

RH: Missing morphological data in living mammals

## Missing morphological data in living mammals

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**Abstract**

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## INTRODUCTION

Studying both living and fossil taxa together in macroevolutionary studies is becoming increasingly common among evolutionary biologists [1, 2, 3, 4, 5]. One trending method, called Total Evidence allows to combine molecular data from living taxa and morphological data from both living and fossil taxa (e.g. [6, 7, 8, 4, 9, 10]). This promising method allows to apply integrative phylogenetic inference methods such as tip-dating [7, 11, 12]. However, because the Total Evidence method requires a lot of data (both molecular and morphological for both living and fossil taxa), this method has been shown to be sensible to missing morphological data [13].

In fact, [13] demonstrates that when few living taxa coded, topological recovery is bad. For example, a given phylogeny containing two clades A and B containing only living taxa, when using a Total Evidence method, molecular data is available for both clades but morphological data is only available for clade A for any reason. Then, the addition of any fossil taxa X related to clade B will lead to a wrong topological placement of this fossil taxa X, branching it somewhere in the clade A instead of the clade B because no morphological data is available to support the placement of the fossil taxa X in clade B.

If there is no overlapping characters between a living clade and a fossil one, then it is impossible to branch and fossil taxa to that clade. This can be due to evolutionary history (i.e. a fossil angiosperm has no overlapping characters with a living mammal) and is expected. However, this can also be due to missing data (i.e. a fossil primates has

no overlapping data with living primates because no data is available for living primates) and will produce artefactual wrong phylogenies (i.e. the fossil primate NOT branching in the primate clade).

