.nex")

#Most parsimonious trees: randomly sample 100 (out of 540?)

treesMPT<-read.tree("TNT_most_parsimonious_trees.tre")
sampleTreesMPT<-sort(sample(1:length(treesMPT),size=100))
treesMPT<-treesMPT[sampleTreesMPT] #subsampling to 100!

#get time data
timeList_birds<-dget("timeList_sorted_asIs_theropods_DWB_11-05-14.txt")

```

Trait Data and Data-Cleaning

In this case, I went with the smaller body-size dataset I constructed by examining the overlap between our Lee and Worthy bird dataset and Benson et al.'s (2014) body-size estimates. These are estimates of (adult?) body mass in units of log₁₀ kilograms. I'm not certain where differences with Graeme's similar dataset comes from, but apparently I was a little more conservative, and I specifically tried to obtain the exact same values used by Benson et al in their analyses for the exact same species. That all said, I doubt the results here will differ at all if I was to use Graeme's dataset instead.

```

#getting trait data, cleaning all datasets

#get body size data
bodySizes1<-read.table("mass_data_for_PCMs_BensonEtal14_10-27-14.txt"
,head=TRUE,stringsAsFactors=FALSE)
bodySizes<-as.numeric(bodySizes1[,2])
bodySizes1[bodySizes1[,1]=="Confuciusornis_sanctus4",1]<-"Confuciusornis_sanctus"
names(bodySizes)<-bodySizes1[,1]
bodySizes<-bodySizes[order(names(bodySizes))]

#cleaning data

#make names in MPTs match the BEAST trees and timeList
treesMPT<-lapply(treesMPT,function(x){
  x$tip.label[x$tip.label=="43Compsognathus_longipes"]<-"Compsognathus_longipes"

```

```

x$tip.label[x$tip.label=="IGM100_1015_undescribed_dromaeosaurid" ]<-"IGM100_1015_UndesDromaeosaurid"
x$tip.label[x$tip.label=="IGM100_42_unnamed_oviraptorid"]<- "IGM100_42_UnnamedOviraptorid"
x$tip.label[x$tip.label=="IGM100_44_unnamed_troodontid"]<- "IGM100_44_unnamedtroodontid"
x$tip.label[x$tip.label=="NGMC91_unnamed_dromaeosaurid" ]<- "NGMC91_UnnamedDromaeosaurid"
return(x)
})
class(treesMPT)<-"multiPhylo"

# rename Mei_lon as Mei_long in MrB trees
attr(treesMrB,"TipLabel")[attr(treesMrB,"TipLabel")==="Mei_lon"]<-"Mei_long"

# checks

#make a list containing taxon names from above datasets
taxonNames<-cbind(
  sort(rownames(timeList_birds[[2]])),
  sort(treesMPT[[1]]$tip.label),
  sort(treesB2BDSS[[1]]$tip.label),
  sort(treesB2SABD[[1]]$tip.label),
  sort(treesMrB[[1]]$tip.label)
)

nameCheck<-apply(taxonNames,2,identical,taxonNames[,1])

if(!all(nameCheck)){
  stop("Not all taxon labels match!")
}

#check body size data (which doesn't have all taxa)

#are any missing?
missingBodySize<-is.na(match(sort(names(bodySizes)),taxonNames[,1]))

if(any(missingBodySize)){
  stop("some taxon names on body size data don't match the tree data sets")
}

```

Post data-cleaning, this particular analysis had body-size data for 47 taxa, of the total 89 taxa contained within the original Lee and Worthy dataset.

```

#Now onto Time-scaling! (post data cleaning)

#For all trees to be comparable, we will use the $root.time convention from paleotree (Bapst, 2012)

#add $root.time to BEAST and MrBayes trees
#do all have Zanz. jr at 0?

whatIsYoungest<-function(tree){
  nodeDates<-suppressMessages(dateNodes(tree=tree))
  youngest<-which(nodeDates==min(nodeDates))[1]
  youngest<-c(tree$tip.label[[youngest]],min(nodeDates))
  youngest
}

```

```

#check to see if the youngest taxon in every tree is "Zanabazar_junior" with an age of 0
youngTruth<-c("Zanabazar_junior",0)
youngTest<-c(sapply(treesB2BDSS,function(tree) identical(whatIsYoungest(tree=tree),youngTruth)),
             sapply(treesB2SABD,function(tree) identical(whatIsYoungest(tree=tree),youngTruth)),
             sapply(treesMrB,function(tree) identical(whatIsYoungest(tree=tree),youngTruth)))
if(!all(youngTest)){
  stop(paste0("Zanabazar junior is not youngest taxon on trees ",
             paste0(which(!youngTest),collapse = " ")))
}

#set root age
setRootAgeZanz<-function(tree){
  tree$root.time<-max(node.depth.edgelen(tree))+zanaDate
  return(tree)
}

treesB2BDSStime<-lapply(treesB2BDSS,setRootAgeZanz)
treesB2SABDtime<-lapply(treesB2SABD,setRootAgeZanz)
treesMrBtime<-lapply(treesMrB,setRootAgeZanz)

```

Post-Hoc Time-scaling

I'm pretty certain that the tip-dating analyses used FAD for all taxa, except Zanz. jr which was fixed at 66. This necessitates making a new timeList that fixes zanz at 66 for use with a posteriori time-scaling methods so that all methods are working with identical data

```

timeList_birds_mod<-timeList_birds
timeList_birds_mod[[1]]<-rbind(timeList_birds_mod[[1]],KTboundary=c(66,66))
timeList_birds_mod[[2]][89,]<-c(nrow(timeList_birds_mod[[1]]),nrow(timeList_birds_mod[[1]]))

#time-scale the MPTs: basic, MBL, cal3
  #MBL (1 Ma) - following Benson et al. 2014
  #for cal3 use median rate values from posterior of BEAST2 run

#basic
treesBasic<-lapply(treesMPT,function(x)
  bin_timePaleoPhy(tree=x, timeList=timeList_birds_mod, type="basic",
    ntrees=1, add.term=FALSE, plot=FALSE, randres=TRUE)
)

#MBL (1 Ma)
treesMBL<-lapply(treesMPT,function(x)
  bin_timePaleoPhy(tree=x, timeList=timeList_birds_mod, type="mbl", vartime=1,
    ntrees=1, add.term=FALSE, plot=FALSE, randres=TRUE)
)

```

Now do cal3 with ancestors, with ranges at FADs

Also do with ranges at LADs, even though that isn't comparable really

```

# FAD only
treesCal3FAD<-lapply(treesMPT,function(x)
  bin_cal3TimePaleoPhy(tree=x, timeList=timeList_birds_mod, ntrees = 1,
    brRate=brRate, extRate=extRate, sampRate=sampRate,
    nonstoch.bin = FALSE, sites = NULL, point.occure = FALSE, anc.wt = 1,
    node.mins = NULL, dateTreatment = "firstLast", FAD.only = TRUE,
    adj.obs.wt = TRUE, root.max = 200, step.size = 0.1, randres = FALSE,
    noisyDrop = TRUE, plot = FALSE)
)

# LAD only
treesCal3LAD<-lapply(treesMPT,function(x)
  bin_cal3TimePaleoPhy(tree=x, timeList=timeList_birds_mod, ntrees = 1,
    brRate=brRate, extRate=extRate, sampRate=sampRate,
    nonstoch.bin = FALSE, sites = NULL, point.occure = FALSE, anc.wt = 1,
    node.mins = NULL, dateTreatment = "firstLast", FAD.only = FALSE,
    adj.obs.wt = TRUE, root.max = 200, step.size = 0.1, randres = FALSE,
    noisyDrop = TRUE, plot = FALSE)
)

```

time-scale to LAD for anc-desc comparisons? ah, but then its not comparable!!! A fundamental problem with tip-dating: need to use FADs...

```

#reset these lists to be multiPhylo
class(treesBasic)<-class(treesMBL)<-class(treesCal3FAD)<-class(treesCal3LAD)<- "multiPhylo"
class(treesB2BDSStime)<-class(treesB2SABDtime)<-class(treesMrBtime)<- "multiPhylo"

# combine tree sets into single tree list

timeTrees<-list(basic=treesBasic,mb11=treesMBL,cal3=treesCal3FAD,
  B2BDSStime=treesB2BDSStime, B2SABDtime=treesB2SABDtime, MrB=treesMrBtime)

# check that they all have 100 trees

testLength<-sapply(timeTrees,length)==100
if(!all(testLength)){
  stop("Not all sets of trees in timeTrees are length 100")
}

```

Results : TOPOLOGY

Get published trees from prior lit and half compatibility (i.e. majority rule) trees for tip-dating
 NB posteriors are hard to plot in R, see treeviewer pdfs for posteriors

```

# get published trees

treeLeeWorthy<-read.nexus("theropod_tree_LeeWorthy2011_RAXML_02-01-16.nex")
treeXuEtAl<-read.nexus("theropod_tree_XuEtAl12011_FigS6_02-01-16.nex")

# half compatibility trees

```

```
treeB2SABD<-read.nexus("B2SABD_majrule_burn03.nex")
treeB2BDSS<-read.nexus("B2BDSS_majrule_burn03.nex")
treeMrB<-read.nexus("MrBayesFBD_majrule_burn03.nex")
```

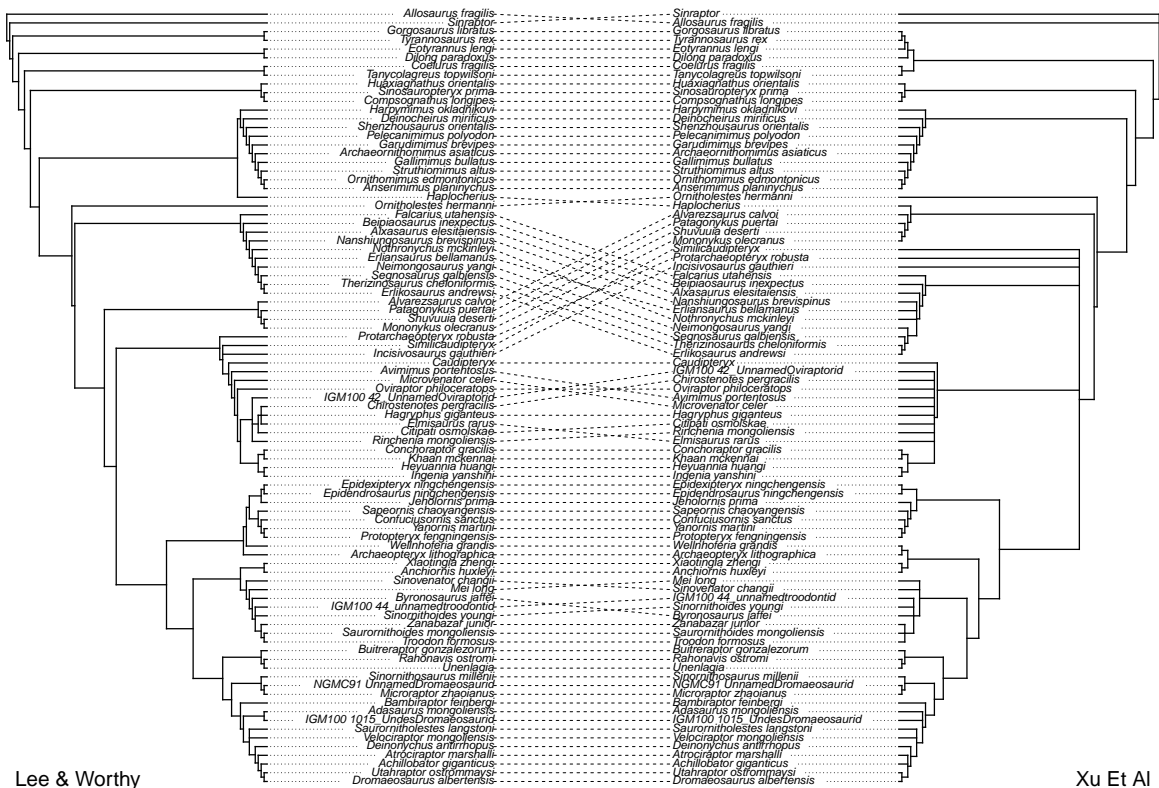
Now plot tanglegrams

```
prepTree<-function(tree){
  compute.brLen(ladderize(tree))
}

plotCophylo<-function(tree1,tree2,label1,label2){
  res<-cophylo(prepareTree(tree1),prepareTree(tree2))
  plot.cophylo(res,fsize=0.87,lwd=1.5,pts=FALSE)
  text(x=-0.5,y=0,label1,cex=1.5,pos=4)
  text(x=0.5,y=0,label2,cex=1.5, pos=2)
}

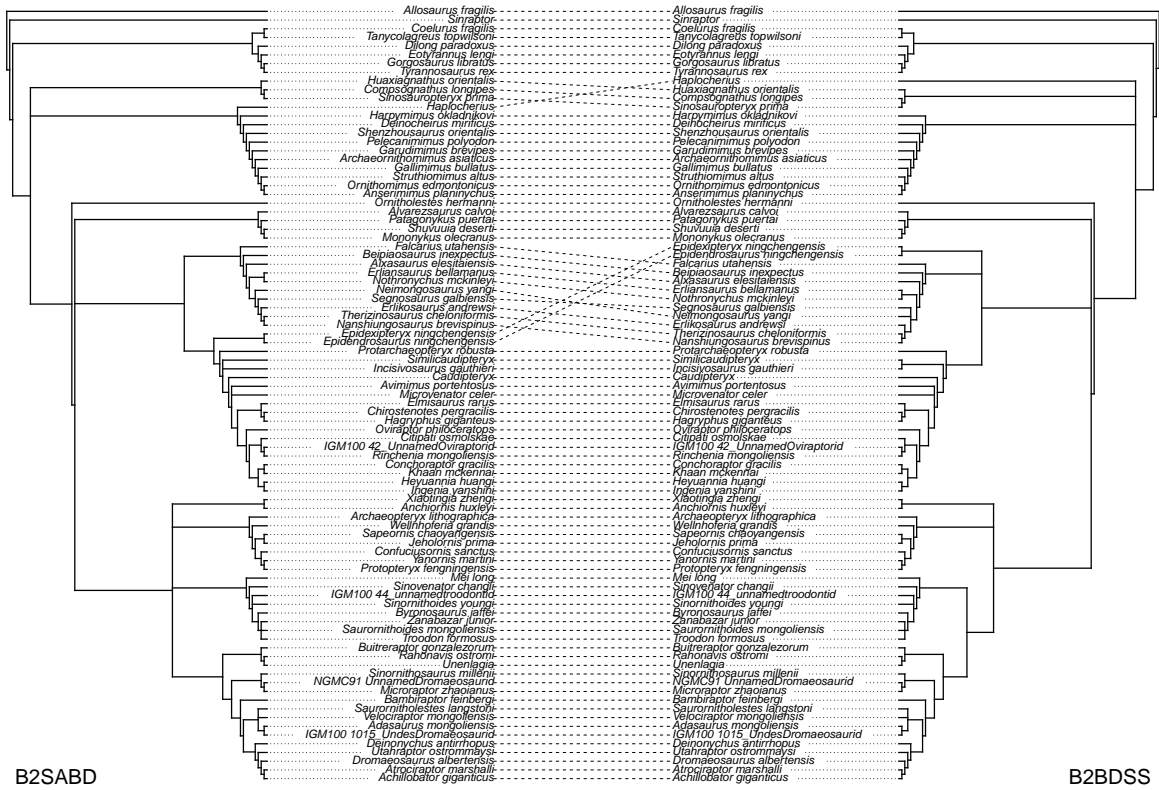
plotCophylo(treeLeeWorthy,treeXuEtAl,"Lee & Worthy","Xu Et Al")
```

