

# rphenoscape: An R package for semantic-aware evolutionary analyses of anatomical traits

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<sup>15</sup> **Running headline:** Semantic-aware evolutionary analyses

## Abstract

<sup>17</sup> 1. Organismal anatomy is a complex hierarchical system of interconnected anatomical entities  
<sup>18</sup> often producing dependencies among multiple morphological characters. Ontologies provide a formal-  
<sup>19</sup> ized and computable framework for representing and incorporating prior biological knowledge about  
<sup>20</sup> anatomical dependencies in models of trait evolution. Further, ontologies offer new opportunities for  
<sup>21</sup> assembling and working with semantic representations of morphological data.

<sup>22</sup> 2. In this work we present a new R package—*rphenoscape*—that enables incorporating ontolog-  
<sup>23</sup> ical knowledge in evolutionary analyses and exploring semantic patterns of morphological data. In  
<sup>24</sup> conjunction with *rphenoscape* it also allows for assembling synthetic phylogenetic character matrices  
<sup>25</sup> from semantic phenotypes of morphological data. We showcase the new package functionalities with  
<sup>26</sup> three data sets from bees and fishes.

27 3. We demonstrate that ontology knowledge can be employed to automatically set up ontology-  
28 informed evolutionary models that account for trait dependencies in the context of stochastic charac-  
29 ter mapping. We also demonstrate how ontology annotations can be explored to interrogate patterns  
30 of morphological evolution. Finally, we demonstrate that synthetic character matrices assembled from  
31 semantic phenotypes retain most of the phylogenetic information of the original data set.

32 4. Ontologies will become an increasingly important tool not only for enabling prior anatomical  
33 knowledge to be integrated into phylogenetic methods but also to make morphological data FAIR  
34 compliant—a critical component of the ongoing ‘phenomics’ revolution. Our new package offers key  
35 advancements toward this goal.

36 **Keywords:** morphology, ontology, PARAMO, Phenoscape, rphenoscape, structured Markov models

## 37 1 Introduction

38 Biological realism in models of trait evolution—*i.e.*, accurate modeling of biological processes underlying  
39 trait changes through time—is often an overlooked but important feature in phylogenetic comparative  
40 modeling (Boyko and Beaulieu, 2021). For example, it is common in statistical phylogenetics to treat  
41 each character as an independent realization of the evolutionary process. While this assumption may  
42 be questionable for molecular data, it is certainly dubious for morphological data. Nevertheless, this  
43 assumption is commonly applied in morphological analyses (see discussions in Lewis, 2001; Wright, 2019).  
44 Non-independence among anatomical traits can result from multiple causes (*e.g.*, see the distinction  
45 among *biological*, *semantic* and *ontological* dependencies in Vogt, 2018a) and alternative models have  
46 been proposed to properly deal with them (*e.g.*, Tarasov, 2019, 2022). While researchers often attempt  
47 to at least partially deal with such challenges via expert character construction, there is a pressing need  
48 for such knowledge to be repeatable and computable. What if we could reliably inform phylogenetic  
49 models with prior knowledge on anatomical trait relationships, including potential biological and/or  
50 logical dependencies, in a repeatable and computable framework? In this paper, we present a new R  
51 package for addressing this challenge, *rphenoscape*, that enables semantically-aware evolutionary analyses  
52 by integrating morphological knowledge present in anatomy ontologies.

53 The ‘dependency problem’—how to code and model dependent traits—often associated with missing  
54 or inapplicable characters, is a longstanding issue in phylogenetics with morphological data (the ‘tail  
55 color problem’ from Maddison, 1993 as referred in Tarasov, 2019) and has received considerable attention  
56 in recent years (Tarasov, 2019, 2022; Goloboff et al., 2021; Hopkins and St. John, 2021; Simões et al.,  
57 2022). This issue is especially relevant if we want to improve the biological realism of evolutionary models  
58 for morphological traits, as organismal anatomy is highly structured and phylogenetic characters often  
59 refer to multiple anatomical entities and/or phenotypes exhibiting complex hierarchical relations (Porto  
60 et al., 2021, 2022). Advances in model-based phylogenetics now allow researchers to employ different

61 models and coding strategies to deal with character dependencies (Tarasov, 2019, 2022). Although there  
62 still is a discussion on how to properly set up these models and represent dependencies in a coding  
63 scheme (see Goloboff et al., 2021; Simões et al., 2022), ontologies can offer an answer to ‘what the  
64 dependencies are’. Thus, anatomy ontologies are important sources of computable biological knowledge  
65 about organismal anatomy and are the key to enabling reproducibility and integration of biological  
66 knowledge into phylogenetic workflows.

