The Evolution of Labiodental Articulation in Indo-European

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S4.1 Introduction

Indo-European comparative linguistics has identified what is called *correspondence sets*: words with related meanings show systematic sound correspondences. For example, there is a large set of related words that begin with bilabial w in some languages, e.g. in English (will, word, wind etc.). These word-initial sounds systematically correspond to a bilabially articulated sound in some related languages (e.g. Latin $uol\bar{o}$, uerbum, uentus etc.) and to a labiodentally articulated sound in others (e.g. German wollen, Wort, Wind etc.). This establishes a set of correspondences that contains the articulations $\{w, v\}$ (among others). Each set reflects descent (with or without modification) from an ancestral proto-sound, but the reconstruction of the phonetic quality of this sound is an unresolved problem. Despite this problem, correspondence sets are traditionally labeled by a symbol that makes a vague suggestion on the phonetics, e.g. the $\{w, v\}$ set is conventionally labelled "*w" (with a distinctive asterisk), suggesting a bilabial realization. It is clear for experts, however, that these labels are mere suggestions and do not reflect an actual reconstruction of phonetics. To avoid confusion, we refer to the label of a correspondence set as a 'correspondeme'. Unlike a phoneme, a correspondence is not associated with a well-defined range of phonetic values. A correspondence only represents a distinct (meaning-differentiating) proto-sound from which all modern variants in a set derive, whatever that sound might have been phonetically. This observation challenges any inference from correspondeme labels to the presence or absence of labiodental places of articulation (an inference that was explicitly made by Hockett (1)).

Traditional attempts at reconstructing actual phonetic values of correspondemes are chiefly based on qualitative considerations of maximum parsimony in the phylogeny, coupled with a tacit assumption that the values closely reflect what is reported in the earliest phonetic descriptions of well-investigated western languages (e.g. bilabial realization in Latin and Ancient Greek for decendants of the $\{w, v\}$ set). This approach incurs two problems. First, maximum-parsimony methods are problematic because sound changes can be completely reversed within relatively short time spans. For example the Germanic nasal m became f before n in North Germanic (Old Norse, early Old Swedish nafn 'name') and reverted to m in late Old Swedish (namn). Second, arguments based on earliest descriptions or even attestations are problematic because all current estimates show that the time that elapsed between Proto-Indo-European and the earliest attested languages is at least as long as the time between these languages and now. This is true even for relative young age estimates (2).

Here we take a fresh approach to the problem and model sound change as Continuous-Time Markov Chains (CTMC), allowing for reversals and different transition rates between states (Section 3). We fit CTMC models using the Markov Chain Monte Carlo Sampling (MCMC) implemented in BayesTraits (3). We then take the best fitting models to estimate ancestral values (Section S4.4) and to reconstruct values for each time interval of Indo-European (Section S4.5). For this we apply Stochastic Character Mapping (4-6), a method that has proven valid for linguistic reconstruction elsewhere (7).

S4.2 Data and Phylogenies

Etymological research in Indo-European linguistics has established ten major correspondences which have a labiodential reflex in at least one daughter language: $*b^h$, *p, *w, *m, $*g^w$, $*g^{wh}$, $*k^w$, $*d^h$, $*k^j$, and *b. The phonetic values of correspondences are justified in detail in Section S6:

```
labiodental.data <- read.csv('../data/ie_labiodental_data_d.csv', stringsAsFactors=F)</pre>
```

Extant languages have 76% labiodentals. Figures S5.1 and S5.2 show their distribution in two different phylogenies of Indo-European (using the ggtree(8)). We use phylogenies from Chang and colleagues(2) (identified by the suffix .c here) and from Bouckaert and colleagues(9) (suffix .b):

```
ie.c.sum.tree <- read.nexus('../data/indoeuropean-C-sum-matched.nex')
ie.c.sum.tree$tip.label <- gsub('(.*)(<.*>)','\\1', ie.c.sum.tree$tip.label)
ie.c.sum.tree <- drop.tip(ie.c.sum.tree,</pre>
```

```
setdiff(ie.c.sum.tree$tip.label, labiodental.data$language))
ie.b.sum.tree <- read.nexus('.../data/indoeuropean-B-sum-matched.nex')</pre>
ie.b.sum.tree$tip.label <- gsub('(.*)(<.*>)','\\1', ie.b.sum.tree$tip.label)
ie.b.sum.tree <- drop.tip(ie.b.sum.tree,</pre>
                         setdiff(ie.b.sum.tree$tip.label, labiodental.data$language))
ie.c.trees <- read.nexus('../data/indoeuropean-C-20k-matched.nex')</pre>
ie.c.trees <- lapply(ie.c.trees, function(t) {</pre>
    t$tip.label <- gsub('(.*)(<.*>)','\\1', t$tip.label)
    t <- drop.tip(t, setdiff(t$tip.label, labiodental.data$language))</pre>
    return(t)
    })
    class(ie.c.trees) <- 'multiPhylo'</pre>
    attributes(ie.c.trees)$TipLabel <- ie.c.trees[[1]]$tip.label</pre>
ie.b.trees <- read.nexus('../data/indoeuropean-B-10k-matched.nex')</pre>
ie.b.trees <- lapply(ie.b.trees, function(t) {</pre>
    t$tip.label <- gsub('(.*)(<.*>)','\\1', t$tip.label)
    t <- drop.tip(t, setdiff(t$tip.label, labiodental.data$language))</pre>
    return(t)
    })
    class(ie.b.trees) <- 'multiPhylo'</pre>
    attributes(ie.b.trees)$TipLabel <- ie.b.trees[[1]]$tip.label</pre>
```

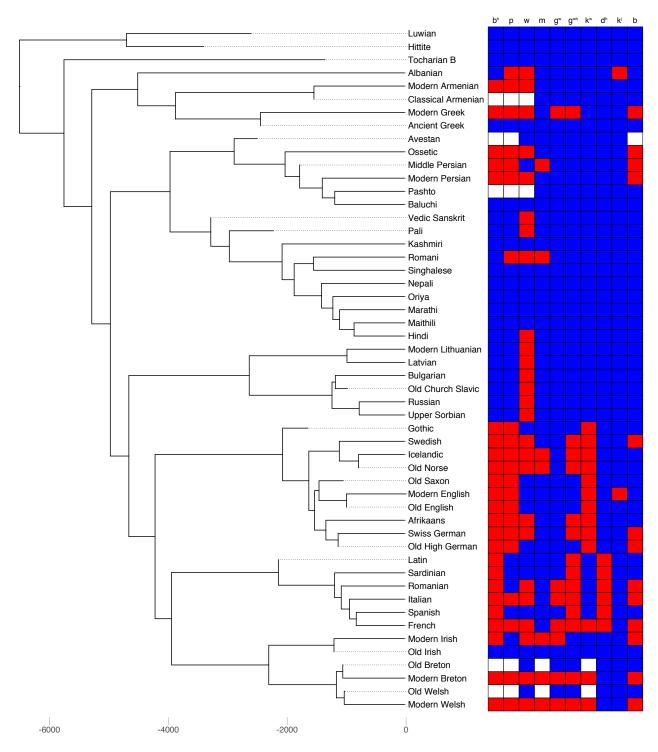


Figure S4.1: Labiodental reflexes in each correspondeme that contains at least one labiodental reflex. Red indicates presence, blue absence a labiodental reflex. White indicates unknown or uncertain data. Maximum clade consensus tree from Chang et al.

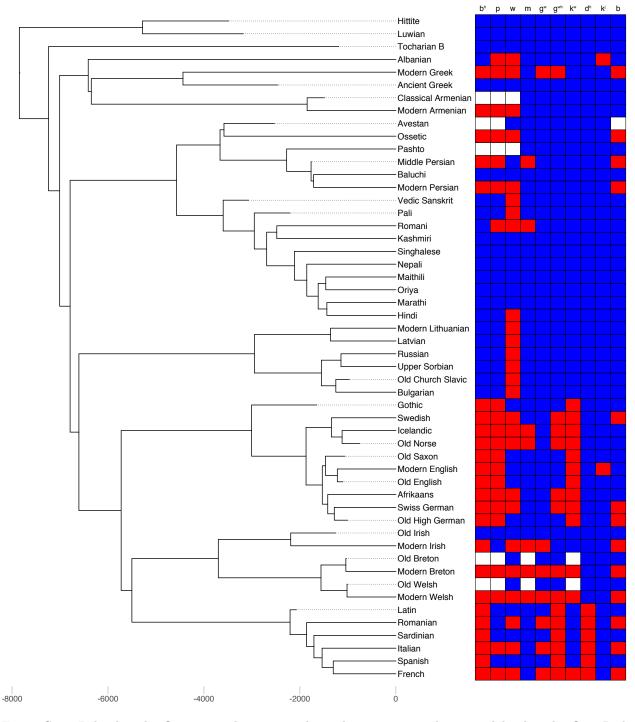


Figure S4.2: Labiodental reflexes in each correspondeme that contains at least one labiodental reflex. Red indicates presence, blue absence a labiodental reflex. White indicates unknown or uncertain data. Maximum clade consensus tree from Bouckaert et al

S4.3 Modeling transition rates

We model language change as CTMCs with the two states:

- Y: yes, the reflex of a given correspondence is labiodental
- N: no, the reflex of a given correspondeme is not labiodental

We then estimate the rates of change q between two states in a Bayesian framework (5, 10-12):

- qYN: instantaneous rate of loosing a labiodental realization (Yes>No)
- qNY: instantaneous rate of gaining a labiodental realization (Yes>No)

In order to assess whether there is a diachronic bias in either direction, e.g. whether gains are favored over losses, we compare two models for each correspondeme:

- ARD: all rates different, i.e. rates of change towards vs away from a labiodental realization are different: qYN\neqqNY. This model therefore has two parameters.
- ER: equal rates, i.e. rates of change towards vs away from a labiodental realization are the same: qYN=qNY. This model therefore has one parameter.