```
## Rotating nodes to optimize matching...
## Done.
```



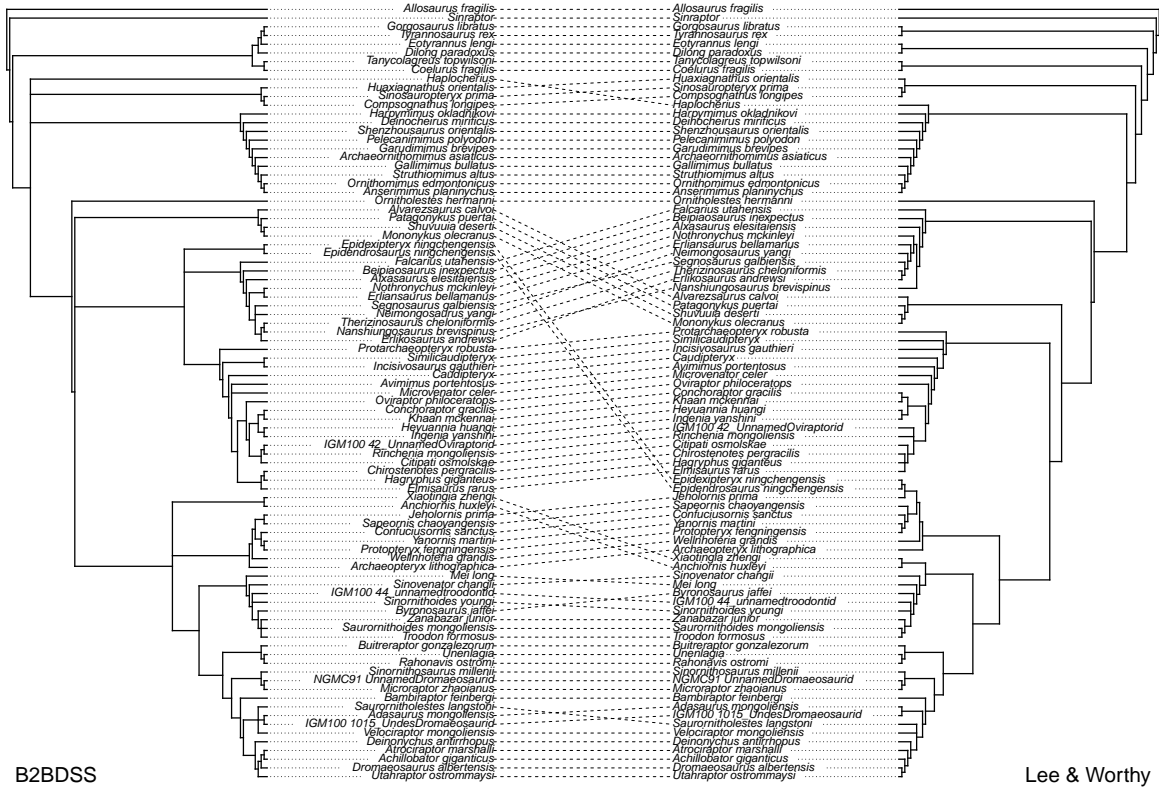
```
plotCophylo(treeB2SABD,treeB2BDSS,"B2SABD","B2BDSS")
```

```
## Rotating nodes to optimize matching...
## Done.
```



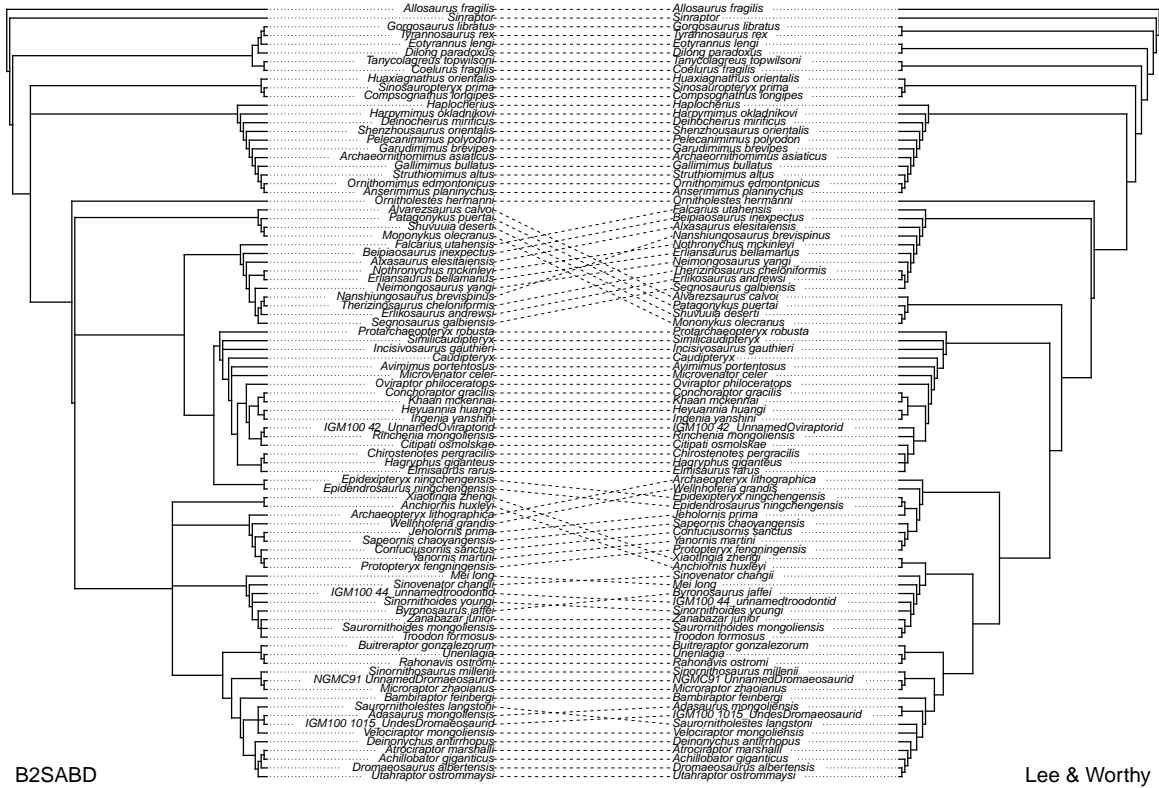
```
plotCophylo(treeB2BDSS,treeLeeWorthy,"B2BDSS","Lee & Worthy")
```

```
## Rotating nodes to optimize matching...
## Done.
```

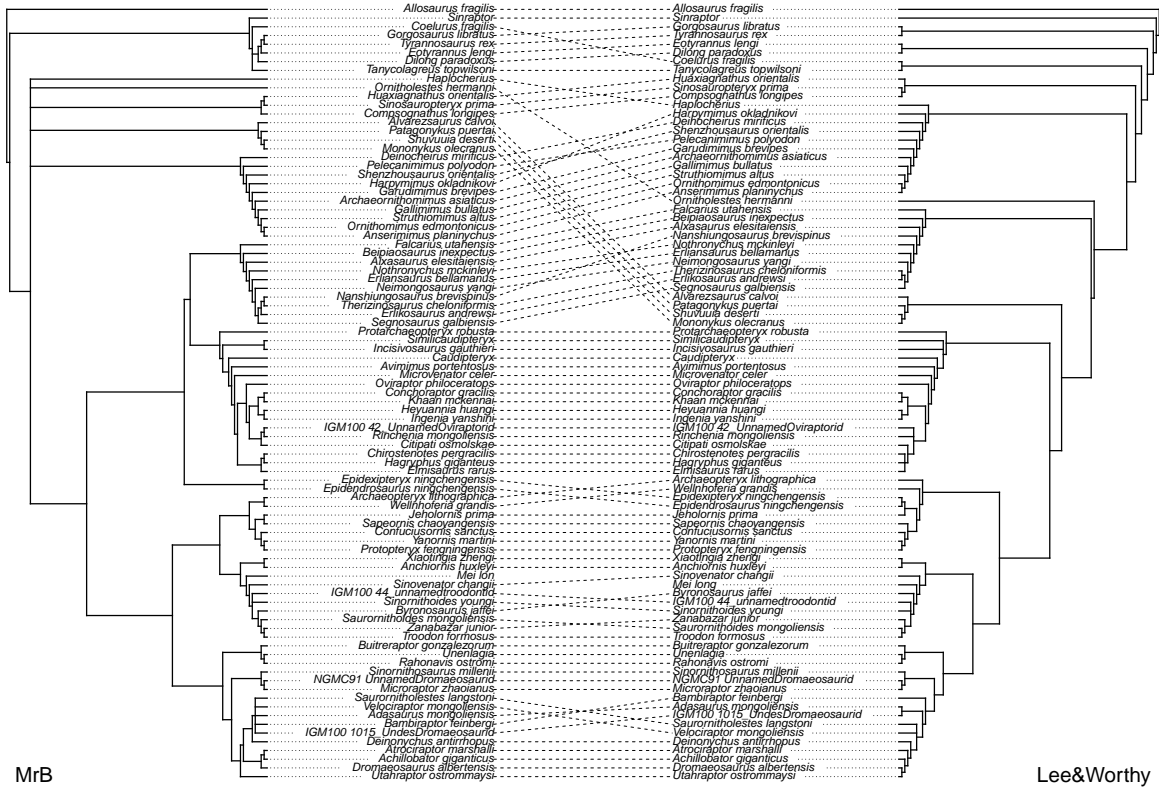
```
plotCophylo(treeB2SABD,treeLeeWorthy,"B2SABD","Lee & Worthy")
```

```
## Rotating nodes to optimize matching...
## Done.
```



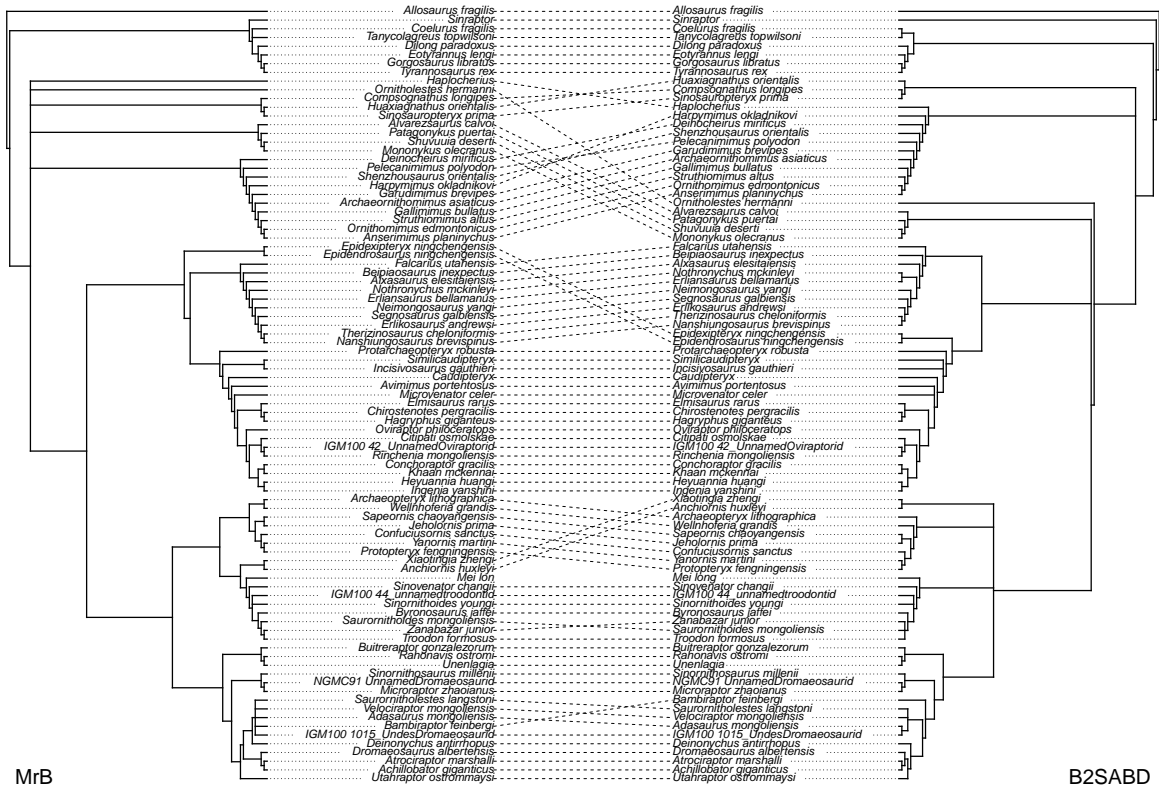
```
plotCophylo(treeMrB, treeLeeWorthy, "MrB", "Lee&Worthy")
```

```
## Rotating nodes to optimize matching...
## Done.
```



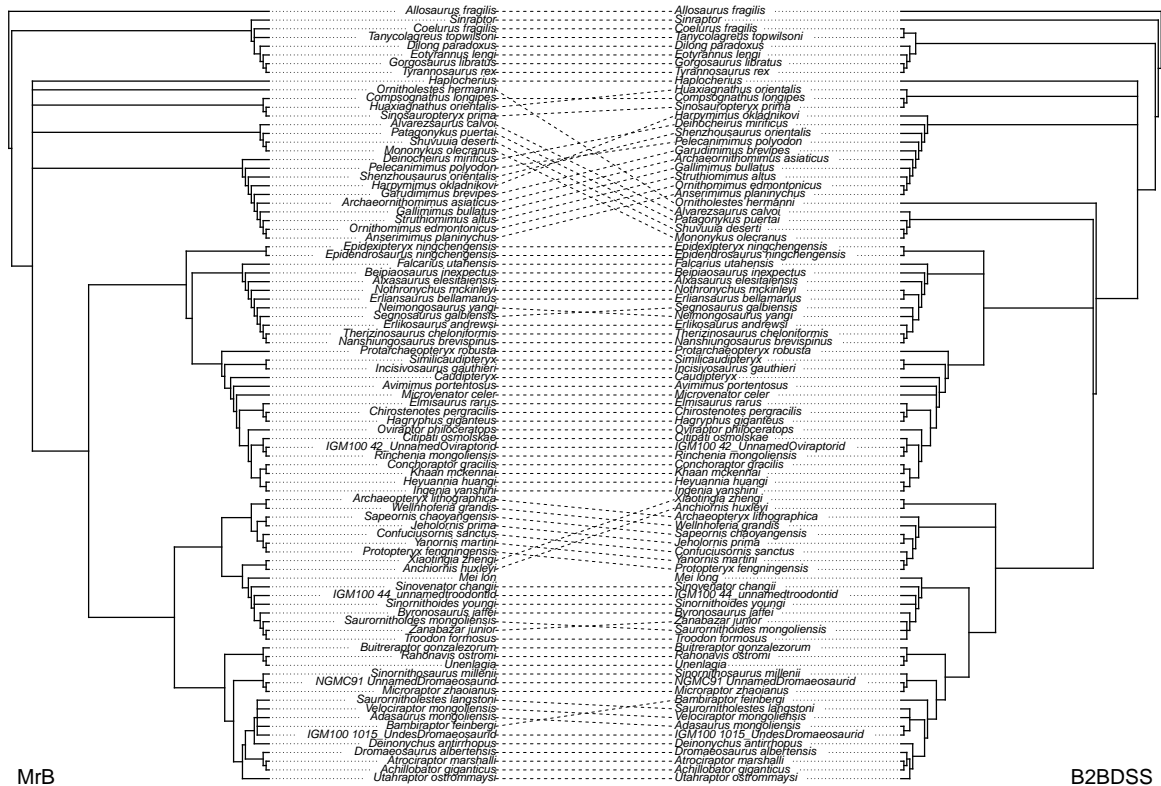
```
plotCophylo(treeMrB,treeB2SABD,"MrB","B2SABD")
```