67 Ontologies are formal representations of domain knowledge using structured vocabularies (Balhoff  
68 et al., 2010; Dahdul et al., 2010b, 2012; Vogt, 2018a,b). Anatomy ontologies, in particular, allow one to  
69 express knowledge about different anatomical concepts in a particular group of organisms (Dahdul et al.,  
70 2010b). For example, ontologies can formalize that the anatomical concept ‘dorsal fin ray’ is *part\_of*  
71 ‘dorsal fin’. Therefore, the condition of a character representing a ‘dorsal fin ray’ (e.g., shape or number  
72 of rays) depends on the presence of a ‘dorsal fin’. Despite being a rather simple statement for a trained  
73 fish anatomist, this type of biological knowledge is crucial for computers to be able to autonomously  
74 reason about trait evolution—yet such relationships are increasingly likely to be lost as analyses tran-  
75 sition from expertly curated data sets to large automated data syntheses. If trait dependencies are not  
76 accounted for, for example, this can result in overestimating the true amount of evolutionary change,  
77 potentially affecting divergence time estimates using fossilized birth-death models (Ronquist et al., 2012;  
78 Wright et al., 2022). Additionally, ignoring dependencies can result in biologically unrealistic combina-  
79 tions of states at internal nodes when performing ancestral character state reconstruction with multiple  
80 traits (Forey and Kitching, 2000; Tarasov, 2019; Boyko and Beaulieu, 2021). Even when these are not  
81 the direct target of inference, many comparative methods such as state-dependent diversification mod-  
82 els (FitzJohn, 2012) and character correlation tests (e.g. Pagel, 1994) integrate over these ancestral  
83 probabilities and therefore can be affected by considering implausible character histories. Therefore,  
84 employing appropriate models is not only desirable for improving biological realism but also necessary  
85 to avoid misleading results. By providing tools that automate model specification when dependent traits  
86 are present using the formalized knowledge in anatomy ontologies (e.g., Tarasov, 2019, 2022), our new  
87 R package enables researchers to quickly and easily structure biologically-plausible models of character  
88 evolution for phenomic-scale matrices.

89 Besides informing models, ontologies open up new questions for researchers interested in the evolution  
90 of morphological traits. Dependencies among anatomical entities—and the phylogenetic characters pro-  
91 posed from them—can be of several types (Vogt, 2018a; see some useful definitions of concepts discussed  
92 along the text in Table 1). Using ontology annotations to phylogenetic characters one can, for exam-  
93 ple, automatically assemble all characters representing traits that are *part\_of* ‘cranium’ (e.g., bones:  
94 ‘endopterygoid’, ‘parasphenoid’, ‘parietal’), *is\_a* type of ‘anatomical projection’, or *develops\_from* the  
95 ‘mesoderm’ in a fish, and then test to see if different bones from the same cluster evolve at similar rates.

96 Alternatively, one can use such clusters to further investigate if the phylogenetic characters linked to  
97 the anatomical entities share other parameters in their evolutionary models (e.g., transition bias). For  
98 example, are certain types (*is-a*) of anatomical entities or entities belonging to a certain body region  
99 (*part\_of*) more prone to be lost during evolution? These are just a few examples of the utility of ontolo-  
100 gies in evolutionary analyses (see also Dahdul et al., 2010a; Ramírez and Michalik, 2014; Vogt, 2018a,b;  
101 Tarasov et al., 2019; Tarasov, 2019; Porto et al., 2022).