In each case, the models are compared with Bayes Factors (BF), which are defined as double the difference between the log marginal likelihood of the more complex model, i.e. the ARD model, and the log marginal likelihood of the simpler model, i.e. the ER model. BF > 2 are considered to give "positive evidence" for the better-fitting model; between 5 and 10 "strong evidence" and > 10 "very strong evidence".

We replicate all MCMC analyses several times(3) and report the median and the median absolute deviation across these replications. The parameters of each run of the analysis were determined on the basis of visual inspections of trace plots of the likelihoods and (in the case of posterior tree sample) of the tree mixing.

S4.3.1 Procedures

We use wrapper scripts which run BayesTraitsV2 (3) in the background and allow various steps of post-processing the output:

```
fit.mcmc <- function(variable, tree=ie.sum.tree, data=labiodental.data,</pre>
                prior="uniform 0 .005", assumed.mrca=NULL,
                iterations=mcmc.iterations, burn.in=mcmc.burn.in,
                sampling.rate=mcmc.sampling.rate, covarion=F, reuse.tree=T) {
    test.ard <- Discrete(tree, data[,c('language', variable)], "Bayesian",</pre>
            pa=prior, it=iterations, bi=burn.in, sa=sampling.rate,
            rm=T, fo=assumed.mrca, cv=covarion, reuse.tree=reuse.tree)
    test.er <- Discrete(tree, data[,c('language', variable)], "Bayesian",</pre>
            resall='qNY', it=iterations, pa=prior, bi=burn.in, sa=sampling.rate,
            fo=assumed.mrca, cv=covarion, reuse.tree=reuse.tree)
    summary.er <- tail(test.er[,5],1)</pre>
    summary.ard <- tail(test.ard[,grep('q', colnames(test.ard), value=T)],1)</pre>
    bfres <- bftest(test.er, test.ard)</pre>
    bfres$Better <- ifelse(bfres$BetterModel %in% 'Model 1', 'ER', 'ARD')
    return(list(ARD=test.ard,
            ER=test.er,
            ER.vs.ARD=bfres[,c(1,3)],
            ER.rate=summary.er,
            ARD.rates=summary.ard
            ))
```

Function for tracing the MCMC iterations:

```
trace.plots <- function(mcmc.res, model=c('ARD','ER'), which=c('Likelihood', 'Rates', 'Trees')) {
    switch (model.
        ARD = {df <- do.call(rbind, lapply(seq along(mcmc.res), function(r) {
               x <- mcmc.res[[r]][['ARD']]</pre>
               x$replicate <- r
               return(x)
               }))
              },
        ER = {df <- do.call(rbind, lapply(seq_along(mcmc.res), function(r) {
               x <- mcmc.res[[r]][['ER']]</pre>
               x$replicate <- r
               return(x)
               }))
              }
    )
    switch (which,
    Likelihood = { ggplot(df, aes(x=Iteration,y=Harmonic.Mean)) + geom_line(size=.2) +
                    facet_wrap(~replicate) + theme_bw(base_size = 12) },
                 { gather(df, rate, value, qNY:qYN) %>%
    Rates =
                            ggplot(aes(x=Iteration, y=value, colour=rate)) +
                             geom_line(size=.2) + theme(legend.position='top') +
                             guides(colour = guide_legend(override.aes = list(size=2))) +
                            facet_wrap(~replicate) + theme_bw(base_size = 12)
                         },
                {  #ggplot(df, aes(x=Iteration, y=Tree.No)) + geom_line(size=.2)
    Trees =
                   ggplot(df, aes(x=Tree.No)) + geom_density(size=.2) +
                facet_wrap(~replicate) + theme_bw(base_size = 12) }
    )
}
```

Some helpers for exploring and plotting the results:

```
)}
ml.rates <- function(m) {</pre>
    x <- do.call(rbind, sapply(m, rbind))
    x$model \leftarrow rep(c('ER', 'ARD'), nrow(x)/2)
    return(x[,c('model',grep('q', colnames(x), value=T))])
    }
transition.matrix <- function(m, aggr=c("median", "mad"), model=NULL, prob=T, years=100) {
    if(is.null(model)) {res <- sapply(m, function(x) unlist(tail(x,1)))} else {</pre>
        test_that('If you request a specific model, there should be a choice', {
            expect_true(any(names(m[[1]]) %in% c('ARD', 'ER')))
    switch (model,
        ARD = {res <- sapply(m, function(x) unlist(tail(x$ARD,1)))},
        ER = {res <- sapply(m, function(x) unlist(tail(x$ER,1)))}</pre>
    }
    switch(aggr,
        median = {rates <- apply(res[grepl('q', rownames(res)),], 1, median)},</pre>
               = {rates <- apply(res[grepl('q', rownames(res)),], 1, mad)}
    # extract names, and do it in the right order so we can use it below for labeling:
    symbols <- unique(substr(gsub('q','',names(rates)),1,1))</pre>
    q.mat.diagonal <- sapply(split(rates, ceiling(seq_along(rates)/(length(symbols)-1))),
    q.mat <- matrix(NA, ncol=length(symbols), nrow=length(symbols))</pre>
    diag(q.mat) <- q.mat.diagonal</pre>
    idx <- which(is.na(q.mat), arr.ind=T)</pre>
    q.mat[idx[order(idx[,1]),]] <- rates # reordered indices by rows first</pre>
    # perform matrix exponentiation if requested:
    if(prob) { q.mat <- matexpo(years*q.mat) }</pre>
    dimnames(q.mat) <- list(symbols,symbols)</pre>
    return(q.mat)
plot.matrix <- function(m, label='x', legend=T, colors=color.scheme[-1],</pre>
                         node.size=20, padding=.8, weight.range=c(.5,1),
                         label.dodge=-.1, label.size=3) {
    gg <- graph_from_adjacency_matrix(adjmatrix=m, weighted=TRUE, mode="directed", diag=T)
    myarrow <- arrow(angle = 30, length = unit(0.3, "cm"), ends = "last", type = "closed")</pre>
    if(ncol(m)==2) \{ directions=rep(c(180,0),2) \} else
                         { directions=rep(c(30,270,150),3) } # unelegant... but how else?
    p <- ggraph(gg, layout = 'linear', circular=ncol(m)>2) +
         geom_edge_fan(aes(width=round(weight,2), label=round(weight,2)), n=200,
                    angle_calc='along', label_dodge=unit(label.dodge, "cm"),
                    label_size=label.size,
                    arrow=myarrow , end_cap = circle(padding, 'cm'),
                    start_cap = circle(padding, 'cm')
                       ) +
         geom_edge_loop(aes(width=round(weight,2)), direction=directions, label=round(weight,2)), arrow=m
                       label_size=label.size,
                         end_cap = circle(padding, 'cm'),
                         start_cap = circle(padding, 'cm')
```

Functions for estimating ARD models and then using the resulting transition rates for Stochastic Character Mapping (see the explanation in Section 3.3 below):

```
years.per.change <- function(variable, trees=ie.trees, sum.tree=ie.sum.tree, data=labiodental.data,
                               tree.simulations=nsim, rate.replications=replications,
                              prior='uniform 0 .0025', reuse.tree=T) {
  # fit model with BayesTraits:
  model <- replicate(rate.replications,</pre>
      Discrete(trees, data[,c('language', variable)],
               mode="Bayesian", pa=prior, it=mcmc.iterations, bi=mcmc.burn.in,
               sa=mcmc.sampling.rate, cv=F, reuse.tree=reuse.tree),
               simplify=F)
  # prepare data for simmap:
  nas <- c('-','?') # catch NAs
  states <- data[, variable]</pre>
  names(states) <- data$language</pre>
  state.symbols <- setdiff(as.character(unique(states)),nas)</pre>
  n.states <- length(state.symbols)</pre>
  if(any(states %in% nas | is.na(states))) { # see ?make.simmap
    states <- to.matrix(states, state.symbols)</pre>
    states[rowSums(states)==0,] <- rep(1/n.states) # equal probability
  # extract Q matrix:
  q.mat <- transition.matrix(model, 'median', prob=F)</pre>
  # estimate simmaps with a flat root prior:
  treemaps <- make.simmap(sum.tree, states, Q=q.mat, pi='estimated',</pre>
                           nsim=tree.simulations, message=F)
  # extract number of changes, translate into how many years a change takes:
  simmap.description <- describe.simmap(treemaps, message=F)</pre>
  median.n.changes <- median(simmap.description$count[,'N']) # N = N(transitions)</pre>
  min.n.changes <- min(simmap.description$count[,'N'])</pre>
  max.n.changes <- max(simmap.description$count[,'N'])</pre>
  return(list(simmap.description=simmap.description,
```

```
median.years = round(sum(sum.tree$edge.length)/median.n.changes),
    min.years = round(sum(sum.tree$edge.length)/max.n.changes),
    max.years = round(sum(sum.tree$edge.length)/min.n.changes)
    ))
}
est.changes <- function(simmap.description, sum.tree) {
    apply(sapply(simmap.description, function(x) x$count[,'N']), 2, function(col) {
        sum(sum.tree$edge.length)/col
        }) %>% as.data.frame %>%
        gather(correspondeme, years)
    }
}
```

S4.3.2 Parameters

Replications:

```
B=10
```

Replications of covarion models:

```
B.cv=3
```

MCMC iterations:

```
mcmc.iterations=1e+07
```

Burn in:

```
mcmc.burn.in=1e+05
```

Sampling rate:

```
mcmc.sampling.rate=1e+03
```

S4.3.3 Evaluation of priors

We defined the prior distribution for each model so that the estimated number of changes is within a realistic ballpark. To assess this ballpark we explored transition rate estimates obtained with priors of $\mathcal{U}(0,.0025)$, $\mathcal{U}(0,.005)$ and $\mathcal{U}(0,.01)$ by performing Stochastic Character Mapping (see Section 5 below). For this purpose we focus on models allowing for rate differences (ARD). This allows a larger range of rates to explore. We then also compare the rates obtained with these priors with rates estimated from Maximum-Likelihood models.