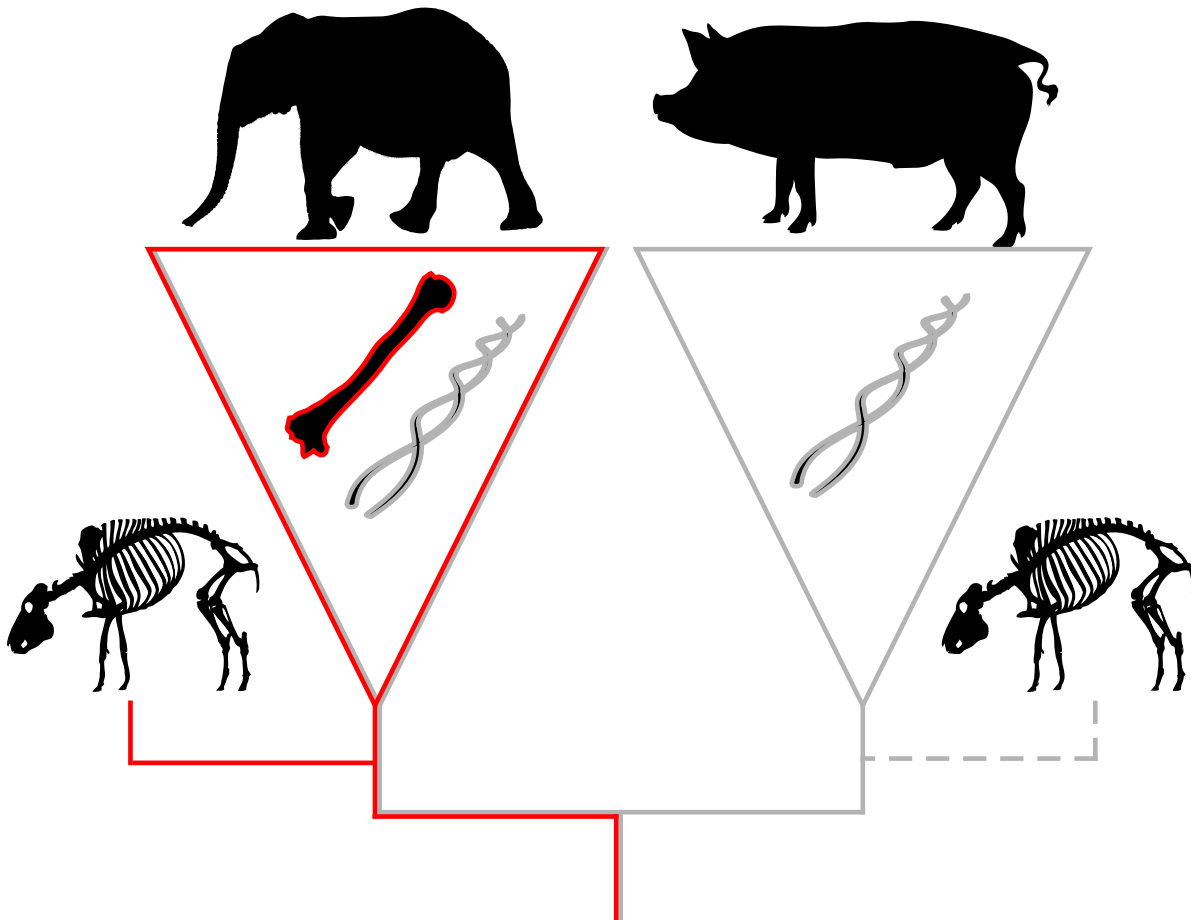


Figure 1: Example of topological errors due to missing morphological data in living taxa. If a phylogeny contains two clades, for example Proboscidea and Cetartiodactyla, with molecular data for both but only morphological data for Proboscidea. If an additional Cetartiodactyla fossil (with no molecular data) will be added to the phylogeny, it will erroneously branch with the Proboscidea clade instead of the Cetartiodactyla one.

In this study we investigate the amount of living mammal taxa with available morphological data to assess the potential caveats in building Total Evidence mammal phylogenetic trees. As well as the data availability, we calculate the structure of the data to make sure that clades with a relatively high amount of data are not only containing all taxa from a single clade and none from another clade.

Questions:

1. -How many taxa with morphological data are available among each living mammals order?
2. -Within each order, how is this data distributed?
3. -How can we improve the data coverage in taxa with non random distributed data

# MATERIAL AND METHODS

## *Matrices search*

To investigate the available living taxa with morphological data, we downloaded morphological matrices from three main public databases: morphobank, graeamlloyd.com and rossmounce's github. We downloaded all the matrices containing any fossil or living mammal taxa from these data bases. Additionally we ran a thorough search for matrices that might not have been uploaded on the previously cited data bases through a Google Scholar search. We downloaded the eventual additional morphological matrices from any of the 20 first papers matching with our selected key words and with any of the 35 taxonomic levels (see supplementary materials for detailed description of the procedure). We downloaded 256 matrices containing a total of 9411 operational taxonomic units (OTUs) from the combination of both searches (public repositories and Google Scholar).

We then transformed all the matrices to be in the same nexus format. We then standardised the taxonomic nomenclature by fixing invalid binomial inputs to match with the official taxonomic nomenclature rules (i.e. *H. sapiens* was transformed in *Homo sapiens*). We assigned each species as being either living or fossil using a taxonomic matching algorithm. We considered living all the OTUs that where either present in [?] or [?]. We considered fossil all the OTUs that where present in the Paleobiology database. For the OTUs neither labelled as living or fossil we tried to decompose the

OTUs name (i.e. *Homo\_sapiens* became *Homo* and *sapiens*) and tried to match the to Wilson Reeder's taxonomy at any taxonomic level (Family, Genus, *Genus\_species*, etc.). The matching OTUs were labelled as living and the ones still not matching were ignored and labelled as not applicable (NA).

### *Data availability analysis*

*Number of characters threshold.*— From all the 256 matrices, we selected only the ones that had at least 100 morphological characters. This arbitrary threshold number of morphological characters was chosen to be in adequacy with [13] and [14]. Also this threshold avoids biases towards small matrices that could be either not informative (e.g. too few characters) or made of non-applicable characters (e.g. antlers which are sexual dimorphic characters proper to a specific clade).

*Data availability.*— To assess the data availability per mammal order, we calculated the percentage of OTUs with morphological data for three different taxonomic levels (Family, Genera and Species). We highlighted all the orders containing less than 25% of living taxa with morphological data because their amount of missing data (>75%) was higher than in [13] and therefore highly probable of suffering from the effect of missing data.