```
## Rotating nodes to optimize matching...
## Done.
```



```
plotCophylo(treeMrB,treeB2BDSS,"MrB","B2BDSS")
```

```
## Rotating nodes to optimize matching...
## Done.
```



Our tip-dating analyses had considerable differences in topology, particularly between the analyses run under different programs. There is weak support for troodonts as sister to Avialae in the MrBayes analyses (posterior 0.5142), while the converse relationship of troodonts as sister to dromeosaurs is better supported in the BEAST2 BDSS analysis (posterior 0.53). BEAST2 SABD does not assign either hypothesis a posterior greater than 0.5, with the majority-rule of the posterior showing a polytomy of the troodonts, dromeosaurs, Avialae and a small clade composed of Anchiornis and Xiaotinga.

The Alvarezsauridae are poorly constrained; the MrBayes analysis doesn't find any stronger support for them beyond an unresolved polytomy of multiple lineages composed of non-tyrannosauroid coelurosaurs. The BEAST2 BDSS and SABD analyses resolves Alvarezsauridae as either sister to Paraves or to a group composed of therinzosaurs and oviraptors (neither solution has a posterior probability greater than 0.5; however their inclusion in that group is supported; posterior probabilities of 0.93 and 0.94 respectively).

Is Archeopteryx a bird?

The posterior probability for both B2 BDSS and B2 SABD for Archeo+Avialae is 1 the PP for archeopteryx to be with the avialae (i.e. for Archeo to be a bird) is 0.68 for MrB

```
avialaePosterior<-c(NA,NA,NA,1,1,0.68)
```

Criticisms of Lee and Worthy (Xu and Pol 2014, Turner et al., 2012, Spencer and Wilburg, 2013)

Relationship of Archaeopteryx and Wellnhoferia Paraphyletic on L&W monophyletic on MrB, posterior 0.9991 paraphyletic on both B2 trees BDSS posterior - 0.75 SABD posterior - 0.77

Archaeopteryx and Wellnhoferia become a paraphyletic stem to the Avialae in Lee and Worthy’s analysis, which Xu and Pol (2014) view with suspicion given that these two taxa have been considered possible synonyms, and thus should be monophyletic in their view (although, this would preclude the possibility that Archaeopteryx and Wellnhoferia are the same taxon *and* ancestral to more derived Avialae).

Epidexipteryx and Epidendrosaurus (the Scansoriopterygidae) Turner et al. (2012) criticized the derived placement of Epidexipteryx and Epidendrosaurus within the Avialae, which is very stratigraphically incongruent for these early occurring taxa, in the RAXML topology presented by Lee and Worthy (2011). Turner et al.’s own cladistic analysis, based on a revision of the Xu et al. character set, placed these taxa in different groups. One would de facto expect that tip-dating analyses would, indeed, also correct for awkward stratigraphically incongruent placements. Indeed, this bears out in this study, with the BEAST2 SABD analysis placing them as a monophyletic group (posterior probability = 1) sister to the oviraptors (posterior probability of 0.53). The BDSS analysis also places them as a monophyletic group (posterior probability of 1), but the majority-rule tree leaves them in an unresolved polytomy with the oviraptors and the therizosaurs (posterior 0.58). The MrBayes FBD tree also finds them to be monophyletic (posterior probability = 1), but places them as sister to a clade composed of both the oviraptors and therizosaurs (posterior probability of 0.53).

non- monophyletic Tyrannosauroida (Turner et al., Xu and Pol, 2014) Paraphyletic in Lee and Worthy’s tree

Posterior probability of Tyrannosauroida monophyly in B2 BDSS and SABD are 0.97 and 0.99 respectively the posterior on the monophyly of the tyrannosauroida is 0.9994 for MrB

```
tyranPosterior<-c(NA,NA,NA,0.97,0.99,1)
```

OVERALL

demonstrates how differences in tip-dating methodology impacts resulting topology, sometimes in large ways

Results: Ancestor Inference

ancestors in cal3

While the BEAST2 BDSS algorithm does not consider the possibility for taxa to be directly ancestral, the poor sampling of the theropod record might suggest that sampling ancestors is unlikely *a priori*. The MrBayes FBD, BEAST2 SABD and cal3 algorithms do consider the possibility for ancestral taxa, placing such relationships stochastically. Thus the number of taxa found to be ancestral becomes an interesting question.

cal3 can recognize two different sort of ancestor-descendant relationships, which in my opinion are the same two possibly recognizable patterns in the fossil record: apparent budding cladogenesis (i.e. a taxon is considered to persist through a branching event) or apparent anagenesis (i.e. the supposed ancestor’s range terminates at its LAD before the supposed origin of its later-appearing sister taxon).

Note that in both cases, the apparent pattern of ancestor-descendant relationships is not the same as the true pattern of ancestor-descendant relationships. We would expect in any incompletely sampled fossil record for some cladogenetic ancestors to ‘look’ like anagenetic ancestors, because the terminal portion of their range is unsampled. Both of these potential patterns are ‘apparent’ events because (a) the timing of the descendant’s origin may be misestimated and (b) taxon ranges are incompletely sampled, so taxa that did overlap may appear to not overlap temporally at all, allowing for the possible incorrect assessment of anagenesis.

The only case where we can be definite is with cladogenesis, which **must** have occurred if the two ranges of taxa overlap in time. Note that not everyone agrees with this principle (Ezard et al., 2011; Aze et al., 2013) but I don't agree with them.

We are biased to mistake cases of cladogenetic ancestors for anagenetic ancestors because the incompletely sampled fossil record may have removed portions of the ancestral taxon's earlier range, producing a gap between the taxa and lowering the chances that the pair would be recognized as a cladogenetic ancestor-descendant relationship. Thus, one would suspect inflation of anagenetic ancestors, even if anagenesis never occurs at all. Conversely, if a fossil record is poorly sampled and the degree of sampling is used to inform the probable placement of branching events (e.g. cal3), it may be difficult to recognize anagenetic ancestors because there is too much uncertainty involved in dating divergences. However you would expect this to also work against placing taxa as cladogenetic ancestors.

WELL THIS IS DUMB, NO ANCESTORS IF WE USE CAL3 FAD SO LET'S USE CAL3 LAD AND JUST SEE WHAT HAPPENS THIS WON'T MAKE THE MAIN PAPER ANYHOW, send to suppmat

```
#for cal3-LAD
```

```
(nBudd<-sapply(treesCal3LAD,function(x) length(x$budd.tips)))
```

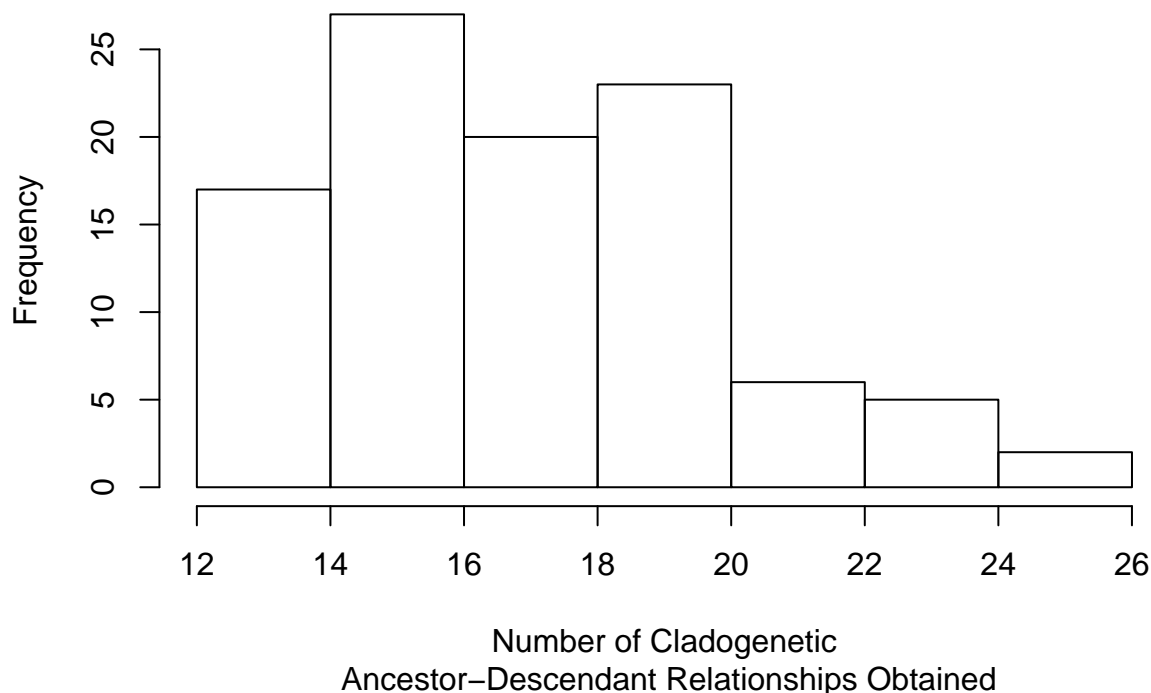
```
## [1] 15 20 15 18 19 19 18 15 19 14 13 14 16 16 25 15 14 14 13 22 16 19 15
## [24] 18 20 25 15 13 16 19 23 14 16 18 19 19 17 18 18 15 17 24 19 14 16 15
## [47] 17 14 14 16 16 14 16 18 19 20 16 19 19 17 18 13 18 15 19 15 13 20 19
## [70] 20 19 18 21 18 16 16 20 16 22 19 21 23 12 16 14 21 15 18 20 17 13 23
## [93] 17 19 17 18 22 23 16 16
```

```
(nAnag<-sapply(treesCal3LAD,function(x) length(x$anag.tips))) # none!
```

```
## [1] 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
## [36] 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
## [71] 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
```

```
layout(1)
hist(nBudd,
     xlab=c("Number of Cladogenetic", "Ancestor-Descendant Relationships Obtained"),
     main="Results from Stochastic cal3 Samples")
```


Results from Stochastic cal3 Samples



```
# number of ancestors per cal3-LAD tree  
summary(nBudd)
```

```
##      Min. 1st Qu.  Median    Mean 3rd Qu.    Max.   
## 12.00  15.00  17.00  17.43  19.00  25.00
```

Despite the expected bias against inferring cladogenetic ancestors, however, (almost?) no taxa were sampled as anagenetic ancestors in the 100 cal3 runs applied in this analysis. The mean number of anagenetic ancestors was 0 with a maximum of 0. On the contrary, 17.43 taxa were found on average to be cladogenetic ancestors, which is 19.5842697% of the total taxa in the dataset.

what about in tip-dating (now that we have SA tip-dating)

then ancestors are just zero length branches

probably would be good to do something comparing cal3, B2SABD and MrB ancestor assignments

```
#get a list of all the taxa listed as ancestors on tip-dating trees  
# i.e. all terminal ZLBs
```

```
getAncZLB<-function(tree,threshold=0.01){  
  termBranches<-which(tree$edge[,2]<=Ntip(tree))  
  zeroTermBranches<-termBranches[tree$edge.length[termBranches]<threshold]  
  anc<-tree$tip.label[tree$edge[zeroTermBranches,2]]  
  anc
```



```

}

ancB2SABD<-lapply(timeTrees$B2SABD,getAncZLB)
ancMrB<-lapply(timeTrees$MrB,getAncZLB)

# how many ancestors per tree

nAncB2SABD<-sapply(ancB2SABD,length)
nAncMrB<-sapply(ancMrB,length)

summary(nAncB2SABD) # number of ancestors per tree for B2SABD

```

```

##      Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##      0.00   1.00   2.00   1.94   3.00   6.00

```

```

summary(nAncMrB) # number of ancestors per tree for MrB FBD

```

```

##      Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##      0.00   0.00   1.00   7.38   7.25   33.00

```

Let's combine and plot with cal3-LAD ancestor inferences

```

#get ancestors from cal3
ancCal3<-lapply(treesCal3LAD,function(x)
  c(x$budd.tips,x$anag.tips))

#unlist and tabulate

ancList<-list(B2SABD=unlist(ancB2SABD),MrB=unlist(ancMrB),
  cal3=unlist(ancCal3))

tabAnc<-lapply(ancList,table)

#and combine them
tabAncMat<-lapply(tabAnc,function(x) t(as.matrix(x)))
tabAncMat<-rbind.fill.matrix(tabAncMat)
tabAncMat[is.na(tabAncMat)]<-0

#turn into proportions
tabAncMat<-tabAncMat/100

#sort
tabAncMat<-tabAncMat[,order(apply(tabAncMat,2,sum))]

```

and plot it

```

#plot

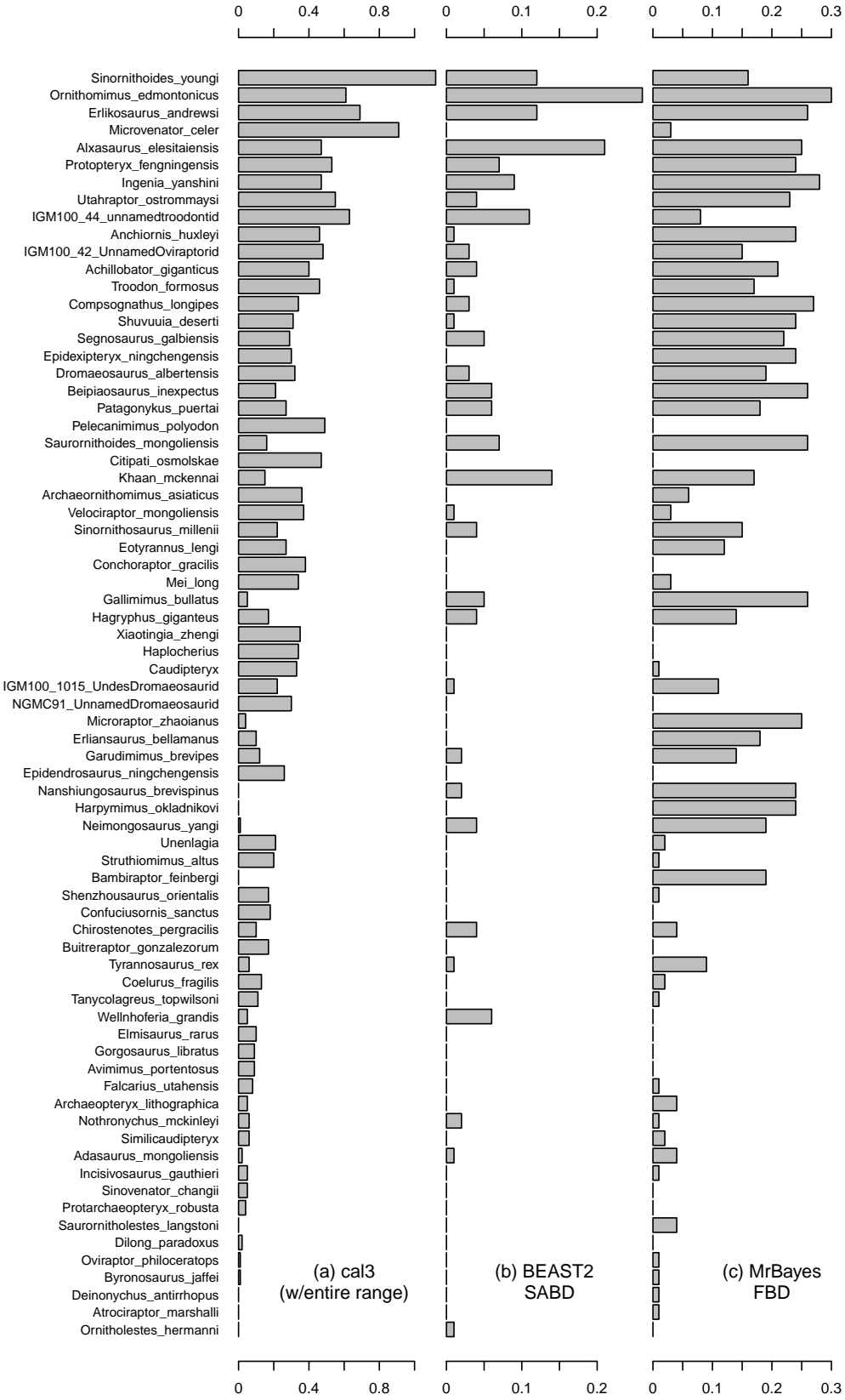
oldPar<-par(no.readonly = T)
layout(matrix(1:3,,3),widths=c(2.2,1,1))
#

```