Parameters:

 $Stochastic\ character\ mappings:$

```
nsim=100
```

Replications of rate estimates:

```
replications=5
```

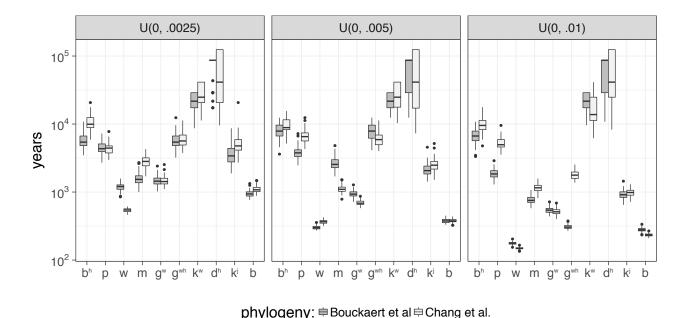


Figure S4.3: Estimated number of years per change per prior assumptions about rates of change

S4.3.3.1 Speed of change allowed under various prior distributions on rates

```
correspondemes <- c('bh','p','w','m','gw','gwh','kw','dh','ky','b')</pre>
```

Phylogenies from Chang et al.

Phylogenies from Bouckaert et al.

S4.3.3.2 Maximum Likelihood estimates of rates

Phylogenies from Chang et al.

0.00014 0.00012 1e-04 4e-05

3.11028 0.00017 0.00084 1.29729 0.07283 1e-04 2.72577 1e-05 4.23726 0.00269

1e-05 0.00011 0.00057

Phylogenies from Bouckaert et al.

median 0.00012 0.00017 8e-04

```
(ml.estimates.b <- sapply(correspondemes, function(crsp) {
    ml <- replicate(B, fit.ml(crsp, tree=ie.b.sum.tree), simplify=F)
    rates <- unlist(ml.rates(ml)[,-1])
    return(data.frame(median=round(median(rates),5), max=round(max(rates),5)))
}))</pre>
```

```
##
          bh
                  р
                                   m
                                                    gwh
                                                             kw
                                                                              ky
                                                                                        b
## median 7e-05
                  0.00012 0.00068 1e-04
                                                                              1e-04
                                           7e-04
                                                    7e-05
                                                             3e-05
                                                                      1e-05
                                                                                        0.00292
          2.43028 0.76684 3.40766 2.95999 2.82243 1.48305 28.73511 1.03078 48.16946 1.34079
```

S4.3.4 Individual analyses

Given the results of the previous section, a prior of $\mathcal{U}(0,.01)$ seems reasonable, i.e. it is large enough without allowing unrealistically fast or unrealistically slow rates of change:

```
prior="uniform 0 .01"
```

S4.3.4.1 Phylogenies from Chang et al.

```
Reflexes of *b^h:
bh.mcmc.c <- replicate(B, fit.mcmc('bh',</pre>
                                             tree=ie.c.trees, prior=prior), simplify=F)
Reflexes of *p:
p.mcmc.c <- replicate(B, fit.mcmc('p',</pre>
                                              tree=ie.c.trees, prior=prior), simplify=F)
Reflexes of *w:
w.mcmc.c <- replicate(B, fit.mcmc('w',
                                              tree=ie.c.trees, prior=prior), simplify=F)
Reflexes of *m:
m.mcmc.c <- replicate(B, fit.mcmc('m',</pre>
                                              tree=ie.c.trees, prior=prior), simplify=F)
Reflexes of *q^w:
gw.mcmc.c <- replicate(B, fit.mcmc('gw',</pre>
                                              tree=ie.c.trees, prior=prior), simplify=F)
Reflexes of *a^{wh}:
gwh.mcmc.c <- replicate(B, fit.mcmc('gwh', tree=ie.c.trees, prior=prior), simplify=F)
Reflexes of k^w:
kw.mcmc.c <- replicate(B, fit.mcmc('kw', tree=ie.c.trees, prior=prior), simplify=F)</pre>
```

```
Reflexes of *d^h:
dh.mcmc.c <- replicate(B, fit.mcmc('dh', tree=ie.c.trees, prior=prior), simplify=F)</pre>
Reflexes of *k^j:
ky.mcmc.c <- replicate(B, fit.mcmc('ky',</pre>
                                             tree=ie.c.trees, prior=prior), simplify=F)
Reflexes of *b:
b.mcmc.c <- replicate(B, fit.mcmc('b', tree=ie.c.trees, prior=prior), simplify=F)
S4.3.4.2 Phylogenies from Bouckaert et al.
Reflexes of *b^h:
bh.mcmc.b <- replicate(B, fit.mcmc('bh', tree=ie.b.trees, prior=prior), simplify=F)
Reflexes of *p:
p.mcmc.b <- replicate(B, fit.mcmc('p',</pre>
                                             tree=ie.b.trees, prior=prior), simplify=F)
Reflexes of *w:
w.mcmc.b <- replicate(B, fit.mcmc('w',
                                             tree=ie.b.trees, prior=prior), simplify=F)
Reflexes of *m:
m.mcmc.b <- replicate(B, fit.mcmc('m',</pre>
                                             tree=ie.b.trees, prior=prior), simplify=F)
Reflexes of *q^w:
gw.mcmc.b <- replicate(B, fit.mcmc('gw', tree=ie.b.trees, prior=prior), simplify=F)</pre>
Reflexes of *q^{wh}:
gwh.mcmc.b <- replicate(B, fit.mcmc('gwh', tree=ie.b.trees, prior=prior), simplify=F)
Reflexes of k^w:
kw.mcmc.b <- replicate(B, fit.mcmc('kw', tree=ie.b.trees, prior=prior), simplify=F)
Reflexes of *d^h:
dh.mcmc.b <- replicate(B, fit.mcmc('dh', tree=ie.b.trees, prior=prior), simplify=F)</pre>
Reflexes of *k^j:
```

S4.3.5 Results

Reflexes of *b:

ky.mcmc.b <- replicate(B, fit.mcmc('ky',</pre>

Figure S4.4 summarizes the models in terms of the logarithm of the Bayes Factor (logBF) across replications and phylogenies. logBF is defined as double the difference between the log marginal likelihood of the more complex model (assuming unequal rates) and the log marginal likelihood of the simpler model (assuming equal rates). Values above 2 are usually considered to support the complex model and this is indicated by light blue shading in the graphs. Only the correspondences m, g, and b show evidence for more

b.mcmc.b <- replicate(B, fit.mcmc('b', tree=ie.b.trees, prior=prior), simplify=F)

tree=ie.b.trees, prior=prior), simplify=F)

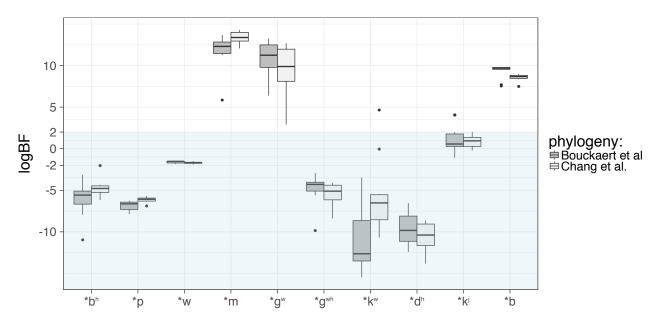


Figure S4.4: Bayes Factor evidence for different-rate model compared to equal-rate model. The blue shading covers the range conventionally considered not to give evidence.

complex models with unequal rates. The rate estimates themselves are plotted in Figure S4.5. The three correspondemes with unequal rates are more likely to lose labiodental reflexes than to gain them.

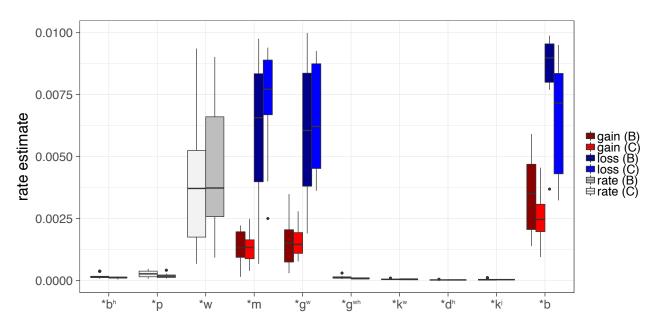


Figure S4.5: Estimated rates of gain and loss of labiodentals in the best models. Gray colors indicate that the best model assumes equal rates of gain and loss. Dark colors indicate phylogenies from Bouckaert et al (B), light colors phylogenies from Chang et al. (C).