*Available data structure.*— For the order with no morphological data for all OTUs at the three different taxonomic levels (Family, Genera and Species), we investigated the

structure of the available data to test if it was either (i) randomly distributed, (ii) over-dispersed or (iii) clustered. To measure the structure of the available data we used classic community structure metric from the *picante* R package [15] where we compared the structure of the available data for each order to the structure of a potentially fully sampled data (i.e. only the OTUs with available morphological data *vs.* all the OTUs). For each orders and taxonomic level that presented OTUs with no available morphological data, we calculated the Net Relatedness Index (NRI) which quantifies the overall distribution of the data with negative values showing more dispersed data and positive values more clustered data than expected by the null model [16]. We choose to present only the NRI values because they have been shown to be slightly less sensitive to the structure of the phylogeny (i.e. branch length and topology) [17, 18] but we also calculated the two other common phylogenetic structure indices: Faith's Phylogenetic Distance (PD)[19] and the Nearest Taxon Index (NTI) [16]. Both metrics are available in the Supplementary results.

All the following procedure is repeatable and available on GitHub.

## RESULTS

### *Data availability*

We extracted 1422 living mammal OTUs from the 256 matrices with a minimum of 6 characters and a maximum of 4541. After removing all the matrices with less than 100



the number of extracted living mammals OTUs was down to 815. 11/28 orders have less than 25% of taxa with morphological data at a species level and 24/28 orders have less than 75% taxa with available morphological data. At the Genus level however only 3/28 orders have less than 25% of taxa with morphological data and 16/28 have less than 75%. Finally, at the family level no order has less than 25% taxa with available morphological data and only 5/28 have less than 75% (table 1).

Table 1: Proportion of available OTUs with morphological data per order and per taxonomic level. We highlighted in bold the orders that have more than 75% of missing data for each taxonomic level. Note that it is possible that more data is available at a higher taxonomic level (Genus > Species) since if the species name for an OTU was not or miss specified, we still counted the OTU for higher taxonomic level analysis.

Order	Taxonomic level	Fraction of OTUs	Percentage of OTUs
Monotremata	Family	2/2	100
Monotremata	Genus	2/3	66.67
Monotremata	Species	2/4	50
Didelphimorphia	Family	1/1	100
Didelphimorphia	Genus	16/16	100
Didelphimorphia	Species	42/84	50
Paucituberculata	Family	1/1	100
Paucituberculata	Genus	3/3	100
Paucituberculata	Species	5/5	100
Microbiotheria	Family	1/1	100
Microbiotheria	Genus	1/1	100
Microbiotheria	Species	1/1	100
Notoryctemorphia	Family	1/1	100
Notoryctemorphia	Genus	1/1	100
<b>Notoryctemorphia</b>	<b>Species</b>	<b>0/2</b>	<b>0</b>
Dasyuromorphia	Family	2/2	100
Dasyuromorphia	Genus	8/22	36.36
<b>Dasyuromorphia</b>	<b>Species</b>	<b>9/64</b>	<b>14.06</b>
Peramelemorphia	Family	2/2	100

Peramelemorphia	Genus	7/7	100
Peramelemorphia	Species	16/18	88.89
Diprotodontia	Family	11/11	100
Diprotodontia	Genus	25/38	65.79
<b>Diprotodontia</b>	<b>Species</b>	<b>31/126</b>	<b>24.6</b>
Afrosoricida	Family	2/2	100
Afrosoricida	Genus	17/17	100
Afrosoricida	Species	23/42	54.76
Macroscelidea	Family	1/1	100
Macroscelidea	Genus	4/4	100
Macroscelidea	Species	12/15	80
Tubulidentata	Family	1/1	100
Tubulidentata	Genus	1/1	100
Tubulidentata	Species	1/1	100
Hyracoidea	Family	1/1	100
Hyracoidea	Genus	1/3	33.33
Hyracoidea	Species	1/4	25
Proboscidea	Family	1/1	100
Proboscidea	Genus	2/2	100
Proboscidea	Species	2/3	66.67
Sirenia	Family	2/2	100
Sirenia	Genus	2/2	100
Sirenia	Species	2/4	50
Cingulata	Family	1/1	100
Cingulata	Genus	8/9	88.89
Cingulata	Species	9/25	36
Pilosa	Family	4/5	80
Pilosa	Genus	4/5	80
<b>Pilosa</b>	<b>Species</b>	<b>5/29</b>	<b>17.24</b>
Scandentia	Family	2/2	100
Scandentia	Genus	2/5	40
<b>Scandentia</b>	<b>Species</b>	<b>3/20</b>	<b>15</b>
Dermoptera	Family	1/1	100
Dermoptera	Genus	1/2	50
Dermoptera	Species	1/2	50