```

par(mar=c(4,14,1.8,0.5),xaxt="n")
#
barplot(tabAncMat[3,],horiz=TRUE,main="",las=1,
        cex.names=0.9,cex.axis=1.1)
text(0.6,4,"(a) cal3\n(w/entire range)",cex=1.2)
par(xaxt="s")
axis(side=1,pos=-1.5,
     labels=c(0,"",0.4,"",0.8,""),
     at=c(0,0.2,0.4,0.6,0.8,1))
axis(side=3,line=-1,
     labels=c(0,"",0.4,"",0.8,""),
     at=c(0,0.2,0.4,0.6,0.8,1))
#
par(mar=c(4,0,1.8,0.5),yaxt="n",xaxt="n")
barplot(tabAncMat[1,],horiz=TRUE,main="",las=1,cex.axis=1.1)
text(0.13,4,"(b) BEAST2\n SABD",cex=1.2)
par(xaxt="s")
axis(side=1,pos=-1.5,
     labels=c(0,"",0.1,"",0.2),
     at=c(0,0.05,0.1,0.15,0.2))
axis(side=3,line=-1,
     labels=c(0,"",0.1,"",0.2),
     at=c(0,0.05,0.1,0.15,0.2))
#
par(mar=c(4,0,1.8,1.5),xaxt="n")
barplot(tabAncMat[2,],horiz=TRUE,main="",las=1,cex.axis=1.1)
text(0.20,4,"(c) MrBayes\nFBD",cex=1.2)
par(xaxt="s")
axis(side=1,pos=-1.5,
     labels=c(0,"",0.1,"",0.2,"",0.3),
     at=c(0,0.05,0.1,0.15,0.2,0.25,0.3))
axis(side=3,line=-1,
     labels=c(0,"",0.1,"",0.2,"",0.3),
     at=c(0,0.05,0.1,0.15,0.2,0.25,0.3))
#
layout(1)
mtext(side=1,line=2.7,at=0.22,"Proportion of Trees Placed As An Ancestor")

```



```
par(oldPar)
```

but what about taxa that never got sampled as ancestors

need to include those in correlations too because the zeroes are also data: taxa that never got placed as ancestors as either

```
# get taxa that are never considered ancestors
missingAncTab<-timeTrees[[1]][[1]]$tip.label[
  sapply(timeTrees[[1]][[1]]$tip.label,
    function(x) all(x!=colnames(tabAncMat)))
  ]
# add on the missing
if(length(missingAncTab>0)){
  # add to tabAncMat as zeroes
  missingAncTabCol<-matrix(0,3,length(missingAncTab))
  colnames(missingAncTabCol)<-missingAncTab
  tabAncMat<-cbind(tabAncMat,missingAncTabCol)
}

#sort
tabAncMat<-tabAncMat[,order(colnames(tabAncMat))]
tabAncMat<-tabAncMat[,order(apply(tabAncMat,2,sum))]

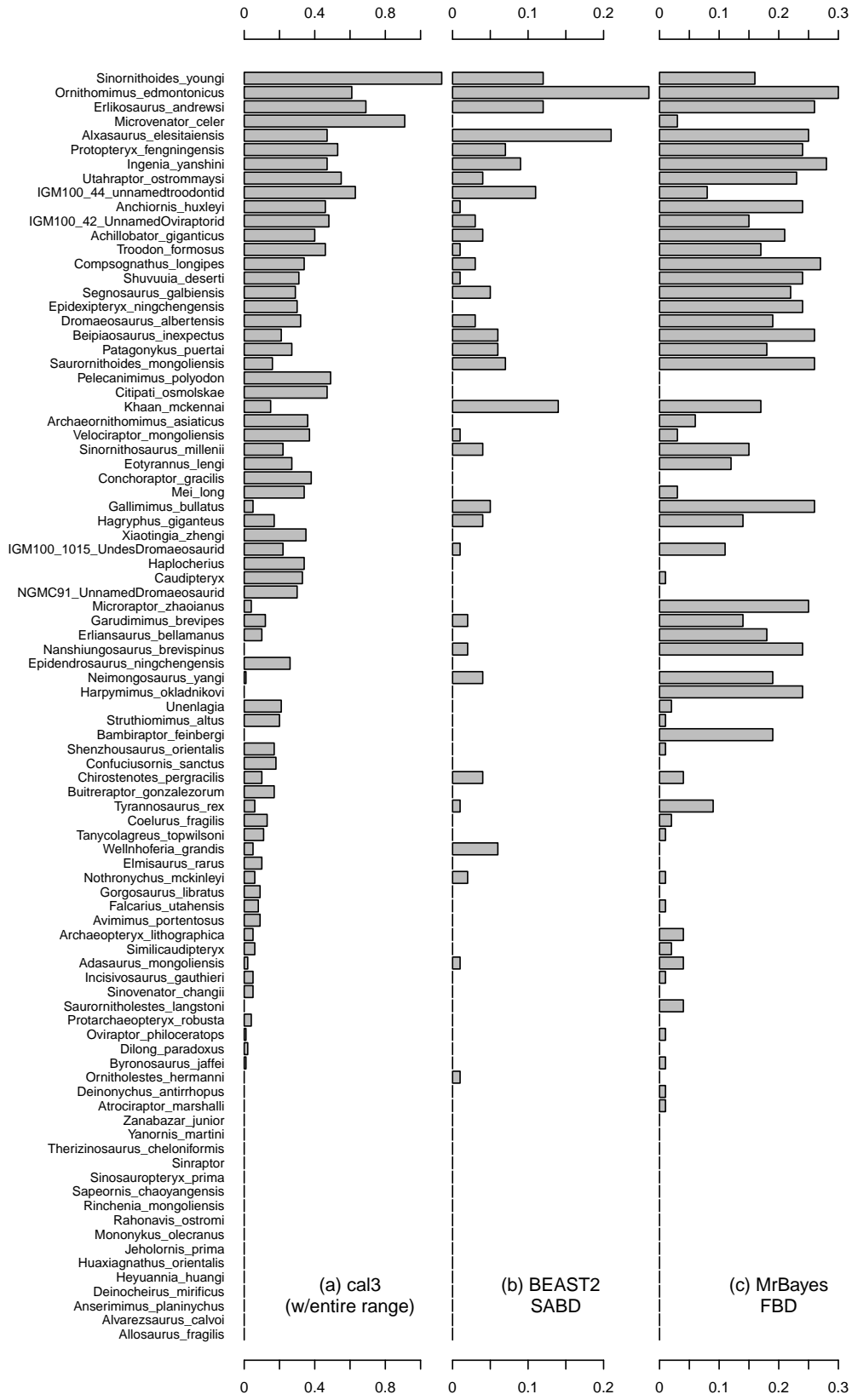
#plot

oldPar<-par(no.readonly = T)
layout(matrix(1:3,3),widths=c(2.2,1,1))
#
par(mar=c(4,14,1.8,0.5),xaxt="n")
#
barplot(tabAncMat[3,],horiz=TRUE,main="",las=1,
  cex.names=0.9,cex.axis=1.1)
text(0.6,4,"(a) cal3\n(w/entire range)",cex=1.2)
par(xaxt="s")
axis(side=1,pos=-1.5,
  labels=c(0,"",0.4,"",0.8,""),
  at=c(0,0.2,0.4,0.6,0.8,1))
axis(side=3,line=-1,
  labels=c(0,"",0.4,"",0.8,""),
  at=c(0,0.2,0.4,0.6,0.8,1))
#
par(mar=c(4,0,1.8,0.5),yaxt="n",xaxt="n")
barplot(tabAncMat[1,],horiz=TRUE,main="",las=1,cex.axis=1.1)
text(0.13,4,"(b) BEAST2\n SABD",cex=1.2)
par(xaxt="s")
axis(side=1,pos=-1.5,
  labels=c(0,"",0.1,"",0.2),
  at=c(0,0.05,0.1,0.15,0.2))
axis(side=3,line=-1,
  labels=c(0,"",0.1,"",0.2),
  at=c(0,0.05,0.1,0.15,0.2))
#
par(mar=c(4,0,1.8,1.5),xaxt="n")
```

```

barplot(tabAncMat[2,],horiz=TRUE,main="",las=1,cex.axis=1.1)
text(0.20,4,"(c) MrBayes\nFBD",cex=1.2)
par(xaxt="s")
axis(side=1,pos=-1.5,
     labels=c(0,"",0.1,"",0.2,"",0.3),
     at=c(0,0.05,0.1,0.15,0.2,0.25,0.3))
axis(side=3,line=-1,
     labels=c(0,"",0.1,"",0.2,"",0.3),
     at=c(0,0.05,0.1,0.15,0.2,0.25,0.3))
#
layout(1)
mtext(side=1,line=2.7,at=0.22,"Proportion of Trees Placed As An Ancestor")

```



Proportion of Trees Placed As An Ancestor

```
par(oldPar)
```

From Nick: - consistent with all of the above, no tip has a high probability of being a direct ancestor. - the highest is *Ornithomimus_edmontonicus* at 20.86%

Overall, it appears cal3 infers many more ancestors, much more often. - DUH BECAUSE WE'RE USING LADs, there weren't any when we used FADs

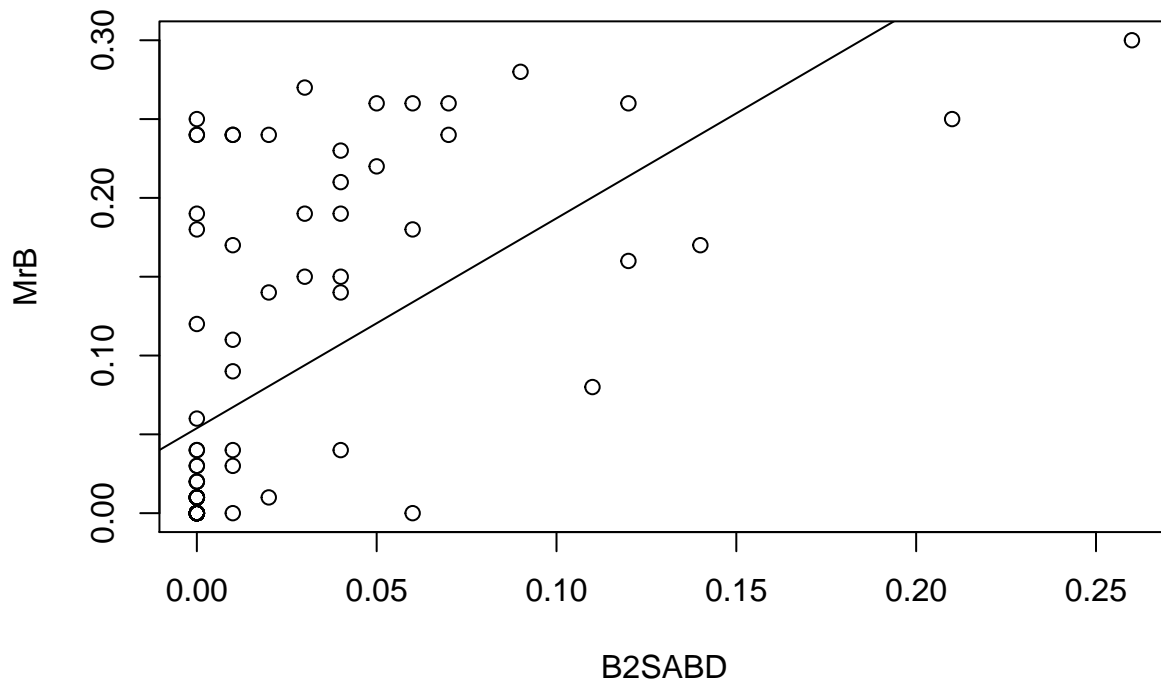
This may be because it looks at taxon ranges, rather than taxa as point occurrences. - that's just saying the same thing, dave

MrBayes infers more ancestors, more often than BEAST2

is there any relationship between being an ancestor in one and another?

```
plot(tabAncMat[1,], tabAncMat[2,],  
     xlab=names(ancList[1]), ylab=names(ancList[2]),  
     main=paste("Anc. Prop. of", names(ancList[1]),  
               "vs.", names(ancList[2])))  
reg<-lm(tabAncMat[2,]~tabAncMat[1,])  
abline(reg)
```

Anc. Prop. of B2SABD vs. MrB



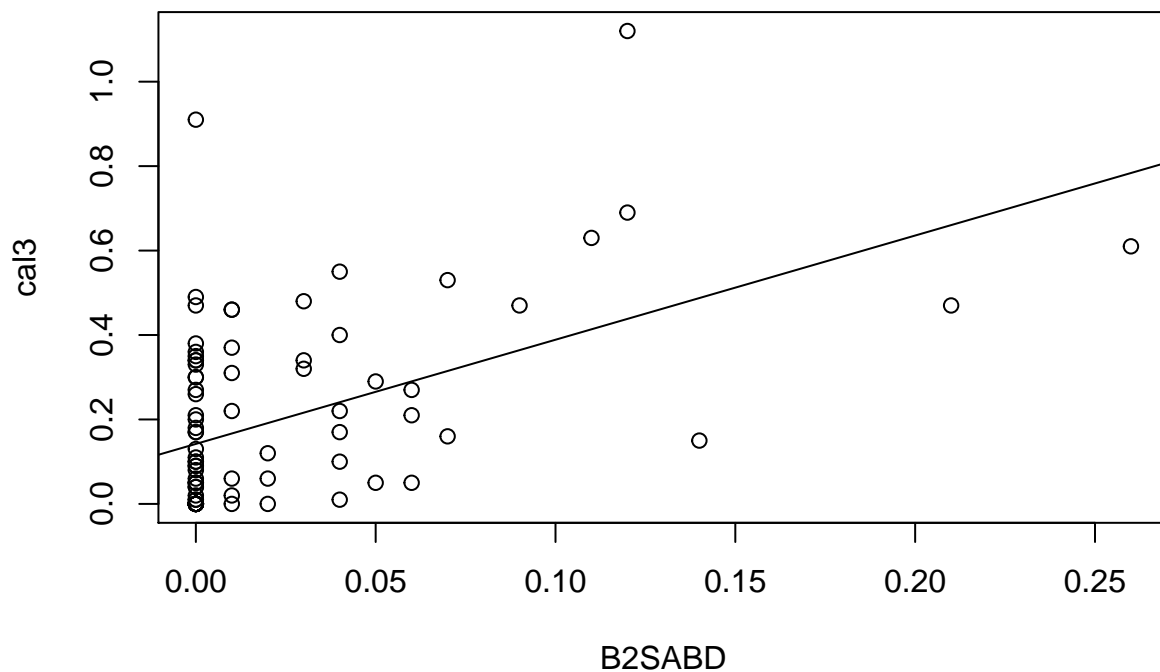
```
#summary(reg)  
cor.test(tabAncMat[2,], tabAncMat[1,], method="spearman")
```

```
## Warning in cor.test.default(tabAncMat[2, ], tabAncMat[1, ], method =  
## "spearman"): Cannot compute exact p-value with ties
```

```
##
## Spearman's rank correlation rho
##
## data: tabAncMat[2, ] and tabAncMat[1, ]
## S = 36073, p-value = 5.307e-14
## alternative hypothesis: true rho is not equal to 0
## sample estimates:
##      rho
## 0.6929473
```

```
plot(tabAncMat[1,],tabAncMat[3,],
     xlab=names(ancList[1]),ylab=names(ancList[3]),
     main=paste("Anc. Prop. of",names(ancList[1]),
               "vs.",names(ancList[3])))
reg<-lm(tabAncMat[3,]~tabAncMat[1,])
abline(reg)
```

Anc. Prop. of B2SABD vs. cal3