S4.4 Ancestral state estimates

CTMC models include an estimate on the probability distribution of the root value. We extract this from the best-fitting models and report the results in Figure S4.6.

```
posterior.size=(mcmc.iterations-mcmc.burn.in)/mcmc.sampling.rate
ace.df <- data.frame(</pre>
           phylogeny=c(rep("Chang et al.'s phylogeny",
                             B*length(correspondemes)*posterior.size),
                       rep("Bouckaert et al.'s phylogeny",
                             B*length(correspondemes)*posterior.size)),
           correspondeme=factor(rep(
                               unlist(lapply(correspondemes,rep,B*posterior.size)),
                               levels=correspondemes,
                               labels=c("*b","*p","*w","*m","*g","*g ","*k ","*d ","*k ","*b")),
           Prob=c(unlist(lapply(correspondemes, function(crsp) {
                   sapply(get(paste0(crsp, '.mcmc.c')), function(x) {
                               if(crsp %in% c('*m','*b','*g')) { x$ARD$Root.P.Y. } else {
                               x$ER$Root.P.Y.
                               }
                           }
                        ) })),
                   unlist(lapply(correspondemes, function(crsp) {
                    sapply(get(paste0(crsp, '.mcmc.b')), function(x) {
                               if(crsp %in% c('*m','*b','*g')) { x$ARD$Root.P.Y. } else {
                               x$ER$Root.P.Y.
                               }
                        ) }))
```

Figure S4.6 suggests that for 8 correspondenes, the probability of a labiodental realization in proto-Indo-European was very low. For two correspondenes — *w and *b — the ancestral state cannot be sufficiently resolved and is estimated at or close to 50% probabilities. In these two cases, there is no decisive evidence in favor of nor against a labiodental realization in proto-Indo-European. One way of resolving this issue is to fit and compare models with vs without assumed proto-states.

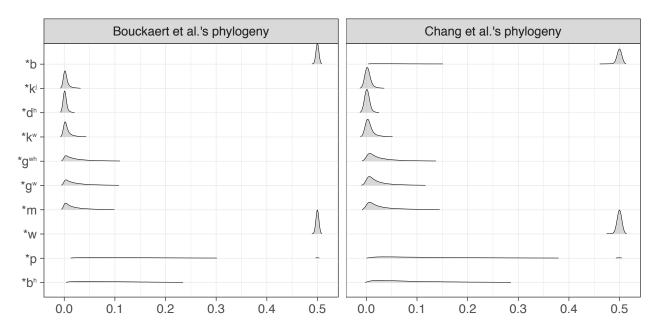


Figure S4.6: Posterior probabilities of labiodentals in PIE, based on the best-fitting models

S4.4.1 Reconstruction comparing assumed proto-states

S4.4.1.1 Based on the phylogenies from Chang et al.

```
Reconstruction of *w:
```

The best fitting model is:

```
unique(model.fits(w.mcmc.c.Y)[,2])
```

```
## [1] "ER"
median(model.fits(w.mcmc.c.Y)[,1])
```

[1] 1.791384

There is no evidence for or against a model that assumes labiodentals:

```
fossil.fits(w.mcmc.c.Y, w.mcmc.c.N, model='ER')
```

```
##
      BayesFactor BetterModel
## 1
         0.004066
                      Model 2
                      Model 1
## 2
         0.000848
## 3
         0.013824
                      Model 2
## 4
         0.005306
                      Model 2
         0.000482
## 5
                      Model 1
## 6
         0.035176
                      Model 2
## 7
         0.163120
                      Model 1
## 8
         0.020978
                      Model 2
## 9
         0.003164
                      Model 1
## 10
         0.000472
                      Model 2
```

Reconstruction of *b:

The best fitting model is:

```
unique(model.fits(b.mcmc.c.Y)[,2])
```

```
## [1] "ARD"
median(model.fits(b.mcmc.c.Y)[,1])
```

```
## [1] 9.792657
```

There is no evidence for or against a model that assumes labiodentals:

```
fossil.fits(b.mcmc.c.Y, b.mcmc.c.N, model='ARD')
```

```
##
      BayesFactor BetterModel
         0.336638
## 1
                      Model 1
## 2
         0.384274
                      Model 2
## 3
                      Model 1
         0.516128
## 4
         0.282814
                      Model 2
## 5
                      Model 1
         2.060142
## 6
         0.858620
                      Model 1
                      Model 2
## 7
         0.392786
## 8
         2.880922
                      Model 2
## 9
                      Model 1
         0.293846
## 10
         0.041236
                      Model 2
```

S4.4.1.2 Based on the phylogenies from Bouckaert et al.

Reconstruction of *w:

The best fitting model is:

```
unique(model.fits(w.mcmc.b.Y)[,2])
```

```
## [1] "ER"
```

```
median(model.fits(w.mcmc.b.Y)[,1])
```

```
## [1] 1.622678
```

There is no evidence for or against a model that assumes labiodentals:

```
fossil.fits(w.mcmc.b.Y, w.mcmc.b.N, model='ER')
```

```
BayesFactor BetterModel
##
## 1
         0.015978
                      Model 2
## 2
         0.019660
                      Model 2
## 3
                      Model 1
         0.016286
         0.004662
                      Model 2
## 5
         0.011198
                      Model 2
## 6
         0.017590
                      Model 2
                      Model 2
## 7
         0.013098
         0.007294
## 8
                      Model 2
## 9
         0.045020
                      Model 1
## 10
         0.005688
                      Model 2
```

Reconstruction of *b:

The best fitting model is:

```
unique(model.fits(b.mcmc.b.Y)[,2])
## [1] "ARD"
median(model.fits(b.mcmc.b.Y)[,1])
```

[1] 9.851225

There is no evidence for or against a model that assumes labiodentals:

```
fossil.fits(b.mcmc.b.Y, b.mcmc.b.N, model='ARD')
```

```
##
      BayesFactor BetterModel
## 1
         0.557948
                       Model 1
## 2
         2.714010
                       Model 1
## 3
         0.250344
                       Model 1
## 4
         0.436856
                       Model 2
## 5
         0.670000
                       Model 1
## 6
         1.626904
                       Model 2
## 7
         0.274046
                       Model 1
## 8
         0.205004
                       Model 1
## 9
         0.600036
                       Model 1
                       Model 1
## 10
         4.628180
```

S4.4.2 Summary

In summary, there is no evidence for or against positing labiodentals as ancestral states of the *w and *b correspondemes. In the case of *b we earlier observed a diachronic bias towards loss of labiodental realizations (Figure S4.5). The rate estimates for *w suggest general instability, with equally high rates of gain and loss. This confirms the qualitative observation that this correspondeme varies substantially in closely related languages (e.g. German vs. English, Spanish vs. Gallo-Romance) and its realization is highly unstable in some extant languages. For example in Hindi, there is substantial variation between [w], $[\beta]$, or [v] (13).

S4.5 Stochastic Character Mapping

Stochastic Character Mapping (4, 5) samples a posterior distribution of character histories given a phylogeny, the current states, and transition rates. We estimate maps using the rate estimates from the best-fitting models estimated in the previous section. The maps are estimated using the algorithm in phytools::make.simmap (6) and relies on Maximum Clade Credibility (MCC) summary trees for easier visualization as probability changes along each branch. Ancestral states at nodes however are estimates using posterior phylogeny samples and are plotted as pie charts.

In all models, we assume constant rates of change over time. This assumption is conservative and disfavors our hypothesis because it will over-estimate the age of innovations. Non-constant rates of change would allow for a late acceleration of innovations.

S4.5.1 Procedures

```
compute.simmap <- function(variable, tree=ie.c.sum.tree, data=labiodental.data,</pre>
         model=c('ER','ARD'), iterations=B, resolution=res) {
        # get the right model based on the tree
        if(grepl('c', deparse(substitute(tree)))) {type='c'} else {type='b'}
        # get Q matrix from BayesTraits results:
        mcmc.results <- get(paste0(tolower(variable), '.mcmc.', type))</pre>
        Q.matrix <- transition.matrix(mcmc.results, 'median', model, prob=F)
        # prepare data for simmap, catching NAs (which will be estimated)
        nas <- c('-','?') # catch NAs
        states <- data[, variable]</pre>
        names(states) <- data$language</pre>
        state.symbols <- sort(setdiff(as.character(unique(states)),nas))</pre>
        n.states <- length(state.symbols)</pre>
            # estimating NAs with a uniform prior:
            if(any(states %in% nas | is.na(states))) {
                     states <- to.matrix(states, state.symbols)</pre>
                     states[rowSums(states)==0,] <- rep(1/n.states)</pre>
                 }
        # make simmaps with a flat root prior:
        treemaps <- make.simmap(tree, states, model=model, Q=Q.matrix,
                     pi='estimated', nsim=iterations, message=F)
```

The following function estimates SCMs on a single tree, but it adds node estimates based on a posterior tree sample:

S4.5.2 Parameters

Number of simulated histories per tree:

```
B=100
```

Resolution (bins): the number of time intervals (bins) is fixed by the resolution parameter of phytools::densityMap, which we set to:

```
res=200
```

Setting the parameter to this value results in bins of about 30 years, roughly reflecting the state at one generation of speakers.