Primates	Family	15/15	100
Primates	Genus	48/68	70.59
<b>Primates</b>	<b>Species</b>	<b>57/351</b>	<b>16.24</b>
Rodentia	Family	16/32	50
<b>Rodentia</b>	<b>Genus</b>	<b>63/451</b>	<b>13.97</b>
<b>Rodentia</b>	<b>Species</b>	<b>76/2095</b>	<b>3.63</b>
Lagomorpha	Family	2/2	100
Lagomorpha	Genus	5/12	41.67
<b>Lagomorpha</b>	<b>Species</b>	<b>12/86</b>	<b>13.95</b>
Erinaceomorpha	Family	1/1	100
Erinaceomorpha	Genus	10/10	100
Erinaceomorpha	Species	21/22	95.45
Soricomorpha	Family	3/4	75
Soricomorpha	Genus	19/43	44.19
<b>Soricomorpha</b>	<b>Species</b>	<b>21/392</b>	<b>5.36</b>
Chiroptera	Family	15/18	83.33
Chiroptera	Genus	77/202	38.12
<b>Chiroptera</b>	<b>Species</b>	<b>155/1054</b>	<b>14.71</b>
Pholidota	Family	1/1	100
Pholidota	Genus	1/1	100
Pholidota	Species	4/8	50
Carnivora	Family	14/15	93.33
Carnivora	Genus	54/125	43.2
Carnivora	Species	76/283	26.86
Perissodactyla	Family	3/3	100
Perissodactyla	Genus	6/6	100
Perissodactyla	Species	10/16	62.5
Cetartiodactyla	Family	20/21	95.24
Cetartiodactyla	Genus	99/128	77.34
Cetartiodactyla	Species	150/311	48.23

*Available data structure*

Among the orders containing OTUs with no morphological data, only two orders (Carnivora and Chiroptera) are significantly clustered both at the species and the genus level but not at the family level (table 2).

Table 2: Data structure for the orders with OTUs without morphological data per taxonomic level. When the Net Relatedness Index (NRI) is negative, the OTUs are more dispersed than expected by chance (random); when the NRI is positive, the OTUs are more clustered by expected by chance. The p-value indicates the significance in difference from the null model (random).

Order	Taxonomic level	Fraction of OTUs	Percentage of OTUs	NRI	p-value
Monotremata	Genus	2/3	66.667	-0.695	0.663
Monotremata	Species	2/4	50	-0.966	0.566
Didelphimorphia	Species	42/84	50	-1.96	0.991
Dasyuromorphia	Genus	8/22	36.364	-0.747	0.768
Dasyuromorphia	Species	9/64	14.062	-0.641	0.789
Peramelemorphia	Species	16/18	88.889	-0.514	0.742
<b>Diprotodontia</b>	<b>Genus</b>	<b>25/38</b>	<b>65.789</b>	<b>2.305</b>	<b>0.021</b>
<b>Diprotodontia</b>	<b>Species</b>	<b>31/126</b>	<b>24.603</b>	<b>2.006</b>	<b>0.042</b>
Afrosoricida	Species	23/42	54.762	1.553	0.089
Macroscelidea	Species	12/15	80	-1.023	0.832
Proboscidea	Species	2/3	66.667	-0.727	0.673
Sirenia	Species	2/4	50	-0.94	0.833
Cingulata	Genus	8/9	88.889	1.366	0.215
Cingulata	Species	9/25	36	1.821	0.055
Pilosa	Family	4/5	80	-0.247	0.48
Pilosa	Genus	4/5	80	-1.21	0.798
Pilosa	Species	5/29	17.241	-1.015	0.861
Scandentia	Genus	2/5	40	-0.785	0.669
Scandentia	Species	3/20	15	-1.462	0.898
Primates	Genus	48/68	70.588	-0.353	0.617
Primates	Species	57/351	16.239	-1.586	0.941
Rodentia	Family	16/32	50	0.956	0.155
Rodentia	Genus	63/451	13.969	-1.614	0.961
<b>Rodentia</b>	<b>Species</b>	<b>76/2095</b>	<b>3.628</b>	<b>5.184</b>	<b>0.001</b>
Lagomorpha	Genus	5/12	41.667	-1.078	0.661