102 Furthermore, ontologies not only offer a solution for the longstanding ‘dependency problem’ among  
103 anatomical traits in phylogenetics (Tarasov, 2019) but also, an interoperable framework for represent-  
104 ing morphological knowledge and integrating it with other knowledge types. Based on theoretical and  
105 practical grounds, recent works have suggested new schema for employing morphological data in phylo-  
106 genetics (Vogt, 2018a,b), for example, by using semantically-enriched character matrices (e.g., Ramírez  
107 et al., 2007; Stefen et al., 2022), semantic instance anatomies (e.g., Vogt, 2018a,b, 2019), or semantic  
108 phenotypes (e.g., Deans et al., 2012; Balhoff et al., 2010, 2014). By representing organismal anatomy  
109 in a semantically-aware format (i.e., ontology-annotated) and moving beyond the standard phylogenetic  
110 character matrices, it is possible to make morphological data more easily reusable, parsable, and inte-  
111 grated across different studies and domains. Some new uses include, but are not restricted to, building  
112 synthetic character matrices from multiple sources (Dececchi et al., 2015; Jackson et al., 2018; Elia-  
113 son et al., 2019), inferring candidate genes for novel phylogenetic traits (Edmunds et al., 2016), and  
114 graph-based phylogenetic algorithms (Vogt, 2018a,b). To enable such analyses, the Phenoscape project  
115 (<https://kb.phenoscape.org/>) has developed key demonstrations of the use of ontologies in the de-  
116 velopment of a logical model of homology (Mabee et al., 2020) and inference of candidate genes from  
117 phylogenetic traits (Edmunds et al., 2016; Manda et al., 2015), as well as gold standards for curation  
118 (Dahdul et al., 2018). These grew from the development of one of the first multispecies anatomy on-  
119 tologies for the biodiversity sciences. Their initial teleost fish ontology (Dahdul et al., 2010b) grew into  
120 a vertebrate ontology (Dahdul et al., 2012) and merged into the Uberon anatomy ontology (Haendel  
121 et al., 2014), used herein. As part of these demonstrations, they developed an expert-curated database  
122 of semantic phenotypes (i.e., the Phenoscape Knowledgebase, e.g., Manda et al., 2015) for more than  
123 4,800 extant and extinct teleost fishes. Our new R package capitalizes on this knowledgebase to provide  
124 some tools for exploring new phylogenetic applications of semantically-aware anatomical data.

125 In this study, we implemented several tools for performing semantic-aware evolutionary analyses and  
126 exploring semantically-aware morphological data in a new R package *rphenoscape*. These tools include  
127 functions for automatically setting up evolutionary models for dependent traits based on a reference  
128 anatomy ontology, a phylogenetic data set, and character annotations to ontology terms. We integrated  
129 the new package with previous R packages tailored to work with phylogenetic data and ontologies, such  
130 as *rphenoscape* (<https://github.com/phenoscape/rphenoscape>), *ontologyIndex* (Greene et al., 2017),

131 *ontoFAST* (Tarasov et al., 2022), and the PARAMO pipeline (Tarasov et al., 2019). We provide tools  
132 to prepare data and models for evolutionary analyses (e.g., stochastic character mapping) that can  
133 be performed in R (e.g., corHMM, Boyko and Beaulieu, 2021) or in RevBayes (Höhna et al., 2016).  
134 *rphenoscape* also offers functions for importing and visualizing results, including tools for investigating  
135 relationships among anatomy ontology term annotations. *rphenoscape* further offers tools for assembling  
136 synthetic character matrices from semantic phenotypes available from the Phenoscape Knowledgebase  
137 (Phenoscape KB). We showcase the package functionality with data sets of two animal groups for which  
138 well-developed anatomy ontologies and/or semantic data are available: bees and fishes. Our new package  
139 provides the foundational tools to foster further advances in the field and incentivize researchers interested  
140 in working in the interface of phylogenetics, comparative methods, and ontologies.

## 141 2 Material and Methods

### 142 2.1 Implementation

143 *rphenoscape* is one of the two main R packages (*rphenoscape* being the other) resulting from the SCATE  
144 project (<https://scate.phenoscape.org/>)—Semantics for Comparative Analyses of Trait Evolution.  
145 It is tailored to facilitate comparative analyses of trait data incorporating domain knowledge from  
146 anatomy ontologies. Our package is intended as an integrative tool for comparative morphologists and  
147 systematists to work with semantic representations of organismal anatomy and/or semantically enriched  
148 phylogenetic data. The package allows working with external ontologies in OBO format but is spe-  
149 cially integrated with the Phenoscape KB. Its sister package under development, *rphenoscape*, is tailored  
150 to work with semantic phenotypes from Phenoscape KB, including tools for quantifying the seman-  
151 tic similarity of phenotype descriptions and algorithms for synthesizing annotated morphological data  
152 from published studies. *rphenoscape* imports and depends on several functions from its sister package,  
153 *rphenoscape*, particularly for accessing semantic phenotypes of vertebrates available at the Phenoscape  
154 KB (<https://kb.phenoscape.org/>), querying absence/presence data with OntoTrace (Dececchi et al.,  
155 2015), and calculating semantic similarity metrics. It relies on *ontologyIndex* (Greene et al., 2017) for  
156 importing and working with external ontologies and *igraph* (Csardi and Nepusz, 2006) for extracting ad-  
157 jacency matrices and other graph manipulations. It also uses some functions from *ontoFAST* (Tarasov,  
158 2022) to post-process semi-automatic annotations of phylogenetic character matrices with anatomy terms  
159 from the external ontologies.