S4.5.3 Individual analyses

A full analysis on the posterior tree sample is computationally extremely expensive (B simulations \times 10 correspondences \times 20,000 trees). In response to this, we use only the last 1000 trees from the posterior sample of each phylogeny:

```
ie.c.trees.sample <- tail(ie.c.trees, 1000)
ie.b.trees.sample <- tail(ie.b.trees, 1000)</pre>
```

The results of this is displayed as pie charts at the nodes. But the stochastic character maps along the branches are based on MCC summary trees.

S4.5.3.1 Reconstruction of labiodental reflexes for $*b^h$

```
correspondeme='bh'
bh.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
bh.density.c <- densityMap(bh.simmaps.c, plot=F, res=res)
bh.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

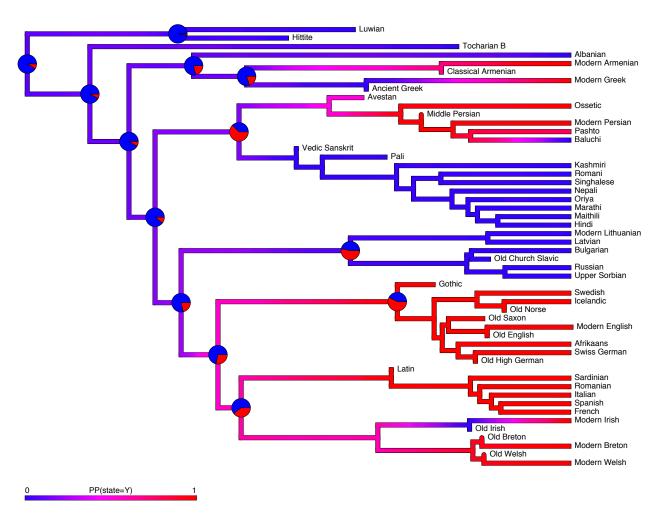


Figure S4.7: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondeme $*b^h$, assuming the phylogenies estimated by Chang et al.

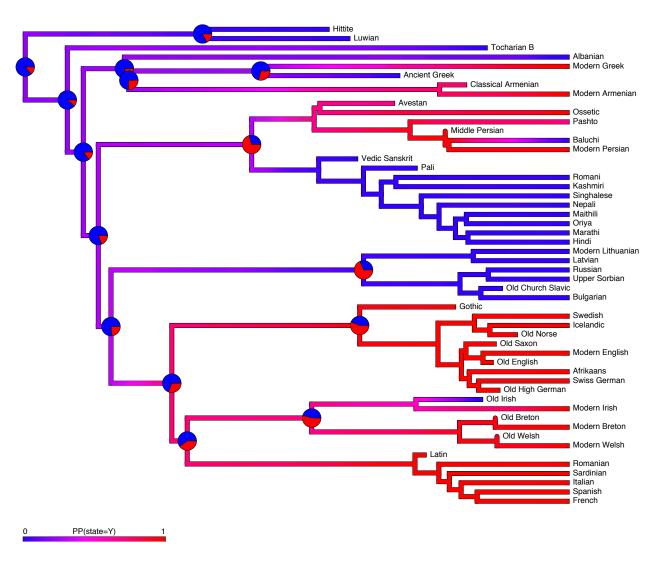


Figure S4.8: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondeme $*b^h$, assuming the phylogenies estimated by Bouckaert et al.

```
bh.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
bh.density.b <- densityMap(bh.simmaps.b, plot=F, res=res)
bh.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```

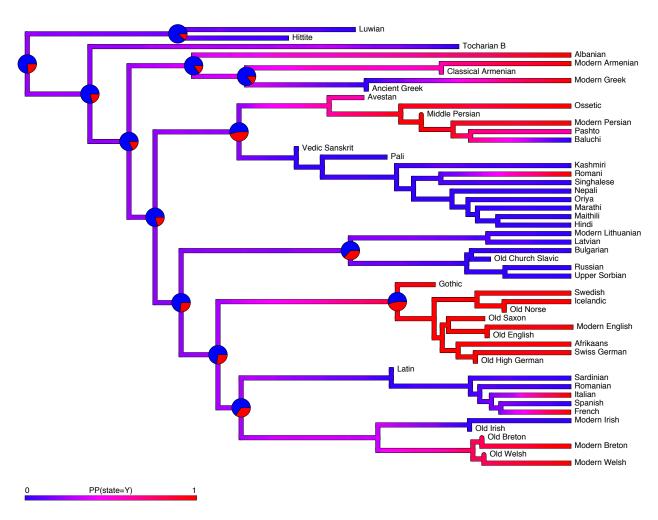


Figure S4.9: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence *p, assuming the phylogenies estimated by Chang et al.

S4.5.3.2 Reconstruction of labiodental reflexes for *p

```
correspondeme='p'
p.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
p.density.c <- densityMap(p.simmaps.c, plot=F, res=res)
p.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

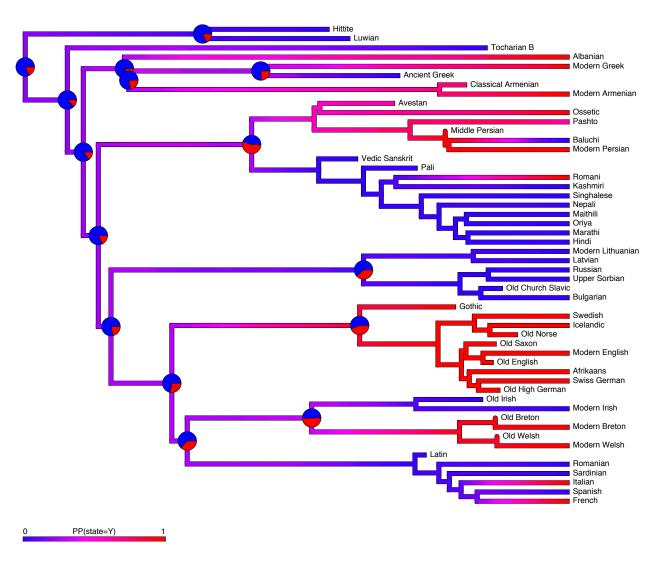


Figure S4.10: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondeme *p, assuming the phylogenies estimated by Bouckaert et al.

```
p.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
p.density.b <- densityMap(p.simmaps.b, plot=F, res=res)
p.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```



Figure S4.11: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondene *w, assuming the phylogenies estimated by Chang et al.

S4.5.3.3 Reconstruction of labiodental reflexes for *w

```
correspondeme='w'
w.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
w.density.c <- densityMap(w.simmaps.c, plot=F, res=res)
w.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

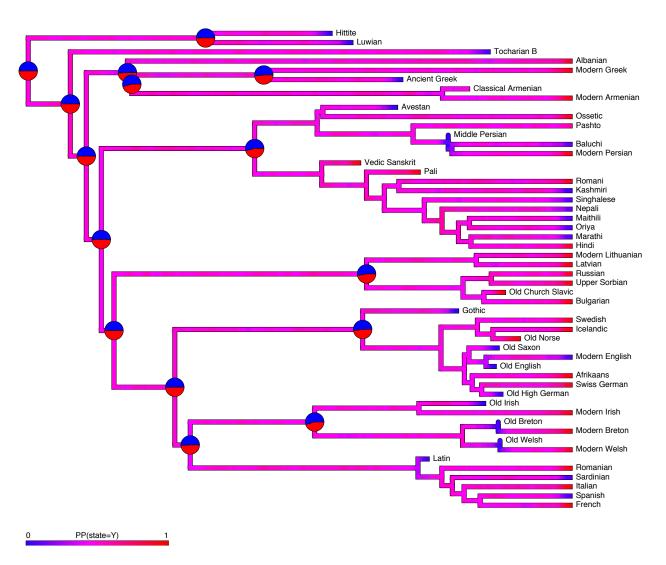


Figure S4.12: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondene *w, assuming the phylogenies estimated by Bouckaert et al.

```
w.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
w.density.b <- densityMap(w.simmaps.b, plot=F, res=res)
w.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```

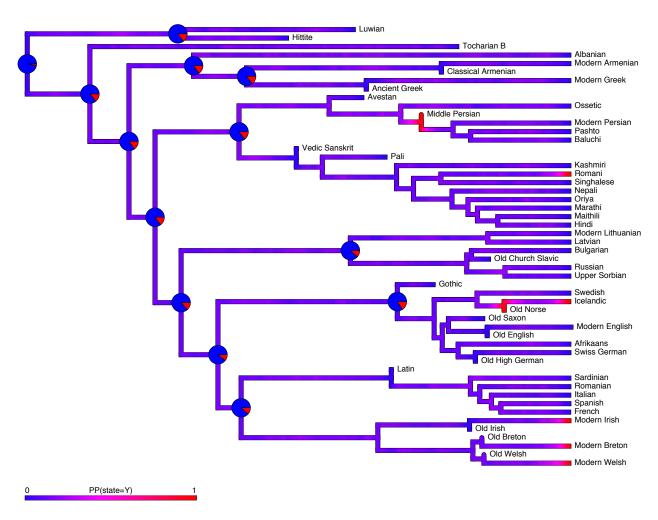


Figure S4.13: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence *m, assuming the phylogenies estimated by Chang et al.