```
#summary(reg)
cor.test(tabAncMat[3,],tabAncMat[1,],method="spearman")
```

```
## Warning in cor.test.default(tabAncMat[3, ], tabAncMat[1, ], method =
## "spearman"): Cannot compute exact p-value with ties
```

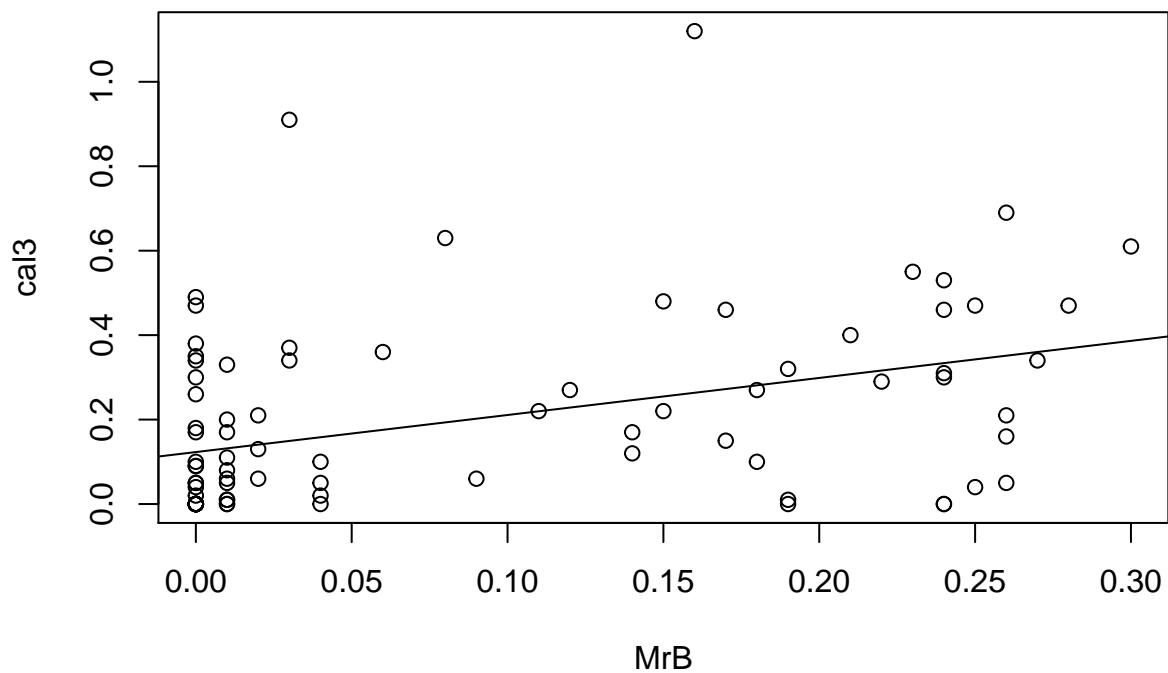
```
##
```



```
## Spearman's rank correlation rho
##
## data: tabAncMat[3, ] and tabAncMat[1, ]
## S = 62741, p-value = 4.193e-06
## alternative hypothesis: true rho is not equal to 0
## sample estimates:
##      rho
## 0.4659468
```

```
plot(tabAncMat[2,],tabAncMat[3,],
      xlab=names(ancList[2]),ylab=names(ancList[3]),
      main=paste("Anc. Prop. of",names(ancList[2]),
                 "vs.",names(ancList[3])))
reg<-lm(tabAncMat[3,]~tabAncMat[2,])
abline(reg)
```

Anc. Prop. of MrB vs. cal3



```
#summary(reg)
cor.test(tabAncMat[3,],tabAncMat[2,],method="spearman")
```

```
## Warning in cor.test.default(tabAncMat[3, ], tabAncMat[2, ], method =
## "spearman"): Cannot compute exact p-value with ties
```

```
##
## Spearman's rank correlation rho
```

```
##
## data: tabAncMat[3, ] and tabAncMat[2, ]
## S = 63483, p-value = 5.868e-06
## alternative hypothesis: true rho is not equal to 0
## sample estimates:
##      rho
## 0.4596302
```

Strong correlations, woah (but not very high Rsq)

Some interesting thoughts -Archeopteryx lithographica has a tiny chance of being an ancestor in any of these analyses (!) - but to who? Wellnhoferia? Avialae? -So does T-rex (presumably to gorgosaurus)

We could measure this...

```
getEarlySister<-function(tree,taxon,threshold=0.01){
  if(length(taxon)>1){stop("more than one taxon given")}
  # check if taxon is on a zero-length branch, if not stop
  tipEdge<-which(tree$edge[,2]==which(tree$tip.label==taxon))
  tipLength<-tree$edge.length[tipEdge]
  # is it on a zero-length branch OR in $budd.tips or $anag.tips ?
  ancTest1<-tipLength<threshold
  ancTest2<- any(taxon == c(tree$anag.tips,tree$budd.tips))
  if(ancTest1 | ancTest2){
    # get sister clade
    mom<-tree$edge[tipEdge,1]
    sister<-tree$edge[-tipEdge,2][tree$edge[-tipEdge,1]==mom]
    # if multiple siblings, kill
    if(length(sister)!=1){stop("where the hell a polytomy come from")}
    # is it a single tip taxon? If so, report that
    if(sister<=Ntip(tree)){
      res<-tree$tip.label[sister]
    }else{
      # is it a clade? if so get descendant taxa of sibling
      sisterDesc<-prop.part(tree)[[sister-Ntip(tree)]]
      # find earliest nodeDate among descendants of sister
      dateDesc<-dateNodes(tree)[sisterDesc]
      # max node date
      earlyDesc<-sisterDesc[which(dateDesc==max(dateDesc))]
      # report that earliest descendant with *
      earlyName<-tree$tip.label[earlyDesc]
      res<-paste0(earlyName, "*")
    }
  }else{
    res<-NA
  }
  return(res)
}
```

```
taxon<-"Archaeopteryx_lithographica"
table(sapply(treesCal3LAD,getEarlySister,taxon=taxon))
```

```
##
```

```
## Wellnhoferia_grandis
##           5
```

```
table(sapply(timeTrees$B2SABD,getEarlySister,taxon=taxon))
```

```
## < table of extent 0 >
```

```
table(sapply(timeTrees$MrB,getEarlySister,taxon=taxon))
```

```
##
## Wellnhoferia_grandis
##           4
```

```
taxon<-"Wellnhoferia_grandis"
table(sapply(treesCal3LAD,getEarlySister,taxon=taxon))
```

```
##
## Archaeopteryx_lithographica
##           5
```

```
table(sapply(timeTrees$B2SABD,getEarlySister,taxon=taxon))
```

```
##
## Confuciusornis_sanctus* Protopteryx_fengningensis*
##           4           2
```

```
table(sapply(timeTrees$MrB,getEarlySister,taxon=taxon))
```

```
## < table of extent 0 >
```

```
taxon<-"Tyrannosaurus_rex"
table(sapply(treesCal3LAD,getEarlySister,taxon=taxon))
```

```
##
## Gorgosaurus_libratus
##           6
```

```
table(sapply(timeTrees$B2SABD,getEarlySister,taxon=taxon))
```

```
##
## Gorgosaurus_libratus
##           1
```

```
table(sapply(timeTrees$MrB,getEarlySister,taxon=taxon))
```

```
##
## Gorgosaurus_libratus
##           9
```

```
taxon<-"Ornithomimus_edmontonicus"  
table(sapply(treesCal3LAD,getEarlySister,taxon=taxon))
```

```
##  
## Anserimimus_planinychus  
## 61
```

```
table(sapply(timeTrees$B2SABD,getEarlySister,taxon=taxon))
```

```
##  
## Anserimimus_planinychus  
## 26
```

```
table(sapply(timeTrees$MrB,getEarlySister,taxon=taxon))
```

```
##  
## Anserimimus_planinychus  
## 30
```

I would not put much faith on these, given that there are many unsampled groups here, so making strong anc-desc pair claims is tough, if not impossible

I mean, the best case would be Ornithomimus but just look how undersampled that clade is in our dataset relative to what it could have been:

<https://en.wikipedia.org/wiki/Ornithomimus#Phylogeny>

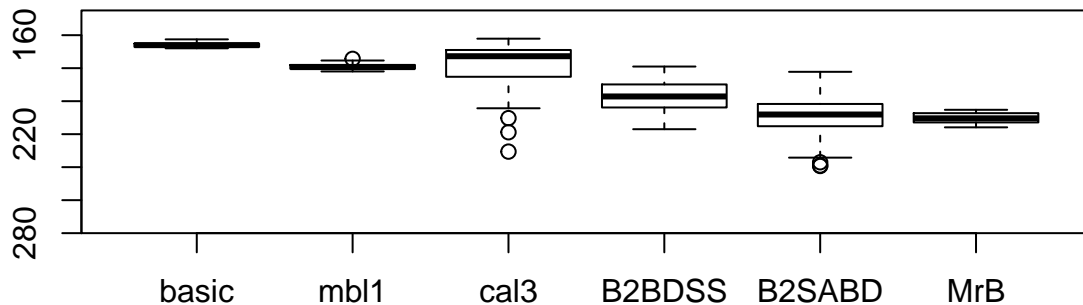
So despite above, I would not rush to say Ornithomimus has the potential to be the ancestor of Anserimas (... but I might in a more complete analysis)

Results: Comparison of divergence dating

Comparing Root Age Estimates

The age of the root divergence is an easy target for comparing trees produced with different timescaling methods. In this case, it is important to remember that cal3 poorly constrains the root age, effectively putting a very flat (and perhaps *overly* flat) prior, and thus we expect that cal3 will produce root ages that can seem unrealistically early.

```
# get root ages  
rootTimes<-lapply(timeTrees,sapply,function(x) x$root.time)  
boxplot(rootTimes,ylim=c(275,150))
```



Oddly, cal3 does **not** provide the oldest age estimates: instead the three tip-dating methods seem to provide the oldest ages, particularly the two sampled-ancestor analyses (~210 Ma). MrBayes provides a remarkably ‘narrow’ range of root ages relative to the BEAST2 SABD run, but they have the same central tendency.

I’m not a vertebrate worker but the extremely old ages produced by tip-dating look like a warning flag to me, as they are tens of millions of years before the first appearance time of any of the taxa in our analysis, and doesn’t overlap at all with the Basic or MBL date estimates. Now, while I admit that those methods are probably wrong, there should still be a sizeable probability that a member of a clade is sampled immediately after the initial branching event, but this seems to be a possibility not given any weight by tip-dating, paradoxically even less so when ancestor-sampling is allowed. (This is a classic aspect of any exponential waiting time model.) Note that cal3 has a long tail that stretches back pretty far, but the majority of the age estimates for cal3 are concentrated closer to the first appearance of the taxa, all of which closely matches expectations under the parallel Poisson processes of the BDSS model (which cal3 also uses, albeit a modification where only first and last appearance dates are known). Remarkably, although cal3 is a sampled-ancestor model, it provides root age estimates very different from BEAST2 or MrBayes under sampled-ancestor.

Compare dating of More Derived Clades

First, the Tyrannosauoidea

```
# get MRCA but only when monophyletic

getMonoMRCA<-function(tree,taxa){
  mrca<-getMRCA(tree,taxa)
  nDesc<-length(prop.part(tree)[[mrca-Ntip(tree)]])
  if(nDesc==length(taxa)){
    res<-mrca
  }else{
    res<-NA
  }
  return(res)
}

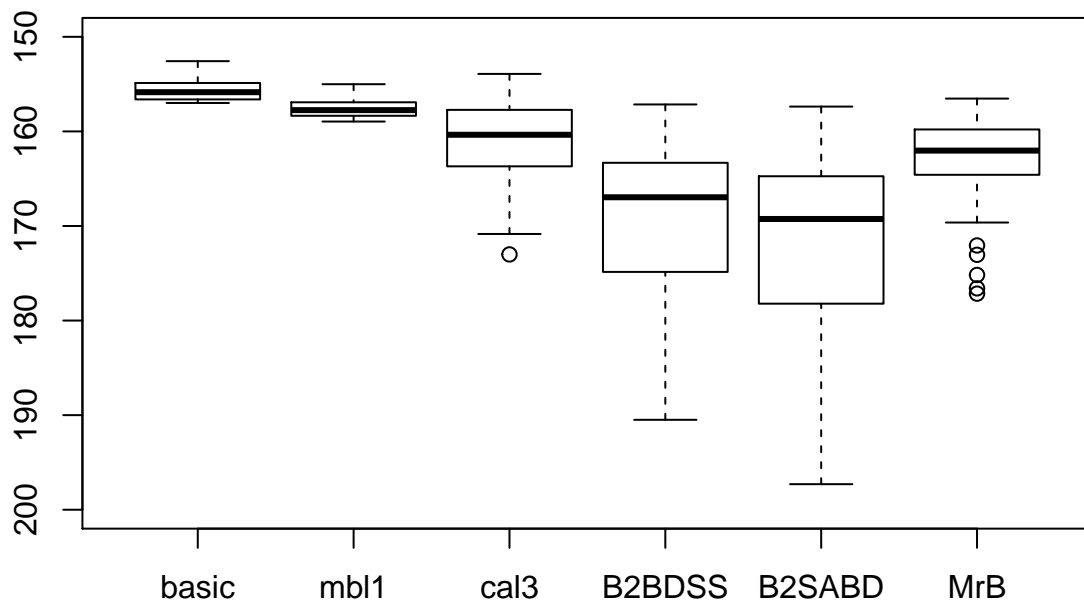
# Tyrannosauoidea
```

```

TyranTaxa<-c("Dilong_paradoxus", "Eotyrannus_lengi", "Gorgosaurus_libratus", "Tyrannosaurus_rex",
tyranTime<-function(tree){
  mrca<-getMonoMRCA(tree,taxa=TyranTaxa)
  if(!is.na(mrca)){
    mrca<-dateNodes(tree)[mrca]
  }
  mrca
}
tyranTimes<-lapply(timeTrees,sapply,tyranTime)
boxplot(tyranTimes,ylim=c(200,150),main="Tyrannosauroida")

```

Tyrannosauroida



```

# num where was not a clade
sapply(tyranTimes,function(x) sum(is.na(x)))

```

```

## basic mbl1 cal3 B2BDSS B2SABD MrB
## 0 0 0 1 1 0

```

```

# proportion where was a clade
sapply(tyranTimes,function(x) 1-sum(is.na(x))/length(x))

```

```

## basic mbl1 cal3 B2BDSS B2SABD MrB
## 1.00 1.00 1.00 0.99 0.99 1.00

```

Now the Avialae

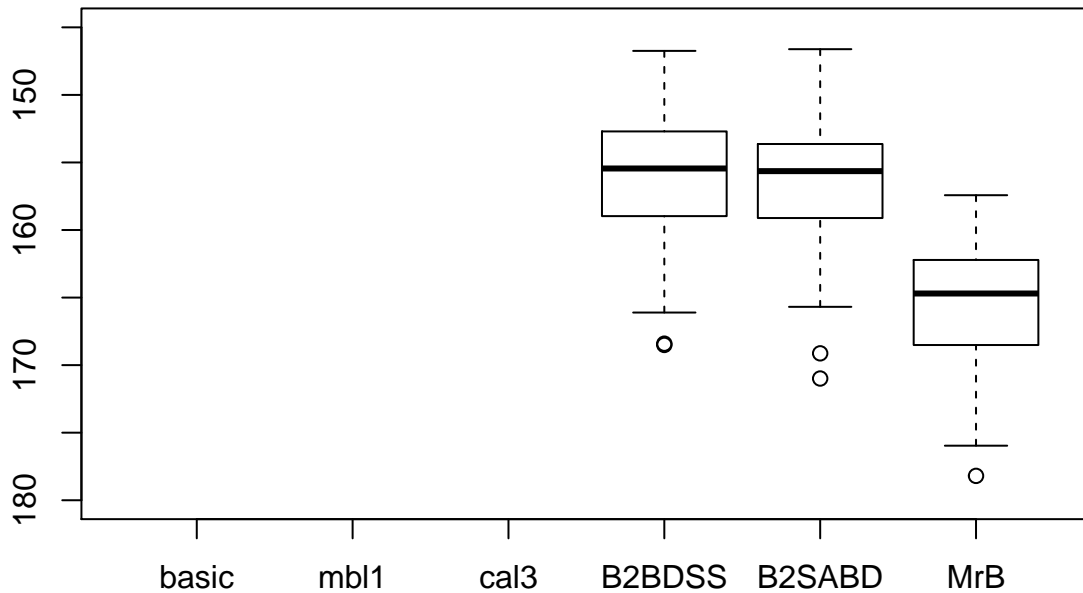
- 1) Avialae (with Archeopteryx, which is a little tricky because it turns out the posterior probability for Archeo in Avialae for MrBayes runs is 0.78)
- 2) Avialae (withOUT Archeopteryx)

```
# Avialae with Archaeopteryx
# mrca of Archaeopteryx and Confuciusornis
# without Deinonychus being a descendant of same ancestor

getInclusiveCladeAge<-function(tree,includedTaxa,excludedTaxon){
  # get mrca
  mrca<-getMRCA(tree,includedTaxa)
  # get children of mrca
  children<-tree$tip.label[prop.part(tree)[[mrca-Ntip(tree)]]]
  # does it contain the raptor? if so, NA
  if(any(children==excludedTaxon)){
    res<-NA
  }else{
    # if not, get age of MRCA
    res<-dateNodes(tree)[mrca]
  }
  return(res)
}

Avialae<-c("Confuciusornis_sanctus","Archaeopteryx_lithographica")
raptor<-"Deinonychus_antirrhopus"

avialaeAge<-lapply(timeTrees,sapply,getInclusiveCladeAge,
  includedTaxa=Avialae,excludedTaxon=raptor)
boxplot(avialaeAge,ylim=c(180,145)) #none for MPT-based trees
```



```
# num where was not a clade
sapply(avialaeAge,function(x) sum(is.na(x)))
```

```
## basic  mbl1  cal3 B2BDSS B2SABD  MrB
## 100    100    100     0     0     9
```

```
# proportion where was a clade
sapply(avialaeAge,function(x) 1-sum(is.na(x))/length(x))
```

```
## basic  mbl1  cal3 B2BDSS B2SABD  MrB
## 0.00   0.00   0.00  1.00   1.00   0.91
```

```
# that's no good
```

Eumaniraptors?