Lagomorpha	Species	12/86	13.953	-1.288	0.954
Erinaceomorpha	Species	21/22	95.455	-0.808	0.916
Soricomorpha	Family	3/4	75	-0.941	0.611
Soricomorpha	Genus	19/43	44.186	1.202	0.11
Soricomorpha	Species	21/392	5.357	-2.298	0.996
Chiroptera	Family	15/18	83.333	0.047	0.434
<b>Chiroptera</b>	<b>Genus</b>	<b>77/202</b>	<b>38.119</b>	<b>14.216</b>	<b>0.001</b>
<b>Chiroptera</b>	<b>Species</b>	<b>155/1054</b>	<b>14.706</b>	<b>11.347</b>	<b>0.001</b>
Pholidota	Species	4/8	50	-0.034	0.482
Carnivora	Family	14/15	93.333	0.671	0.363
<b>Carnivora</b>	<b>Genus</b>	<b>54/125</b>	<b>43.2</b>	<b>4.624</b>	<b>0.001</b>
<b>Carnivora</b>	<b>Species</b>	<b>76/283</b>	<b>26.855</b>	<b>7.448</b>	<b>0.001</b>
Perissodactyla	Species	10/16	62.5	-0.042	0.474
Cetartiodactyla	Family	20/21	95.238	0.461	0.166
Cetartiodactyla	Genus	99/128	77.344	-1.616	0.954
Cetartiodactyla	Species	150/311	48.232	-0.901	0.81

Two contrasted results are shown on figure 2 with randomly distributed data in Cetartiodactyla (Fig. 2A) and clustered available data in Carnivora (mainly Canidae; Fig. 2B).

## DISCUSSION

It's pretty bad

But good news! It's at least mainly random

However, we counted only the raw number of characters here and not there similarity. It might be that actually the amount of available data here is lower due to non overlap of characters....