S4.5.3.4 Reconstruction of labiodental reflexes for *m

```
correspondeme='m'
m.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ARD')
m.density.c <- densityMap(m.simmaps.c, plot=F, res=res)
m.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ARD')</pre>
```

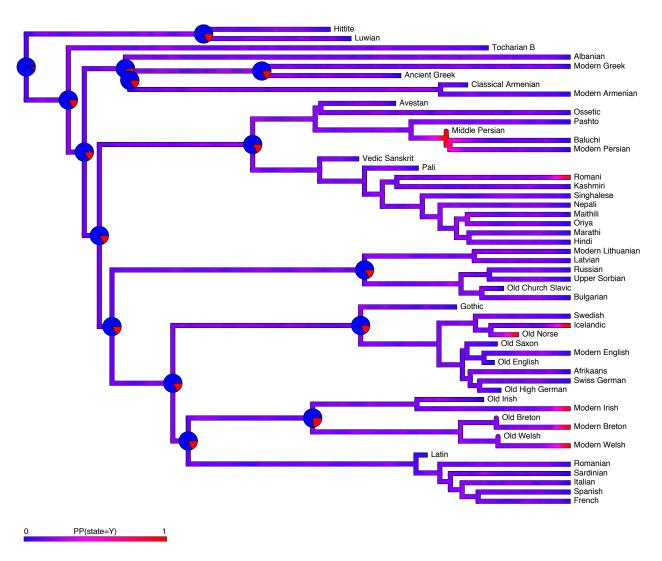


Figure S4.14: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondene m, assuming the phylogenies estimated by Bouckaert et al.

```
m.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ARD')
m.density.b <- densityMap(m.simmaps.b, plot=F, res=res)
m.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ARD')</pre>
```

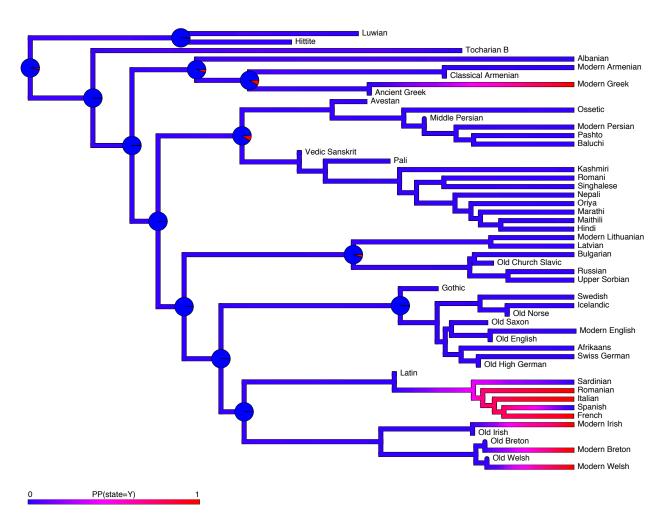


Figure S4.15: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence $*g^w$, assuming the phylogenies estimated by Chang et al.

S4.5.3.5 Reconstruction of labiodental reflexes for $*g^w$

```
correspondeme='gw'
gw.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
gw.density.c <- densityMap(gw.simmaps.c, plot=F, res=res)
gw.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

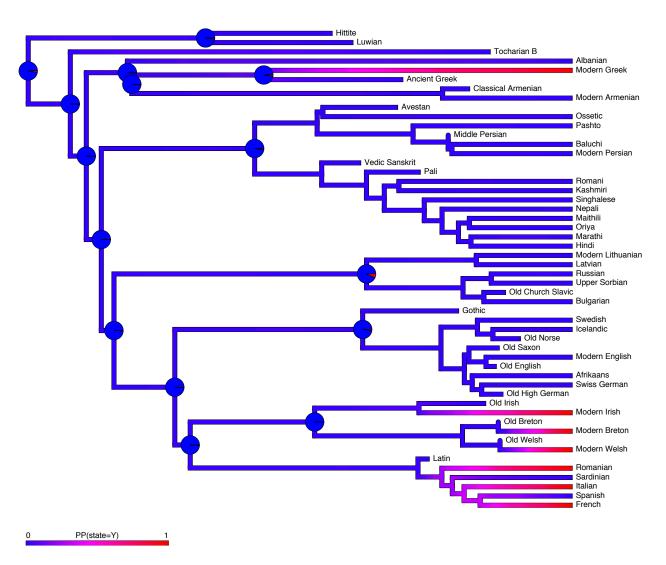


Figure S4.16: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondeme $*g^w$, assuming the phylogenies estimated by Bouckaert et al.

```
gw.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
gw.density.b <- densityMap(gw.simmaps.b, plot=F, res=res)
gw.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```

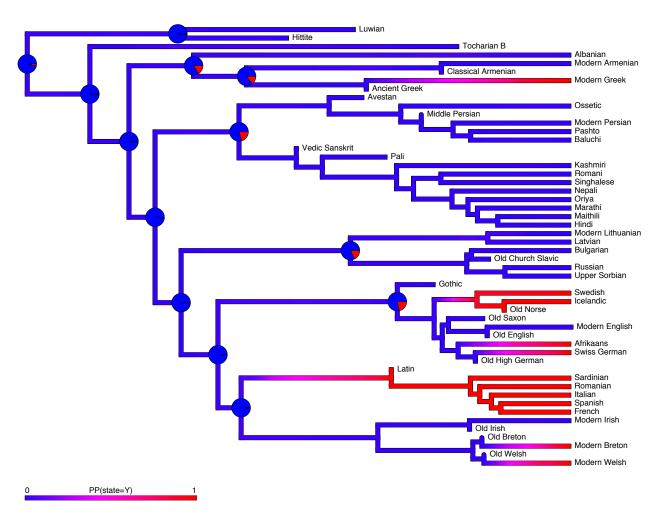


Figure S4.17: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence $*g^{wh}$, assuming the phylogenies estimated by Chang et al.

S4.5.3.6 Reconstruction of labiodental reflexes for $*g^{wh}$

```
correspondeme='gwh'
gwh.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
gwh.density.c <- densityMap(gwh.simmaps.c, plot=F, res=res)
gwh.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

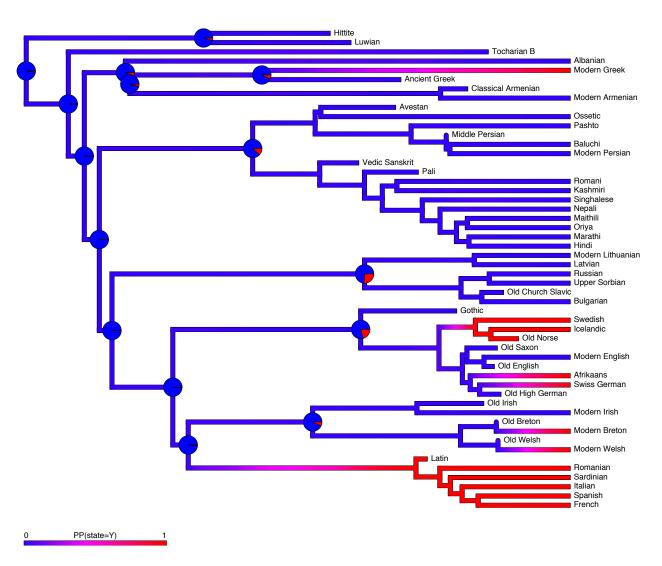


Figure S4.18: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondeme $*g^{wh}$, assuming the phylogenies estimated by Bouckaert et al.

```
gwh.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
gwh.density.b <- densityMap(gwh.simmaps.b, plot=F, res=res)
gwh.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```

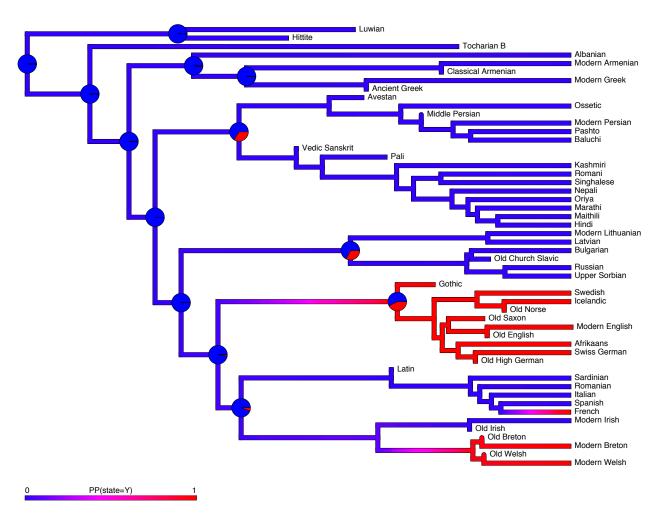


Figure S4.19: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence k^w , assuming the phylogenies estimated by Chang et al.

S4.5.3.7 Reconstruction of labiodental reflexes for $*k^w$

```
correspondeme='kw'
kw.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
kw.density.c <- densityMap(kw.simmaps.c, plot=F, res=res)
kw.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

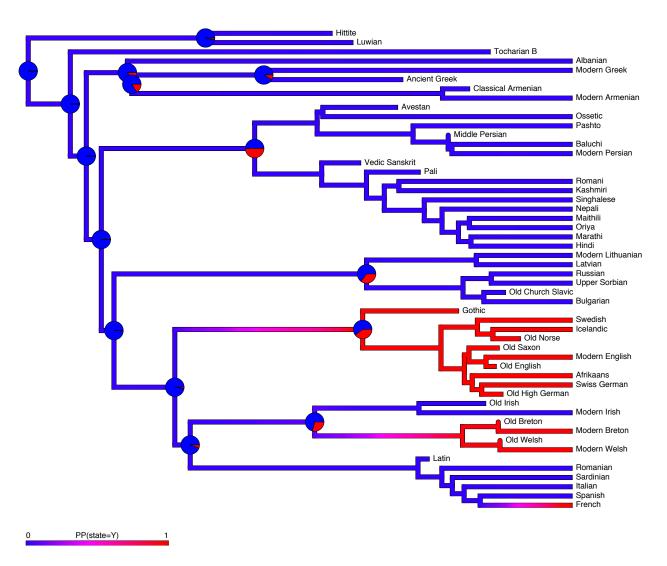


Figure S4.20: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondeme $*k^w$, assuming the phylogenies estimated by Bouckaert et al.