### 160 2.2 Availability

161 The *rphenoscape* package requires R 3.5.0 or higher and the installation of *rphenoscape* from GitHub  
162 (<https://github.com/phenoscape/rphenoscape>). The current version of *rphenoscape* can be installed

163 directly from its GitHub repository (<https://github.com/uyedaj/rphenoscate>). The source code from  
164 the latest stable version of the package as dated from this publication is deposited at Zenodo (XXXX).

### 165 2.3 Overview

166 The functions of *rphenoscate* comprise three main groups. The first group (G1) includes functions for:  
167 (a) assessing the dependency structure of anatomical entities based on annotations with ontology terms  
168 or semantic phenotypes available at Phenoscape KB; (b) setting up and fitting evolutionary models  
169 accounting for trait dependencies; and (c) performing stochastic character mapping using corHMM or  
170 RevBayes. The second group (G2) includes functions for: (a) assessing the relationships among anatomy  
171 ontology terms annotated to phylogenetic characters using semantic similarity metrics calculated with  
172 *rphenoscape*; and (b) visualizing the semantic and phylogenetic structure of the data. Finally, the third  
173 group (G3) includes functions for: (a) constructing phylogenetic characters based on the exclusivity  
174 classes inferred with *rphenoscate*; (b) assembling and exporting synthetic character matrices for phylo-  
175 genetic analyses. A scheme of the main components in *rphenoscate* is presented in Figure 1. Detailed  
176 tutorials with examples of the different applications of *rphenoscate* are given in the Supporting Informa-  
177 tion and are also available at GitHub ([https://github.com/diegosasso/rphenoscate\\_tutorials](https://github.com/diegosasso/rphenoscate_tutorials)).

### 178 2.4 Data sets

179 For demonstrating the package functionality, we employed two animal groups with well-established  
180 anatomy ontologies: bees and fishes. For the bees, we employed a data set based on the matrix of  
181 corbiculate bees (Hymenoptera: Apidae; *e.g.*, honey bees, bumble bees) from Porto and Almeida (2021)  
182 (data set 1). The original character matrix in NEXUS format was first imported in R. Then a sample  
183 of 20 phylogenetic characters referring to the anatomical entities in Table 2 was used. These characters  
184 were selected to represent anatomical entities from the head, mouthparts, and genitalia of bees, for which  
185 many anatomical dependencies can be observed (D.S.P. personal observations), making them suitable to  
186 test the package functionality. Phylogenetic character annotation used anatomy terms from the HAO  
187 ontology (Yoder et al., 2010) employing a semi-automatic pipeline implemented in *ontoFAST* (Tarasov,  
188 2022) and new functions from *rphenoscate*.

189 For the fishes, we employed two data sets comprising skeletal characters for species in the order  
190 Characiformes (Ostariophysi). One data set was an Ontotrace (Dececchi et al., 2015) data matrix of  
191 absence/presence characters inferred for species of the family Characidae (commonly known as characids  
192 and tetras) retrieved from the Phenoscape KB (data set 2), including a search for the anatomical entities  
193 in Table 3. These entities were selected because information for them was available for many species  
194 at the Phenoscape KB and they exhibited anatomical dependencies, thus making them suitable to test  
195 the package functionality. The second data set was the matrix of anostomoid fishes (Characiformes:

196 Anostomoidea) from Dillman et al. (2016) (data set 3). The original character matrix was retrieved from  
197 the metadata available at Phenoscape KB. This data set was selected as the benchmark of the SCATE  
198 project for evaluating the synthetic character matrix assembling functionality because the original study  
199 itself comprises a supermatrix for four families of anostomoid fishes and has semantic phenotypes avail-  
200 able at the Phenoscape KB. For both data sets, anatomical entities were already annotated by experts  
201 (W.M.D. and P.M.M.) with anatomy terms from the UBERON ontology (Mungall et al., 2012; Haendel  
202 et al., 2014; Dahdul et al., 2018).

## 203 2.5 Package showcase

204 For showcasing the package, we consider three study cases, one for each data set presented above. In  
205 the first case (hereafter BEES), a researcher wants to reconstruct the evolutionary history of several  
206 traits and understand how they relate to each other in bee anatomy (data set 1). For example, do traits  
207 from different anatomical regions evolve similarly? How are the anatomical entities represented by such  
208 traits related to each other? The researcher needs first to account for possible dependencies among  
209 anatomical entities in the evolutionary models (*i.e.*, biologically realistic models) before reconstructing  
210 the trait histories using stochastic character mapping. Then, the researcher needs to employ some tool  
211 to visualize the semantic patterns across anatomical entities in the data.