```
# Eumaniraptor is mrca of velociraptor, jelornis and troodon
```

```
ageMRCA<-function(tree,taxa){
  mrca<-getMRCA(tree,taxa)
  res<-dateNodes(tree)[mrca]
  return(res)
}
```

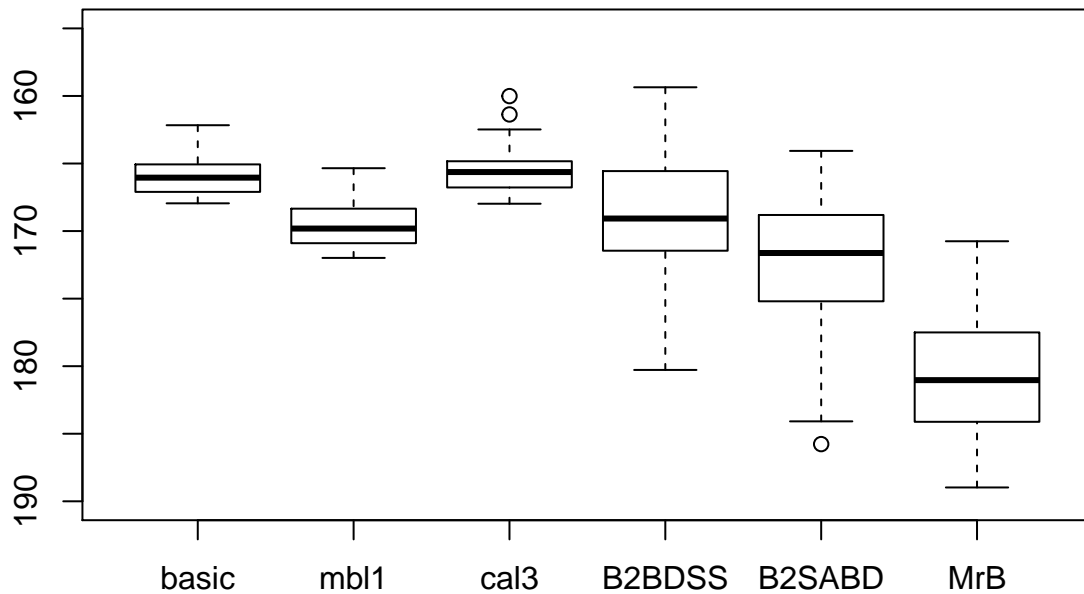


```

Eumaniraptora<-c("Velociraptor_mongoliensis",
  "Troodon_formosus","Jeholornis_prima",
  "Confuciusornis_sanctus","Archaeopteryx_lithographica",
  "Xiaotingia_zhengi","Wellnhoferia_grandis")

eumaniAge<-lapply(timeTrees,sapply,ageMRCA,taxa=Eumaniraptora)
boxplot(eumaniAge,ylim=c(190,155))

```



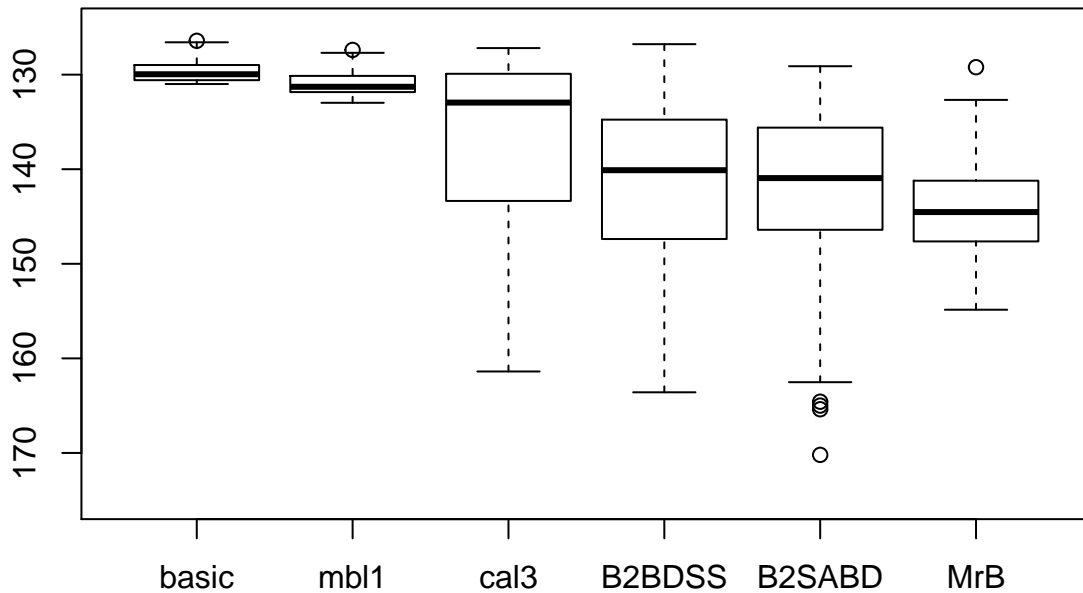
Therinzosaurs?

```

Therinz<-c("Falcarius_utahensis", "Beipiaosaurus_inexpectus",
  "Therizinosaurus_cheloniformis","Segnosaurus_galbiensis")

therinzAge<-lapply(timeTrees,sapply,ageMRCA,taxa=Therinz)
boxplot(therinzAge,ylim=c(175,125))

```



Now let's do some branch-based clades

```
findBranchBasedClade<-function(tree,moreRelatedTo,lessRelatedTo){
  # get descendants of each clade
  nodeDesc<-lapply(prop.part(tree),function(x) tree$tip.label[x])
  # clade size
  nDesc<-sapply(nodeDesc,length)
  # test if contains all moreRelatedTo
  conMRT<-sapply(nodeDesc,function(x)
    all(sapply(moreRelatedTo,function(y) any(y==x))))
  # test if contains any lessRelatedTo
  conLRT<-sapply(nodeDesc,function(x)
    any(sapply(lessRelatedTo,function(y) any(y==x))))
  # are acceptable
  accept<-!conLRT & conMRT
  # are any clades acceptable
  if(any(accept)){
    # find largest acceptable clade
    maxAccept<-max(nDesc[accept])
    # as a node ID
    res<-Ntip(tree)+which(accept)[nDesc[accept]==maxAccept]
    if(length(res)!=1){stop("wtf")}
  }else{
    res<-NA
  }
  return(res)
}
```

```

}

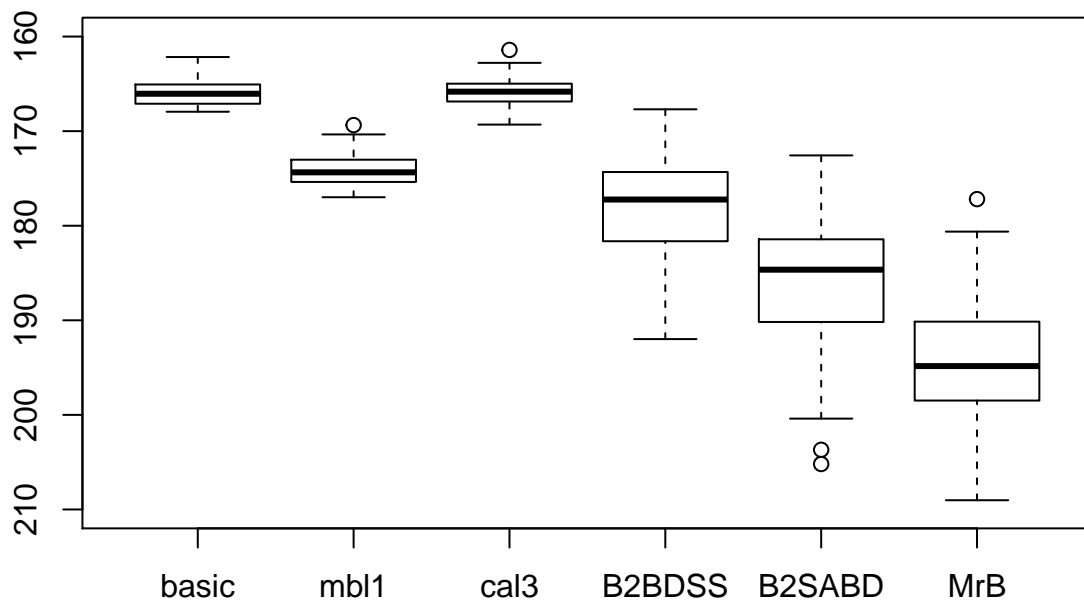
# Maniraptora
# All taxa more closely related to birds than Ornithomimus

dateManiraptora<-function(tree){
  ManiNode<-findBranchBasedClade(tree,moreRelatedTo=Eumaniraptora,
    lessRelatedTo="Ornithomimus_edmontonicus")
  dateNodes(tree)[ManiNode]
}

maniraptoraAge<-lapply(timeTrees,sapply,dateManiraptora)

boxplot(maniraptoraAge,ylim=c(210,160))

```



```

# num where was not a clade
sapply(maniraptoraAge,function(x) sum(is.na(x)))

```

```

## basic mbl1 cal3 B2BDSS B2SABD MrB
## 0 0 0 0 0 0

```

```

# branch-based Avialae
# all taxa more closely related to birds than Deinonychus or Troodon

```

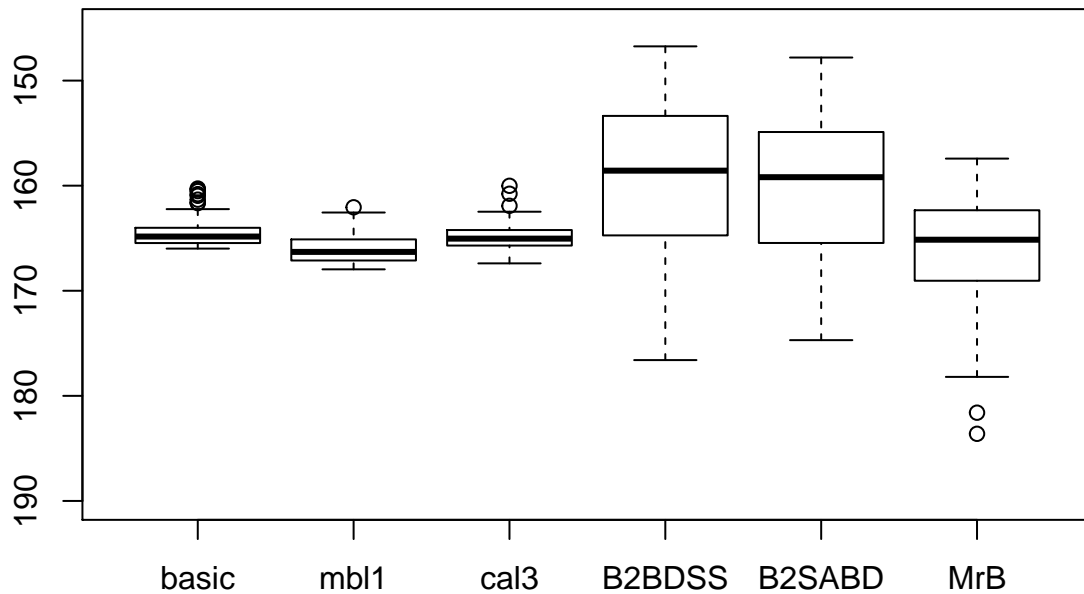
```

dateBranchAvialae<-function(tree){
  aviNode<-findBranchBasedClade(tree,
    moreRelatedTo=c("Jeholornis_prima","Confuciusornis_sanctus"),
    lessRelatedTo=c("Deinonychus_antirrhopus","Troodon_formosus"))
  dateNodes(tree)[aviNode]
}

aviBranchAge<-lapply(timeTrees,sapply,dateBranchAvialae)

boxplot(aviBranchAge,ylim=c(190,145))

```



```

# num where was not a clade
sapply(aviBranchAge,function(x) sum(is.na(x)))

```

```

## basic mbl1 cal3 B2BDSS B2SABD MrB
## 0 0 0 0 0 0

```

```

# Coelurosauria
# all animals closer to birds than to Allosaurus

```

```

dateCoel<-function(tree){
  coelNode<-findBranchBasedClade(tree,
    moreRelatedTo=c("Jeholornis_prima","Confuciusornis_sanctus"),
    lessRelatedTo=c("Allosaurus_fragilis"))
}

```

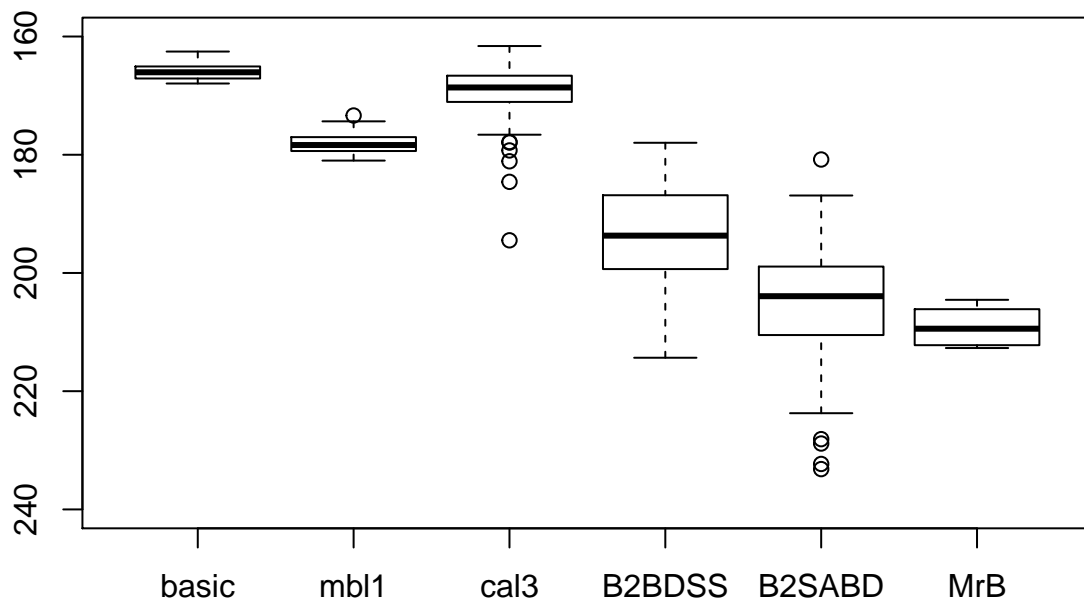
```

dateNodes(tree)[coelNode]
}

coelAges<-lapply(timeTrees,sapply,dateCoel)

boxplot(coelAges,ylim=c(240,160))

```



Somewhere among these is likely a good combination of node ages to use for illustrating phylogenetic uncertainty and dating differences; its interesting how different they are.

Overall, MrBayes trees seem to infer younger dates for more rootward clades relative to B2, and older dates for clades further from the root (??)

cal3 is very much like basic...

Differences Across All Divergence Dates

Describing the structure of differences in node age estimates for samples of trees is a difficult proposition (cough... Bapst, 2014, Paleobiology). A particular difficulty here is that unlike my simulations in the Paleobiology paper is that there is no true set of node dates to compare these trees to.

One reference point we could use would be a single Basic time-scaled tree, as the clades ages in this type of time-scaled tree are identical to the age of their earliest appearing member. Of course, due to the stochasticity of pulling first appearance dates and the differences among MPTs in Graeme's maximum-parsimony analysis, each Basic time-scaled is slightly different, but in this case the choice of a Basic tree is somewhat arbitrary. Here, we will simply use the first tree in the Basic set as our 'exemplar'.

We will use the paleotree function `compareNodeAges` to measure the difference in node ages for those clades that are shared across both the exemplar Basic tree and one of our sets of trees (with the exemplar tree removed from the Basic set). We can then take the median difference in divergence date for each of these shared clades across the entire sample, and then compare the resulting sets of median age differences to examine how time-scaling methods impact the dating of a large number of nodes.

Restricting our analysis to only clades shared with the exemplar (and across the entire given set of time-scaled trees) has the nice secondary effect of focusing our attention on the node ages of widely accepted clades.