```
kw.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
kw.density.b <- densityMap(kw.simmaps.b, plot=F, res=res)
kw.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```

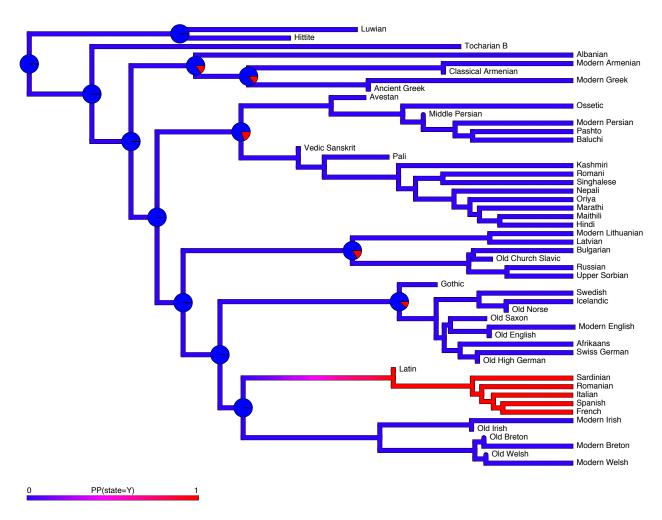


Figure S4.21: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence $*d^h$, assuming the phylogenies estimated by Chang et al.

S4.5.3.8 Reconstruction of labiodental reflexes for $*d^h$

With phylogenies estimated by Chang et al.:

```
correspondeme='dh'
dh.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
dh.density.c <- densityMap(dh.simmaps.c, plot=F, res=res)
dh.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

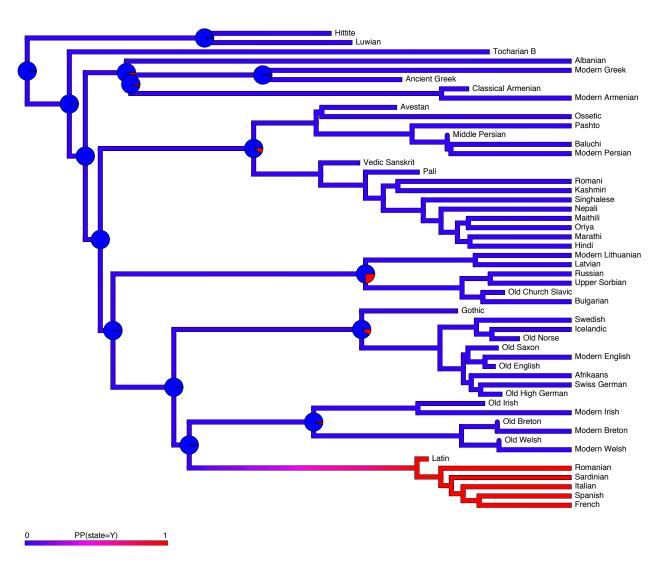


Figure S4.22: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence $*d^h$, assuming the phylogenies estimated by Bouckaert et al.

With phylogenies estimated by Bouckaert et al.:

```
dh.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
dh.density.b <- densityMap(dh.simmaps.b, plot=F, res=res)
dh.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```

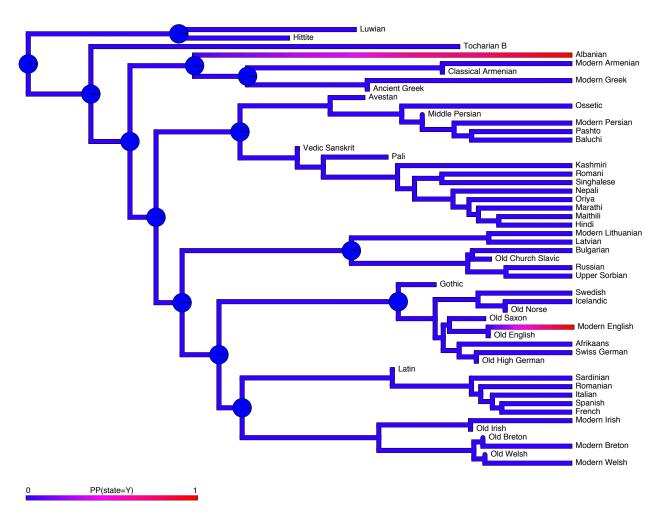


Figure S4.23: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondene $*k^{j}$, assuming the phylogenies estimated by Chang et al.

S4.5.3.9 Reconstruction of labiodental reflexes for $*k^{j}$

With phylogenies estimated by Chang et al.:

```
correspondeme='ky'
ky.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ER')
ky.density.c <- densityMap(ky.simmaps.c, plot=F, res=res)
ky.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ER')</pre>
```

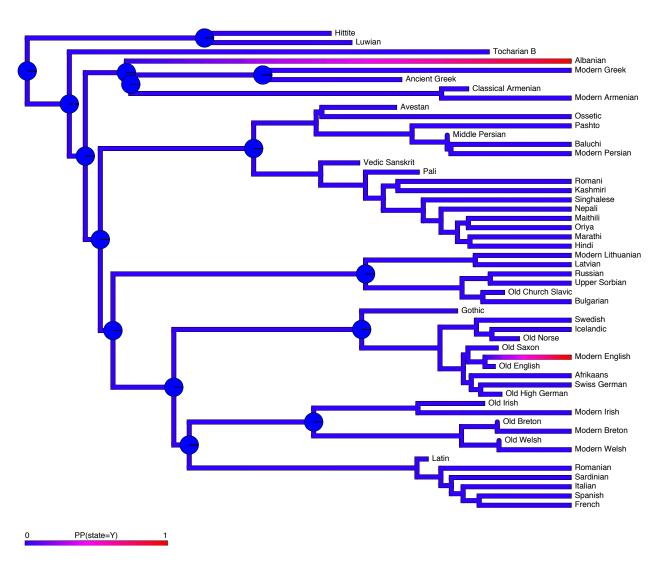


Figure S4.24: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondene $*k^{j}$, assuming the phylogenies estimated by Bouckaert et al.

With phylogenies estimated by Bouckaert et al.:

```
ky.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ER')
ky.density.b <- densityMap(ky.simmaps.b, plot=F, res=res)
ky.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ER')</pre>
```

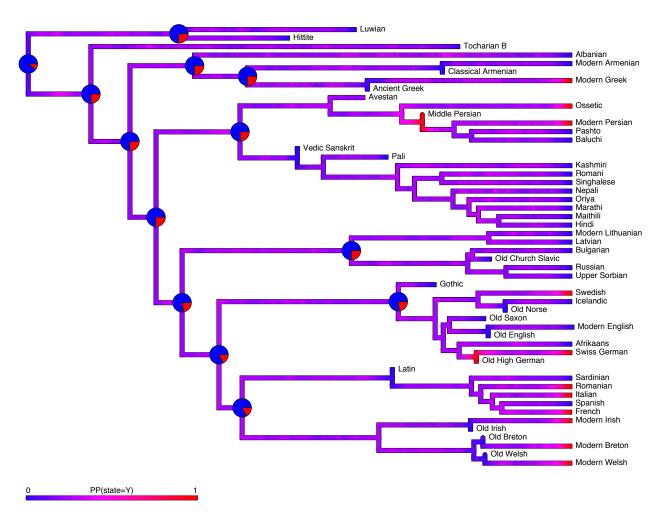


Figure S4.25: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondence *b, assuming the phylogenies estimated by Chang et al.

S4.5.3.10 Reconstruction of labiodental reflexes for *b

With phylogenies estimated by Chang et al.:

```
correspondeme='b'
b.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.sum.tree, model='ARD')
b.density.c <- densityMap(b.simmaps.c, plot=F, res=res)
b.multi.simmaps.c <- compute.simmap(correspondeme, tree=ie.c.trees.sample, model='ARD')</pre>
```



Figure S4.26: Posterior probability (PP) density of labiodental reflexes in some contexts of the correspondeme *b, assuming the phylogenies estimated by Bouckaert et al.