212 In the second case (hereafter CHARA), a researcher has access to the Phenoscape KB and wants  
213 to retrieve all information available for absence/presence of bones in characid fishes (data set 2). The  
214 researcher wants then to reconstruct the evolutionary history of these traits to answer a particular ques-  
215 tion. Do bones from particular body regions get lost more frequently than others in this particular group  
216 of fishes? For that, this researcher also needs to account for possible dependencies among anatomical  
217 entities when reconstructing character histories and employ tools to investigate the association between  
218 the semantic and phylogenetic patterns of the data.

219 In the third case (hereafter ANOST), a researcher also has access to the Phenoscape KB but this time  
220 wants to retrieve all information available for semantic phenotypes in anostomoid fishes. The researcher  
221 wants then to use this information to infer a phylogenetic tree. For that, the researcher needs some  
222 tools for getting the semantic phenotypes (task 1), converting them to phylogenetic characters (task 2),  
223 and assembling them in a synthetic character matrix (task 3). However, how can this researcher be  
224 assured that a synthetic character matrix obtained as such actually contains phylogenetic information?  
225 To answer this question, a benchmark is necessary, thus the matrix of anostomoid fishes from Dillman  
226 et al. (2016) (data set 3) was used.

## 227 2.6 Assessment analyses

228 BEES and CHARA.—Stochastic character mapping was used to reconstruct trait evolution using corHMM  
229 (Boyko and Beaulieu, 2021). For BEES, reconstructions used an ultrametric tree modified from Porto  
230 and Almeida (2021) using *phytools* (Revell, 2012). Note that the transformation was done only for  
231 demonstrative purposes and a proper dating method was not employed. For CHARA, reconstructions  
232 used a dated phylogeny obtained from *fishtree* (Chang et al., 2019). In both cases, for the exploration  
233 of the semantic patterns of the data, clustering dendrograms for the anatomy ontology terms ('trait  
234 trees') were constructed using the Jaccard semantic similarity metric calculated using functions from  
235 *rphenoscape*.

236 ANOST.—Assessment of phylogenetic information was performed by comparing the original data set  
237 from Dillman et al. (2016) to the synthetic character matrix obtained from semantic phenotypes of the  
238 same study using functions from *rphenoscape* (tasks1 and 2) and *rphenoscape* (task 3). Comparisons  
239 were made for both character matrices and for the posterior distributions of trees inferred from them.  
240 Character matrices were compared by calculating the cladistic information content (*sensu* Steel and  
241 Penny, 2005) using functions from the package *TreeTools* (Smith, 2019). Posterior distributions were  
242 compared by calculating the generalized Robinson-Foulds (RF) distances (Smith, 2020a) in reference to  
243 the majority-rule (MJ) consensuses of both analyses using functions from the package *TreeDist* (Smith,  
244 2020b). The generalized RF distance is a metric of dissimilarity between pairs of trees based on the  
245 information content (in bits) of shared splits (Smith, 2020b). In short, posterior distributions of tree  
246 topologies were sampled through Bayesian inferences for both character matrices. Then generalized RF  
247 distances were calculated in reference to the MJ consensus of the original and inferred synthetic matrices,  
248 thus resulting in four distributions of RF distances: distribution from the (i) original matrix vs. original  
249 MJ consensus; (ii) inferred synthetic matrix vs. original MJ consensus; (iii) inferred synthetic matrix  
250 vs. inferred synthetic MJ consensus; and (iv) original matrix vs. inferred synthetic MJ consensus.  
251 A broad overlap between (i) and (ii) and between (iii) and (iv) can then serve as a proxy to assess  
252 whether the Bayesian phylogenetic analyses result in similar posterior distributions of trees and thus  
253 whether character matrices have similar phylogenetic information. Bayesian inferences were performed  
254 in MrBayes (Ronquist et al., 2012) with MCMC settings as indicated in the Supporting Information  
255 available online.

256 Finally, to give an example based on the original intent of the researcher in this study case, an  
257 additional search was performed retrieving all semantic phenotypes available at Phenoscape KB for  
258 fishes in Characidae. This family was selected—instead of the superfamily Anostomoidea—to reduce  
259 computational effort and facilitate downstream analyses (for demonstrative purposes only), but still,  
260 show an example of a relatively large data set retrieved from Phenoscape KB. The data set was then  
261 used to build a synthetic character matrix assembling data from multiple phylogenetic studies (see also

262 Dececchi et al., 2015).

## 263 3 Results

### 264 Automated construction of structured Markov models for dependent traits 265 and exploration of semantic patterns of morphological data