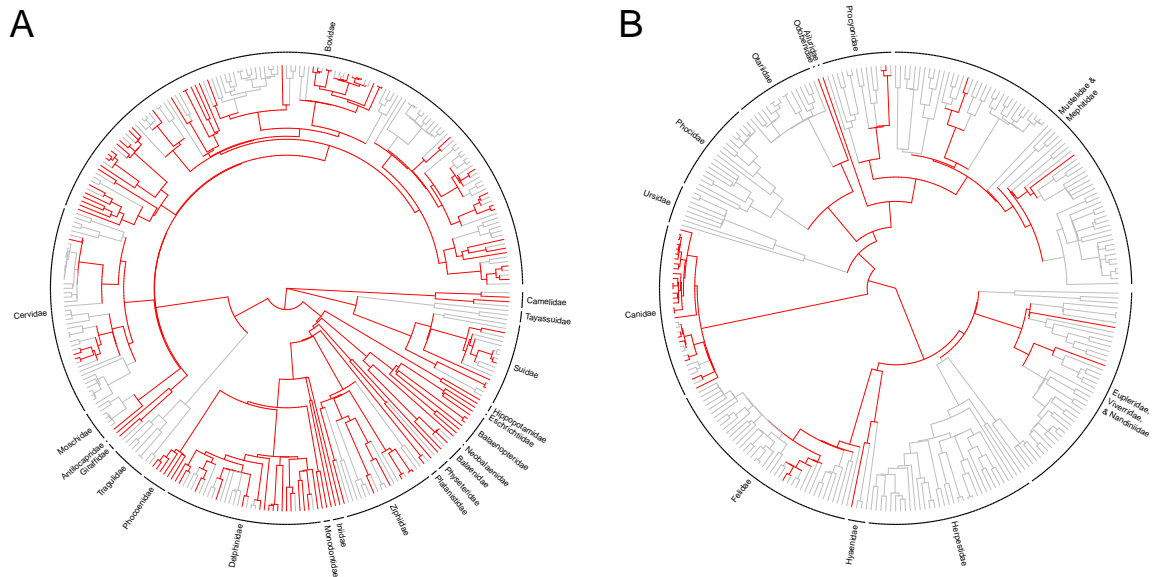


Figure 2: Distribution of available morphological data across cetartiodactyles (A) and carnivores (B). Edges are colored in grey when no morphological data is available or in red when data is available.

So let's go coding some data and using opensource traceable data bases like morphobank!

## ETHICS STATEMENT

## DATA ACCESSIBILITY STATEMENT

All data is available and reproducible on GitHub.

## AUTHORS CONTRIBUTIONS STATEMENT

Conceived and designed the experiments: TG NC. Performed the experiments: TG.

Analyzed the data: TG. Wrote the paper: TG NC.

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## SOM

### Supplementary Material

#### DATA COLLECTION

1- Data collection: key words, clade (ordinal) metacharacters, Google Search terms, Google Search protocol, Google Search rarefaction curve.

#### *search terms*

The searched mammalian order terms are available in *search<sub>t</sub>erms<sub>latin</sub>.txt* or *search<sub>t</sub>erms<sub>meta</sub>.txt*. The file containing the meta names is the Latin name files but with replacing the latin suffixes ([ia—ata—ea—a]) by a joker character (\*) and by replacing the first letter by a upper/lower case meta character (e.g. [Aa]). Mammalia; Monotremata; Marsupialia; Placentalia; Macroscelidea; Afrosoricida; Tubulidentata; Hyracoidea; Proboscidea; Sirenia; Pilosa; Cingulata; Scandentia; Dermoptera; Primates; Lagomorpha; Rodentia; Erinaceomorpha; Soricomorpha; Cetacea; Artiodactyla; Cetartiodactyla; Chiroptera; Perissodactyla; Pholidota; Carnivora; Didelphimorphia;

Paucituberculata; Microbiotheria; Dasyuromorphia; Peramelemorphia;  
Notoryctemorphia and Diprotodontia.

*Ross Mounce data set.*— I selected all the matrices containing at least one of the mammalian orders names from Ross Mounce GitHub *cladistic – data/nexusfiles* repository (accessed on the 02/12/2014).

*Graeme Lloyd.*— Selecting the downloadable matrices

*Morphobank.*— *order*

*Google scholars.*— 20 first results since 2010 with the following exact key words:

*order* ("morphology" OR "morphological" OR "cladistic") AND characters  
matrix paleontology phylogeny

We selected only the 20 first results per search term because only the 50 first of the 660 papers added 425 living OTUs.

### *Wrong Bionmial names and typos*

I fixed the wrong bionomial names format (e.g. H. sapiens) into the correct ones (e.g. Homo sapiens) manually using the abbreviation list in the concerned publications. We then applied our taxonomic matching algorithm to classify the OTUs as either living or fossil.