With phylogenies estimated by Bouckaert et al.:

```
b.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.sum.tree, model='ARD')
b.density.b <- densityMap(b.simmaps.b, plot=F, res=res)
b.multi.simmaps.b <- compute.simmap(correspondeme, tree=ie.b.trees.sample, model='ARD')</pre>
```

S4.5.4 Summary

The estimated root probabilities are as follows:

```
# doing this with lapply exceeds memory, so....; and let's do it externally...
# bh.c <- as.data.frame(describe.simmap(bh.multi.simmaps.c)$ace)</pre>
# p.c <- as.data.frame(describe.simmap(p.multi.simmaps.c)$ace)</pre>
# w.c <- as.data.frame(describe.simmap(w.multi.simmaps.c)$ace)</pre>
# m.c <- as.data.frame(describe.simmap(m.multi.simmaps.c)$ace)
# qw.c <- as.data.frame(describe.simmap(qw.multi.simmaps.c)$ace)</pre>
# qwh.c <- as.data.frame(describe.simmap(qwh.multi.simmaps.c)$ace)
# kw.c <- as.data.frame(describe.simmap(kw.multi.simmaps.c)$ace)</pre>
# dh.c <- as.data.frame(describe.simmap(dh.multi.simmaps.c)$ace)</pre>
# ky.c <- as.data.frame(describe.simmap(ky.multi.simmaps.c)$ace)</pre>
# b.c <- as.data.frame(describe.simmap(b.multi.simmaps.c)$ace)</pre>
load("all_aces_c.rda")
all.aces.c <- list(bh.c, p.c, w.c, m.c, gw.c, gwh.c, kw.c, dh.c, ky.c, b.c)
names(all.aces.c) <- correspondemes</pre>
(root.aces.c <- sapply(all.aces.c, '[', 1, 2))</pre>
##
        bh
                                                  gwh
## 0.08591 0.23692 0.49831 0.02780 0.02537 0.03418 0.00374 0.00057 0.00100 0.10478
mean(root.aces.c)
## [1] 0.101858
median(root.aces.c)
## [1] 0.03099
# bh.b <- as.data.frame(describe.simmap(bh.multi.simmaps.b)$ace)
# p.b <- as.data.frame(describe.simmap(p.multi.simmaps.b)$ace)</pre>
# w.b <- as.data.frame(describe.simmap(w.multi.simmaps.b)$ace)</pre>
# m.b <- as.data.frame(describe.simmap(m.multi.simmaps.b)$ace)</pre>
# gw.b <- as.data.frame(describe.simmap(gw.multi.simmaps.b)$ace)</pre>
# qwh.b <- as.data.frame(describe.simmap(qwh.multi.simmaps.b)$ace)
# kw.b <- as.data.frame(describe.simmap(kw.multi.simmaps.b)$ace)
# dh.b <- as.data.frame(describe.simmap(dh.multi.simmaps.b)$ace)</pre>
# ky.b <- as.data.frame(describe.simmap(ky.multi.simmaps.b)$ace)
# b.b <- as.data.frame(describe.simmap(b.multi.simmaps.b)$ace)
load("all_aces_b.rda")
all.aces.b <- list(bh.b, p.b, w.b, m.b, gw.b, gwh.b, kw.b, dh.b, ky.b, b.b)
names(all.aces.b) <- correspondemes</pre>
(root.aces.b <- sapply(all.aces.b, '[', 1, 2))</pre>
##
                                          gw
                                                 gwh
## 0.13783 0.17755 0.49897 0.03916 0.02567 0.01989 0.00596 0.00114 0.00768 0.13006
mean(root.aces.b)
## [1] 0.104391
```

median(root.aces.b)

[1] 0.032415

Figures S4.27 and S4.28 give a synopsis of all stochastic character maps.

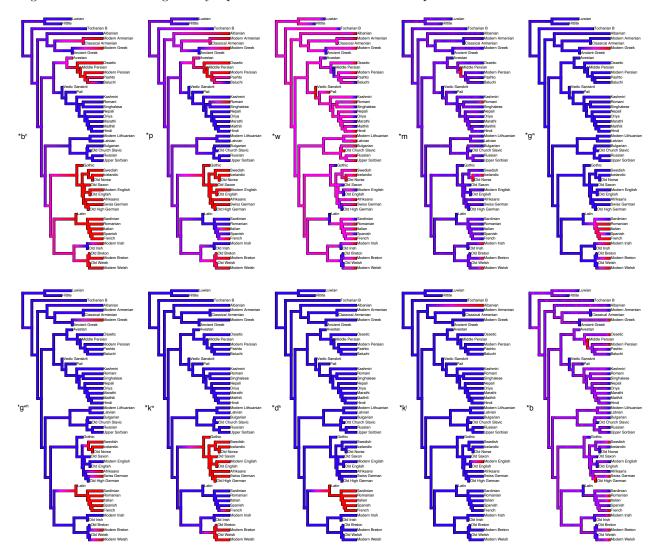


Figure S4.27: Stochastic character maps on the MCC trees estimated by Chang et al.

Figures S4.29 and S4.30 give a synopsis in terms of traitgrams. Each color represents the evolution of a correspondeme over all branches of the phylogeny. The position of the branch on the y-axis reflects the probability of a labiodental articulation.

```
all.maps.c <- list(
    bh=bh.density.c,p=p.density.c,w=w.density.c,m=m.density.c,
    gw=gw.density.c,gwh=gwh.density.c,kw=kw.density.c,
    dh=dh.density.c,ky=ky.density.c,b=b.density.c)

all.maps.values.c <- lapply(all.maps.c, function(density.map) {
    # get node and tip probabilities from densitymap:
    nodes.and.tip.values <- c(as.numeric(names(density.map$tree$maps[[1]])[1]), # the root
    sapply(density.map$tree$maps, function(m) {</pre>
```

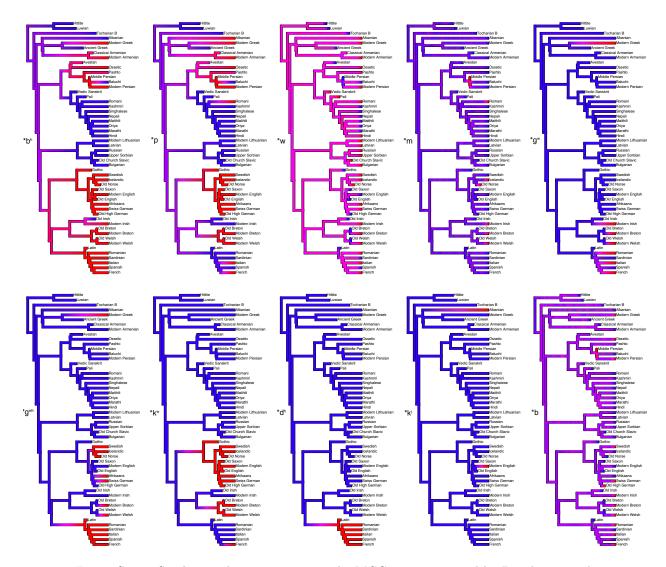


Figure S4.28: Stochastic character maps on the MCC trees estimated by Bouckaert et al.

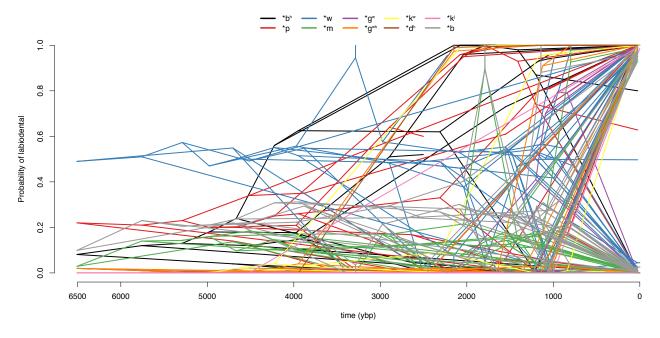


Figure S4.29: Evolution of labiodentals across correspondenes, based on the maximum clade credibility tree of the phylogeny in Chang et al.

```
as.numeric(names(m)[length(m)])}) # the end states, i.e the internal nodes and tips
        )/1000
   names(nodes.and.tip.values) <- as.character(c(53, # the root number
                        density.map$tree$edge[,2]
                        )) # the internal node and tip numbers
   density.map$tree$tip.label <- as.character(1:length(density.map$tree$tip.label)) # name match
   return(list(values=nodes.and.tip.values,tree=as.phylo(density.map$tree)))
   })
tree.c <- all.maps.values.c[[1]]$tree</pre>
all.maps.b <- list(</pre>
   bh=bh.density.b,p=p.density.b,w=w.density.b,m=m.density.b,
    gw=gw.density.b,gwh=gwh.density.b,kw=kw.density.b,
    dh=dh.density.b,ky=ky.density.b,b=b.density.b)
all.maps.values.b <- lapply(all.maps.b, function(density.map) {
    # get node and tip probabilities from densitymap:
   nodes.and.tip.values <- c(as.numeric(names(density.map$tree$maps[[1]])[1]), # the root
            sapply(density.map$tree$maps, function(m) {
               as.numeric(names(m)[length(m)])}) # the end states, i.e the internal nodes and tips
   names(nodes.and.tip.values) <- as.character(c(53, # the root number</pre>
                        density.map$tree$edge[,2]
                        )) # the internal node and tip numbers
   density.map$tree$tip.label <- as.character(1:length(density.map$tree$tip.label)) # name match
   return(list(values=nodes.and.tip.values,tree=as.phylo(density.map$tree)))
   })
```

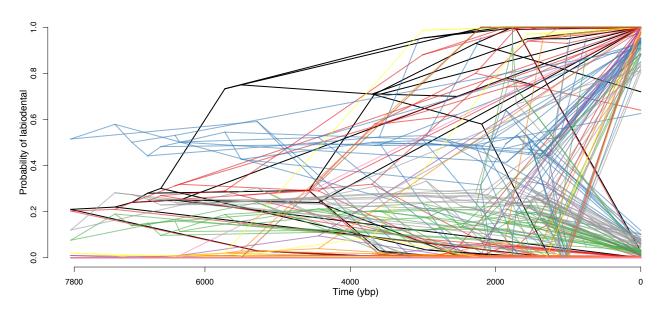


Figure S4.30: Evolution of labiodentals across correspondemes, based on the maximum clade credibility tree of the phylogeny in Bouckaert et al. $\frac{1}{2}$

tree.b <- all.maps.values.b[[1]]\$tree</pre>

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