266 BEES.—The sample of 20 phylogenetic characters from Porto and Almeida (2021) contained 16 anatomical entities (Table 2). In those cases where multiple characters refer to the same anatomical entity, 267 *rphenoscate* automatically detected those characters and set up appropriate evolutionary models, either 268 a standard structured Markov model (SMM-ind) if no ontological dependencies were found; an embedded 269 dependency quality type Markov model (ED-ql) if dependencies based on property instantiation were 270 found (*sensu* Vogt, 2018a); or an embedded dependency absence-presence type Markov model (ED-ap) 271 if dependencies based on parthood relations were found (*sensu* Vogt, 2018a; for additional discussions 272 on types of dependencies and models see Tarasov, 2019, 2022; Vogt, 2018a). Otherwise, different models 273 were automatically assigned to single non-dependent characters based on the number of observed states 274 (Figure 2). For example, amalgamated characters of the ‘posterior tentorial arm’ were assigned an Mk 275 model with 2 states; the ‘anterior tentorial arm’, an ED-ql model with 3 states; the ‘furcula’, an ED-ql 276 model with 6 states; and the ‘hypopharyngeal lobe’, an Mk model with 7 states. Samples of the stochastic 277 maps from these examples are shown in Figure 3a.

278 In this study case, the researcher was interested in reconstructing the evolutionary history of multiple 279 traits and understanding their relationships in the bee anatomy. After accounting for the ontological 280 dependencies among anatomical entities in the evolutionary models, the researcher can observe that 281 reconstructed trait histories show some character states co-occurring in the phylogeny, for example, 282 those in the clades indicated with stars and triangles (Figure 3a). When exploring the semantic patterns 283 of the data, the relationships among the ontology term annotations indicate that some anatomical entities 284 are part of the same anatomical regions of the bee anatomy (*e.g.*, ‘anterior tentorial arm’ and ‘posterior 285 tentorial arm’ are *part\_of* ‘tentorium’; Figure 3b, TEN, purple dashed box) whereas others not (*e.g.*, 286 ‘hypopharyngeal lobe’ and ‘furcula’). Most clusters based on semantic similarity, in this case, actually 287 correspond to anatomically related entities of the bee anatomy, as indicated by parthood relationships 288 to parent terms in the HAO ontology. For example, clusters with anatomical entities that are *part\_of* 289 ‘mandible’, ‘maxilla’, ‘genitalia’, and ‘tentorium’ were recovered (dashed boxes in Figure 3b; MD, MX, 290 GEN, and TEN respectively). Therefore, clustering anatomical entities based on semantic similarity 291 metrics calculated for their ontology term annotations can be used by this researcher to further investigate 292 if such clusters reflect shared parameters in the evolutionary models of traits linked to these anatomical 293 entities, for example, evolutionary rates or transition biases.

295 CHARA.—The data set retrieved from the Phenoscape KB contained 420 species with absence/presence  
296 data available for at least one of the anatomical entities listed in Table 3. From these, 146 species were  
297 also available in the tree obtained from *fishtree*. Data coverage, defined as the number of species for which  
298 absence/presence was asserted or can be inferred by the Phenoscape KB reasoner, ranges from 361 (86%)  
299 to 7 (2%) across all taxa (Table 3). The average presence of anatomical entities across species with data  
300 available ranges from 0.99 for ‘infraorbital 1’ and ‘infraorbital 2’ to 0.14 for ‘supraneural 5 bone’, with  
301 lower values indicating entities commonly absent (e.g., ‘coracoid foramen’, ‘uroneural 2’, ‘supraneural  
302 3 bone’, ‘supraneural 4 bone’). From the anatomical entities in Table 3, ontological relationships were  
303 detected between the pairs ‘scapula’ and ‘scapular process’, and ‘coracoid bone’ and ‘coracoid foramen’,  
304 thus appropriate structured Markov models were automatically set up by *rphenoscape*. In this case, the  
305 model used to account for trait dependencies was the SMM-sw, as discussed in Tarasov (2019, 2022), as  
306 shown in Figure 2. Samples of stochastic maps for some of the anatomical entities, including the two  
307 above pairs of dependent ones, are shown in Figure 4.

308 As observed for ‘supraneural 4 bone’, ‘supraneural 5 bone’, and ‘uroneural 1’, for example, stochastic  
309 character maps reconstructed no transitions at all, possibly due to many taxa being coded as polymorphic  
310 (i.e., states 0 and 1 or 1 and 0) or ‘?’ (missing) and/or due to low data coverage, as is observed in  
311 ‘supraneural 4 bone’ and ‘supraneural 5 bone’. In the case of the combined character ‘coracoid bone  
312 + coracoid foramen’, all instances of presence of ‘coracoid foramen’ seem to be correctly inferred in  
313 branches where ‘coracoid bone’ was also present, as indicated with the arrowheads in Figure 4.