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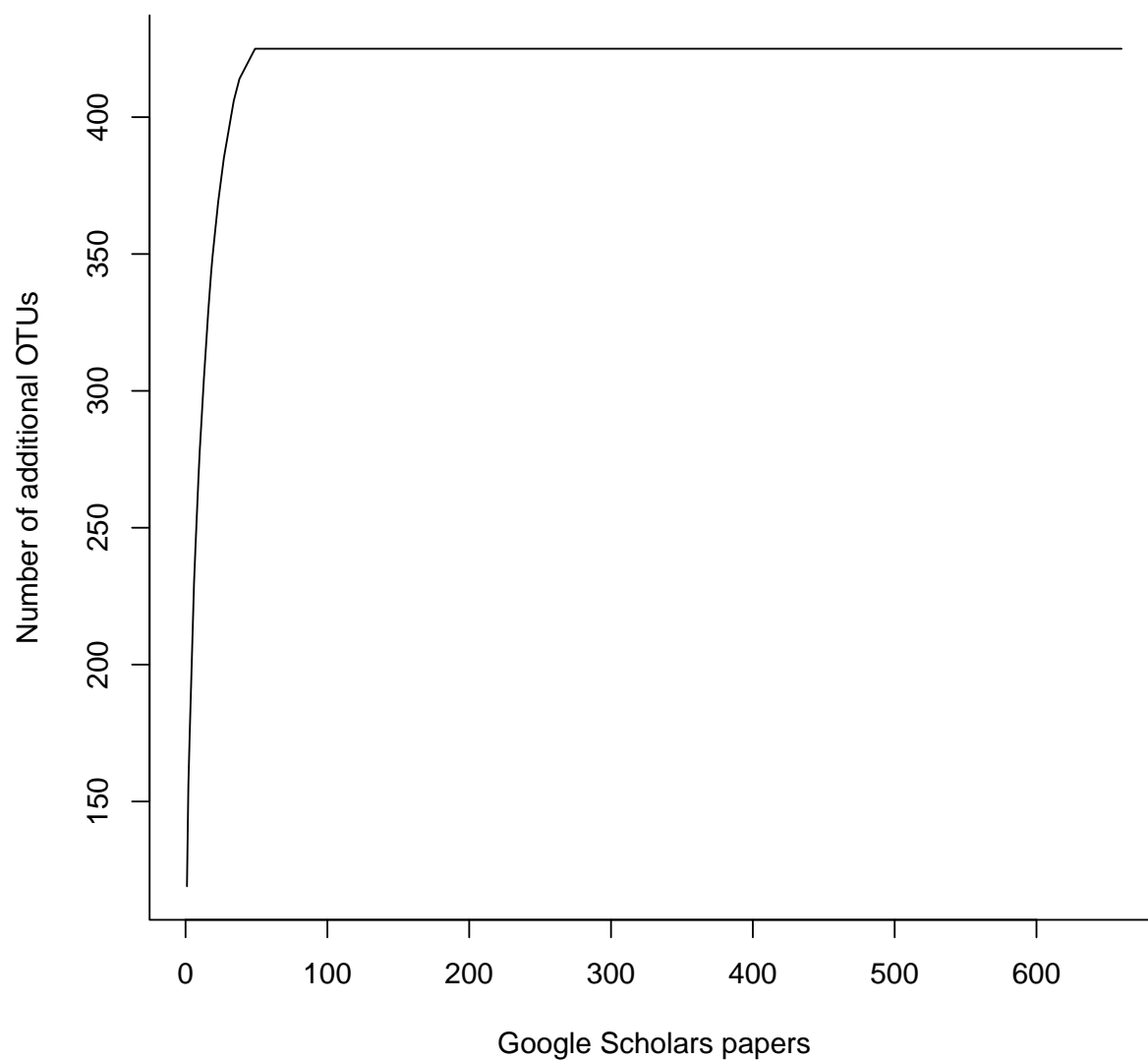


Figure 3: Google searches additional OTUs rarefaction curve. The x axis represent the number of google scholar matches (papers, books or abstracts) and the y axis represents the cumulative number of additional living OTUs per google scholar match.