```
#let's look at the whole distribution of ages, relative to the first Basic tree

BasicOne<-timeTrees$basic[[1]]

shiftAges<-lapply(timeTrees,function(x)
  compareNodeAges(BasicOne,x,dropUnshared=TRUE))

#remove that first node age comparison from shiftAges
isBasic<-which(names(timeTrees)=="basic")
shiftAges[[isBasic]]<-compareNodeAges(BasicOne,timeTrees[[isBasic]][-1],dropUnshared=TRUE)

#how many nodes did we recover from each set
sapply(shiftAges,dim)
```

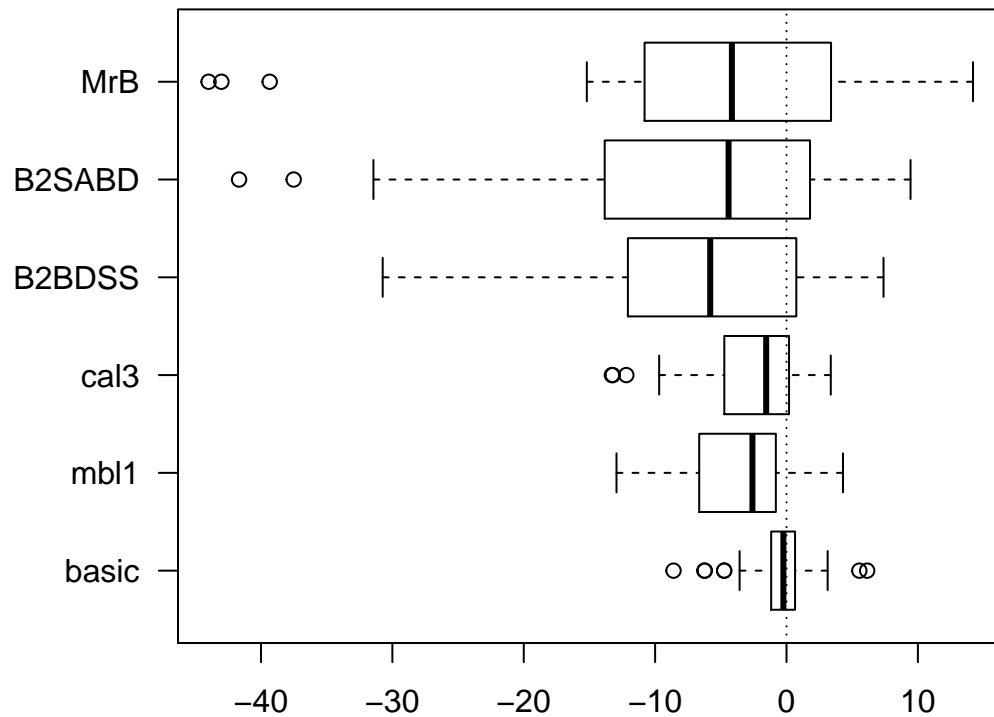
```
##      basic mbl1 cal3 B2BDSS B2SABD MrB
## [1,]   99  100  100   100   100  100
## [2,]   67   67   67    29    30  27
```

have about half as many valid comparisons when we get to tip-dating

Median of Per-Node Age Difference

```
#get median shift in node age estimates for each node
shiftAgesMedian<-lapply(shiftAges,function(x) apply(x,2,median))

#plot it!
par(mar=c(5,10,1,1))
boxplot(shiftAgesMedian,
  names=names(timeTrees),horizontal=TRUE,las=1,
  xlab=c("Median Difference in Node Age Estimates",
    " relative to Exemplar Basic Tree (Ma)"))
abline(v=0,lty=3)
```



Median Difference in Node Age Estimates
relative to Exemplar Basic Tree (Ma)

```
par(oldPar)
```

We see here a pattern that partly matches the one for the root ages: tip-dating calculates node ages that are several million years older than the first appearance of taxa in that clade. cal3 does not estimate such old node ages; overall looks a lot like MBL. Interestingly, MrBayes somehow manages to infer slightly younger ages for some nodes than Basic (suggest MrBayes is preferentially pulling younger tip ages from the uniform age priors), and simultaneously some of the oldest nodes ages too

Variance (or Range) of Per-Node Age Difference

A different investigation would examine how consistent a time-scaling method is producing a node age estimate, as could be measured by examining the variance or range in divergence dates for the same clade. Obviously, we would expect Basic to have small ranges (any that exist are entirely due to the uncertain placement of first appearances within stratigraphic intervals). MBL would be expected to behave similarly to Basic, although differences in topology may affect the MBL algorithm such as to add slightly more variation to the node ages produced. cal3 and the tip-dating posterior trees would be expected to have fairly broad uncertainties in the node ages.

We could quantify range in multiple ways; first, let's look at variance in age estimates for a node

```
#calculate var for shiftAges
shiftAgesVar<-lapply(shiftAges,function(x) apply(x,2,var))

#plot it!
par(mar=c(5,10,1,1))
```

```

boxplot(shiftAgesVar,notch=TRUE,
        names=names(timeTrees),horizontal=TRUE,las=1,
        xlab=c("Variance of Differences in Node Age Estimates",
               " relative to Exemplar Basic Tree (Ma)"))

```

```

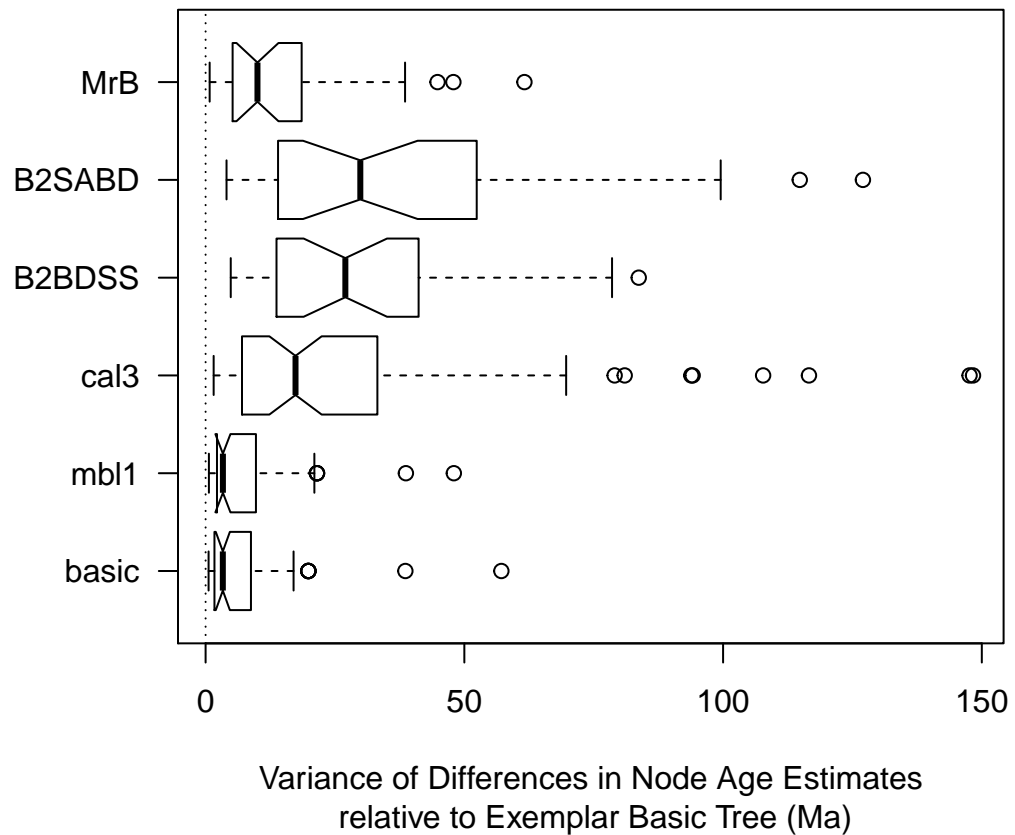
## Warning in bxp(structure(list(stats = structure(c(0.573732253973916,
## 1.70702889355898, : some notches went outside hinges ('box'): maybe set
## notch=FALSE

```

```

abline(v=0,lty=3)

```



```

par(oldPar)

```

As expected, Basic has little variance in node age estimates and MBL has only slightly more.

cal3 and tip-dating have some of the largest variance in node ages (), with MrBayes having the least and Beast2 the most

At least for me, that BEAST2 tip-dating methods produce more uncertain age estimates is shocking: I specifically have recommended in publications (e.g. Bapst, 2014, Paleobio.) that tip-dating methods may 'solve' the issue that cal3 may have less precision than desired, as the morphological clock would provide positive information on the divergence date, while cal3's model of sampling in the fossil record can really only ever provide uncertainty bounds.

Now, I can also plot absolute range (maximum difference in age estimates for a node minus the minimum) and the size of the two-tailed 95% and 50% quantiles (to control for the effect of outliers on absolute range).

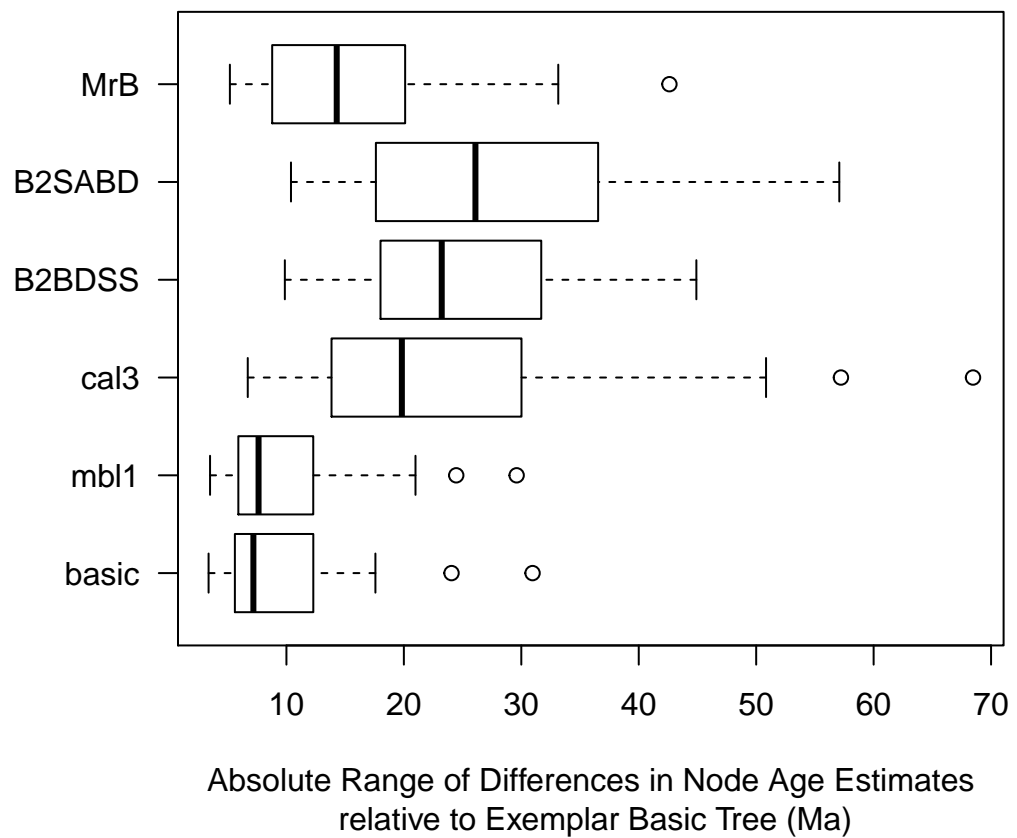

```

#range
range1<-function(x) diff(range(x))

#calculate ranges for shiftAges
shiftAgesRanges1<-lapply(shiftAges,function(x) apply(x,2,range1))

#plot it!
par(mar=c(5,10,1,1))
boxplot(shiftAgesRanges1,
        names=names(timeTrees),horizontal=TRUE,las=1,
        xlab=c("Absolute Range of Differences in Node Age Estimates",
              " relative to Exemplar Basic Tree (Ma)"))
abline(v=0,lty=3)

```



```
par(oldPar)
```

```

#95% quantile size
range2<-function(x) unname(diff(quantile(x,probs=c(0.025,0.975))))

#calculate ranges for shiftAges
shiftAgesRanges2<-lapply(shiftAges,function(x) apply(x,2,range2))

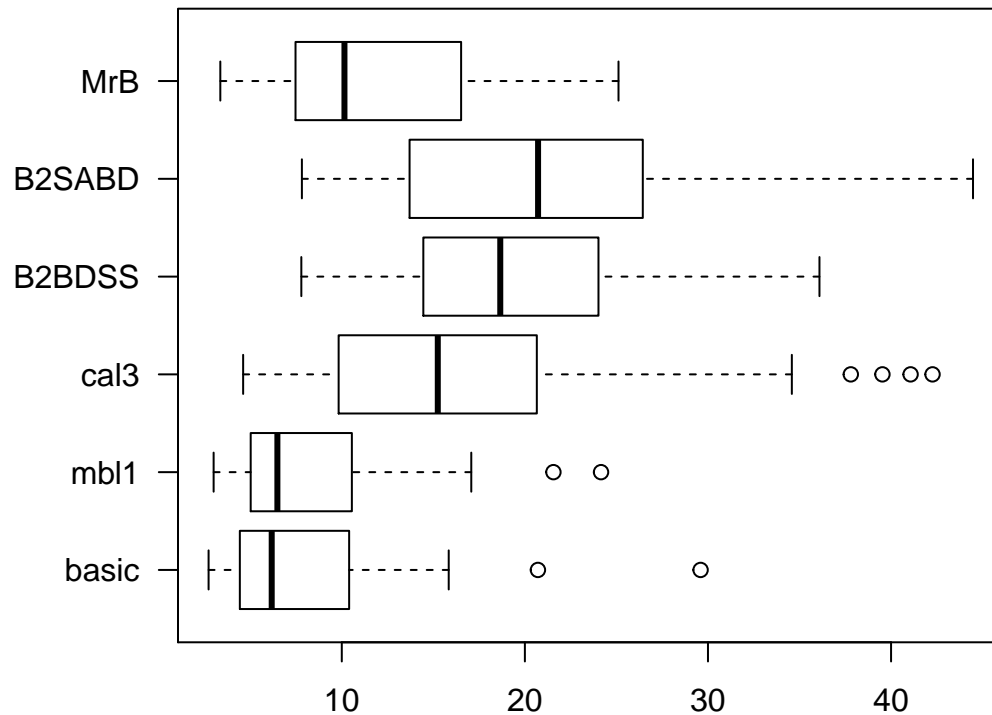
#plot it!
par(mar=c(5,10,1,1))

```

```

boxplot(shiftAgesRanges2,
        names=names(timeTrees),horizontal=TRUE,las=1,
        xlab=c("Size of 95% Quantile of Differences in Node Age Estimates",
               " relative to Exemplar Basic Tree (Ma)"))
abline(v=0,lty=3)

```



Size of 95% Quantile of Differences in Node Age Estimates relative to Exemplar Basic Tree (Ma)