314 In this second study case, the researcher was interested in understanding the history of loss of bones  
315 in characid fishes. By inspecting the stochastic character maps (4), the researcher can observe that some  
316 bones were reconstructed as absent (e.g., ‘supraneural 4 bone’ and ‘supraneural 5 bone’) or present for  
317 all species (e.g., ‘uroneural 1’), possibly due to the issues mentioned above. Some other bones were lost  
318 multiple times in several species (e.g., ‘uroneural 2’) whereas others were lost a few times but seem to  
319 be correlated (e.g., ‘infraorbital 5’ and ‘infraorbital 6’). More complex cases can be observed for the  
320 combined characters. For example, for ‘scapula + scapular process’, ‘scapula’ and ‘scapular process’ are  
321 present in all species, whereas for ‘coracoid bone + coracoid foramen’, ‘coracoid bone’ is present in all  
322 species, but ‘coracoid foramen’ can be absent or present (4, arrowheads).

323 However, the researcher can learn more about the losses of bones in characid fishes by also investi-  
324 gating the semantic patterns of the data with some tools from *rphenoscape*. For example, in Figure  
325 5, the tree shown to the left is the species phylogeny obtained from the *fishtree* package; the clustering  
326 dendrogram at the top right shows the relationships among the anatomical entities from Table 3; and  
327 the heatmap indicates absence/presence of the bones. In this case, some phylogenetic patterns of the  
328 data set can be easily identified, such as the absence of ‘infraorbital 5’ and ‘infraorbital 6’ supporting  
329 the clade indicated with a red dashed-box in the phylogenetic tree of Figure 5. Additionally, a clear

330 pattern in this data set is that information-poor anatomical entities—empty cells in the heatmap—are  
331 not randomly distributed; rather they are predominantly semantically related entities: all bones from  
332 the supraorbital series (Figure 5: clustering dendrogram, star). This might prompt the researcher to  
333 further investigate if this lack of information is simply due to a poorly studied anatomical structure in  
334 this group of fishes or if there are underlying biological causes.

335 **Synthetic character matrices maintain phylogenetic information from manually-  
336 curated matrices**

337 ANOST.—The ability to synthesize data from different studies with characters of varying types presents  
338 a major challenge to data reuse, expansion, and synthesis (Dececchi et al., 2015). In this third study  
339 case, the researcher was interested in retrieving all semantic phenotypes for anostomoid fishes from the  
340 Phenoscape KB, building a character matrix, and inferring a phylogeny. However, this task requires  
341 assessing the phylogenetic utility of this synthetic character matrix. For that, the researcher evaluated  
342 whether the use of character data represented as ontology-annotated phenotypic statements ('semantic  
343 phenotypes') and subsequent construction of synthetic character matrices from these phenotypes re-  
344 sulted in any loss of phylogenetic information. The researcher achieved this by using *rphenoscape* and  
345 *rphenoscape* to compare the semantic phenotypes obtained from the Phenoscape KB to the original  
346 expert-curated matrix from Dillman et al. (2016).

347 The original data set from Dillman et al. (2016) contained 463 phylogenetic characters and 173 taxa.  
348 With *rphenoscape*, it was possible to recover and cluster semantic phenotypes referring to the original  
349 data set resulting in a synthetic matrix with 422 characters. When assessing the phylogenetic information  
350 of both data sets, the cladistic information content (*sensu* Steel and Penny, 2005) for characters in the  
351 original and synthetic matrices are almost identical (Figure 6a) indicating the conservation of potential  
352 phylogenetic information (Porto et al., 2022). When comparing the majority-rule consensus trees inferred  
353 from both matrices (Figure 6b) or their posterior distributions (Figure 6c-d), trees are almost identical  
354 and distributions mostly overlap, demonstrating that the phylogenetic information of the original data  
355 set was retained in the synthetic matrix inferred with *rphenoscape*.

356 As for the additional search on the Phenoscape KB, the synthetic matrix inferred from semantic  
357 phenotypes of Characidae contained 524 species and 739 phylogenetic characters. From all species,  
358 around 45% have data available for at least a quarter of the phylogenetic characters. From all phylo-  
359 genetic characters, at least 37% have data available for at least a quarter of the species. Overall data  
360 coverage—character state information available—is around 20% for the entire matrix (Figure 7). From  
361 all phylogenetic characters, around 20% are phylogenetically non-informative (*i.e.*, non-variable for the  
362 taxa considered).