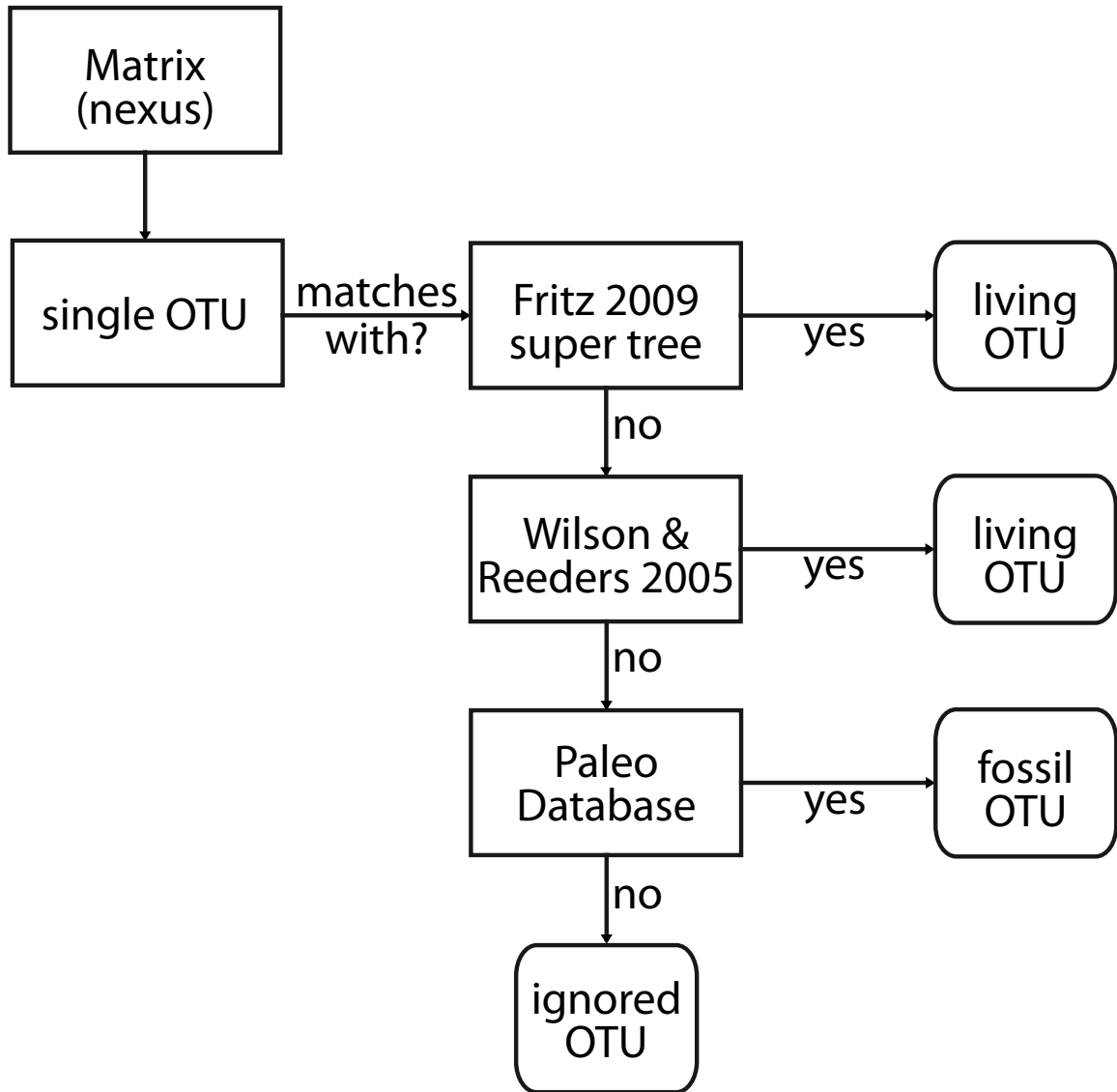


Figure 4: Taxonomic matching algorithm used in this study. For each matrix, each operational taxonomic units (OTU) is matched with the super tree from Fritz 2009. If the OTU matches, then it is classified as living. Else it is matched with the Wilson & Reeders 2005 taxonomy list. If the OTU matches, then it is classified as living. Else it is matched with the Paleo Database list of mammals. If the OTU matches, then it is classified as fossil. Else it is ignored.

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## DATA STRUCTURE

## SUPPLEMENTARY RESULTS