```
par(oldPar)
```

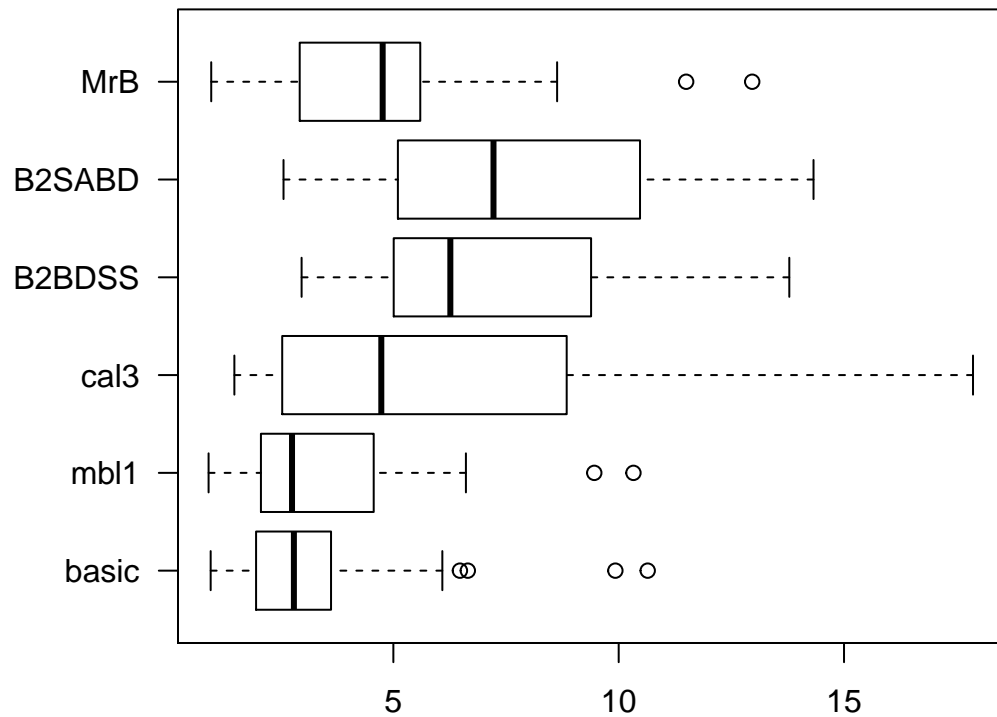
```

#50% quantile size
range2<-function(x) unname(diff(quantile(x,probs=c(0.25,0.75))))

#calculate ranges for shiftAges
shiftAgesRanges2<-lapply(shiftAges,function(x) apply(x,2,range2))

#plot it!
par(mar=c(5,10,1,1))
boxplot(shiftAgesRanges2,
        names=names(timeTrees),horizontal=TRUE,las=1,
        xlab=c("Size of 50% Quantile of Differences in Node Age Estimates",
               " relative to Exemplar Basic Tree (Ma)"))
abline(v=0,lty=3)

```



Size of 50% Quantile of Differences in Node Age Estimates relative to Exemplar Basic Tree (Ma)

`par(oldPar)`

The absolute range and 95% quantiles results are quite similar, as is the 50% quantiles, to the variance measures above

Its important I think to recall that, in simulation, 95% quantiles from cal3 with all bells and whistles (i.e. ancestors, poltomy resolution) contain the true node age about 80% of the time (Bapst, 2013; 2014). Obviously, this suggests that cal3 is too precise. Thus, the tip-dating methods may be more accurately reflecting the node age uncertainty.

Results: Phylogenetic Comparative Methods

Fitting Models of Trait Evolution to Body-Size Data from Benson et al. 2014

Here's the real meat and potatoes: how do the timescaling methods influence the support for different models of continuous trait evolution, as is commonly done? Benson et al. (2014) analyzed the Mesozoic theropoda with avians and found a strong support for Ornstein-Uhlenbeck (OU), especially under MBL. So, using a subset of their data and our trees, what do we find? I apply a more limited range of models here than they apply: as they only find measurable support for OU and Early Burst (EB), I will limit the models tested to OU, EB and their nested relative, Brownian Motion (BM).

Here I'll present results as stacked barplots of Akaike weights which sum to 1, with a different barplot for each tree. I've removed the lines separating the 100 barplots for each set of trees, and sorted the barplots by the weight for BM.

For EB, need to set bounds manually as geiger miscalculates the bounds on EB's for non-ultrametric trees

```

#fitContinuous analyses - first clean the trees of missing taxa
timeTreesATBL<-lapply(timeTrees,function(x)
  lapply(x,function(y) addTermBranchLength(treedata(phy=y,dat=bodySizes)$phy)))

compareModels<-function(tree){
  aBound<-abs(log(10^(-5)))/max(node.depth.edglength(tree))
  akaike.wts(c(
    fitContinuous(phy=tree,dat=bodySizes,model="BM")$opt$aicc,
    fitContinuous(phy=tree,dat=bodySizes,model="OU")$opt$aicc,
    fitContinuous(phy=tree,dat=bodySizes,model="EB",
      bounds=list(a=c(-aBound,0)))$opt$aicc
  ))
}

wtsTrees<-mclapply(timeTrees,function(x) sapply(x,compareModels))

```

now plot it

```

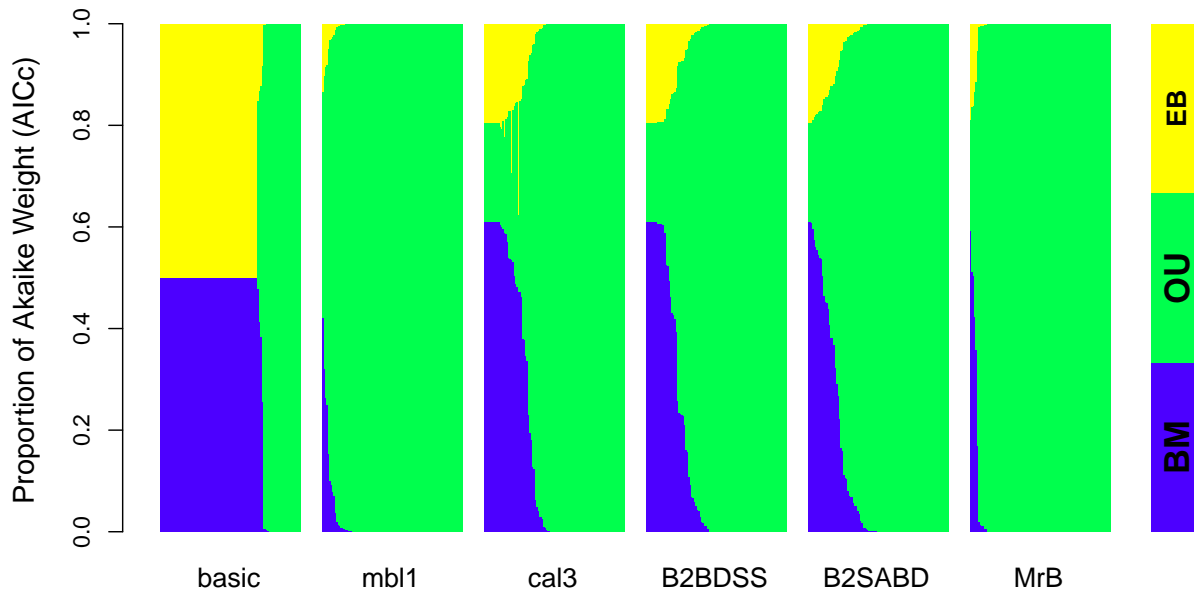
#order the weights by support for BM
wtsTreesSort<-lapply(wtsTrees,function(x) x[,order(-x[1,])])

#collapse to a single table with white bands inbetween

midCol<-matrix(c(0,0,0,1),4,15)
wtsPlot<-lapply(wtsTreesSort,function(x) rbind(x,0))
wtsPlot[1:(length(wtsPlot)-1)]<-lapply(1:(length(wtsPlot)-1),
  function(x) cbind(wtsPlot[[x]],midCol))
wtsPlot<-do.call(cbind,wtsPlot)
namesBar<-rep(NA,ncol(wtsPlot))
namesBar[49+(0:(length(timeTrees)-1))*(100+ncol(midCol))]<-names(timeTrees)
colorsBar<-c(topo.colors(3),"white")

#
#plot
layout(matrix(1:2,1,2),widths=c(7,0.5))
par(mar=c(3,5,1,0))
barplot(wtsPlot,names=namesBar,
  ylab="Proportion of Akaike Weight (AICc)",cex.names=1.2,cex.lab=1.25,
  col=colorsBar,border=NA) # "darkblue", "orangered", "forestgreen"
par(mar=c(3,0,1,1))
barplot(cbind(c(1,1,1,0)/3),col=colorsBar,axes=FALSE,border=NA)
text(x=0.7,y=1/6,"BM",srt=90,font=2,cex=1.5)
text(x=0.7,y=0.5,"OU",srt=90,font=2,cex=1.5)
text(x=0.7,y=1-(1/6),"EB",srt=90,font=2,cex=1.2)

```



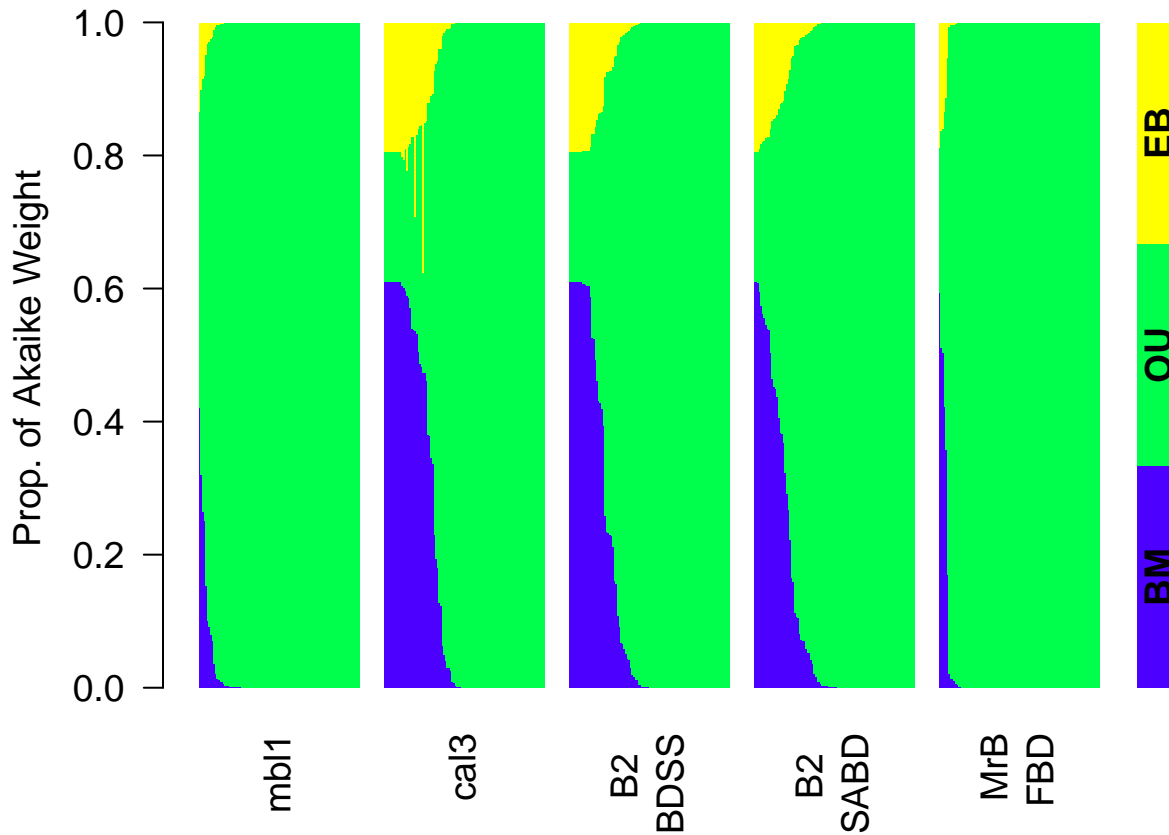
```
par(oldPar)
```

Let's look at results with *just* MBL, get rid of basic - after all, no one uses basic for this sort of thing

```
#order the weights by support for BM
wtsTreesSort<-lapply(wtsTrees,function(x) x[,order(-x[1,])])
# remove MBL
wtsTreesSort<-wtsTreesSort[-1]
namesWts<-names(wtsTreesSort)
namesWts[3:5]<-c("B2 \n BDSS","B2 \n SABD","MrB\nFBD")

#collapse to a single table with white bands inbetween
midCol<-matrix(c(0,0,0,1),4,15)
wtsPlot<-lapply(wtsTreesSort,function(x) rbind(x,0))
wtsPlot[1:(length(wtsPlot)-1)]<-lapply(1:(length(wtsPlot)-1),
  function(x) cbind(wtsPlot[[x]],midCol))
wtsPlot<-do.call(cbind,wtsPlot)
namesBar<-rep(NA,ncol(wtsPlot))
namesBar[49+(0:(length(wtsTreesSort)-1))*(100+ncol(midCol))]<-namesWts
colorsBar<-c(topo.colors(3),"white")

#plot
layout(matrix(1:2,1,2),widths=c(7,0.5))
par(mar=c(4,5,1,0))
barplot(wtsPlot,names=namesBar,cex.axis=1.2,
  ylab="",cex.names=1.2,las=2,
  col=colorsBar,border=NA)
mtext("Prop. of Akaike Weight",side=2,line=3,cex=1.2)
par(mar=c(4,0,1,1))
barplot(cbind(c(1,1,1,0)/3),col=colorsBar,axes=FALSE,border=NA)
text(x=0.7,y=1/6,"BM",srt=90,font=2,cex=1.2)
text(x=0.7,y=0.5,"OU",srt=90,font=2,cex=1.2)
text(x=0.7,y=1-(1/6),"EB",srt=90,font=2,cex=1.2)
```



`par(oldPar)`

The main thing Benson et al found was overwhelming support for OU in the theropods. They were using equal (not applied here) and MBL, which also strongly supports OU here.

The results are complex. I've shown in my Paleobiology paper that Basic and MBL have a known tendency to erroneously support OU in simulations when BM is the true model. Here, Basic shows a bizarre pattern of either being a toss-up between BM and EB, or strong support for OU. Benson et al. used MBL and got strong support for OU, which is also what we see here. Now, I've shown that cal3 minimized this biasing effect, and the results for cal3 are fairly similar to those for the Beast2 tip-dating analyses, with some support for BM, EB or OU in some trees, and some trees having a strong support for OU. MrBayes is perhaps the most worrisome: showing the same strong support for OU across all trees examined for OU.

As this is not a simulation, I cannot make any statements regarding whether this means that BEAST2, cal3 or MrBayes methods are producing more accurate results.

Regardless, the differences between BEAST2, cal3 and MrBayes in this analysis are extremely worrying as the only positive finding for performing model-choice comparative methods in the fossil record would have been if all methods had equally agreed.

[1] "Message was sent to david.bapst@sdsmt.edu! You have 19 messages left."