363 A complete work-through of all the analyses of the three study cases is given in the tutorials in

364 the Supporting Information online and also available on GitHub ([https://github.com/diegosasso/rphenoscate\\_tutorials](https://github.com/diegosasso/rphenoscate_tutorials)).

## 366 4 Discussion

### 367 4.1 Studying complex traits

368 One of the main challenges of studying morphological evolution is modeling complex traits—sets of  
369 related traits often exhibiting multiple levels of dependencies or correlations (e.g., Tarasov, 2022: Fig.  
370 1D). We have demonstrated that morphological knowledge expressed in anatomy ontologies can be  
371 employed for automatically setting up models for ontologically dependent traits. Biologically realistic  
372 models for morphology—e.g., accounting for ontological dependencies or correlations among characters—  
373 can be used for studying complex traits, for example, in the context of understanding adaptations to  
374 particular environments (Tribble et al., 2022); trait-dependent diversification (O’Meara et al., 2016); or  
375 integration/modularity among anatomical structures (Billet and Bardin, 2019).

### 376 4.2 What can be learned from the three study cases?

377 Trait evolution and semantic patterns.—In this work, we have shown the application of ontology-informed  
378 evolutionary models for morphological traits in the context of stochastic character mapping with two data  
379 sets, bees (Figure 3) and characid fishes (Figure 4), annotated with terms from the HAO and UBERON  
380 ontologies, respectively. We then demonstrated how *rphenoscate* can help researchers to investigate trait  
381 evolution and address simple evolutionary questions by assessing semantic patterns in morphological  
382 data.

383 In the study-case BEES, after accounting for ontological (anatomical) dependencies among traits,  
384 the researcher learned that some character states are still reconstructed in similar branches of the tree  
385 (stars and triangles in Figure 3a). Although this pattern is congruent with a scenario of biological  
386 dependency between traits, the limited size of the data set—only one instance of co-occurring states—  
387 precludes any assertive interpretation. Another possibility is that some traits from structurally related  
388 anatomical regions might be evolving similarly due to shared gene regulatory and developmental machin-  
389 ery (Wagner Gunter and Altenberg, 1996; Wagner and Stadler, 2003; Mabee, 2006). By investigating  
390 the semantic patterns of ontology annotations to phylogenetic characters in this data set, the researcher  
391 learned that some traits with congruent character-state reconstructions (triangles in Figure 3a) represent  
392 related anatomical entities—i.e., that are *part\_of* the same anatomical region (Figure 3b, TEN, purple  
393 dashed box). Indeed, this might be an indicator that some traits from a given anatomical region evolve  
394 similarly. However, in the context of phylogenetic inference, it has been demonstrated that the evolution  
395 of morphological characters does not necessarily follow anatomical partitions (Tarasov and Genier, 2015;

396 Casali et al., 2022) or is often incongruent across them (Porto et al., 2021, 2022), thus prompting the  
397 researcher to further investigate for alternative causal explanations.

398 In the study-case CHARA, the researcher learned that some bones representing structurally related  
399 anatomical entities might be evolving independently (*e.g.*, ‘uroneural 1’ and ‘uroneural 2’) whereas others  
400 not (*e.g.*, infraorbital bones) (Figure 4). They could also observe that anatomical entities commonly lost  
401 in characid fishes include both structurally related (*e.g.*, ‘supraneural 3 bone’, ‘supraneural 4 bone’,  
402 and ‘supraneural 5 bone’) and unrelated entities (*e.g.*, ‘coracoid foramen’ and ‘uroneural 2’) (Figure  
403 5). Furthermore, the loss of some structurally related entities (*e.g.*, infraorbital bones) seems to be  
404 phylogenetically informative for some groups of fishes (Figure 5, red dashed box). After this initial  
405 exploration using *rphenoscape*, the researcher can then investigate the observed phylogenetic and semantic  
406 patterns of the data to ask further questions. For example, why are these particular bones absent  
407 altogether in some groups of fish? Are they associated with (*develops\_from*) the same developmental  
408 module?

409 Synthetic character matrices.—Finally, in the study case ANOST, the researcher was able to obtain  
410 a synthetic character matrix from semantic phenotypes and learned that the phylogenetic information  
411 inferred from this matrix is indeed comparable to that inferred from the original manually-curated matrix  
412 (Figure 6). This result is crucial since the main interest of most systematists in assembling character  
413 matrices is to infer the phylogeny of a given group based on the available anatomical evidence. Perhaps  
414 more importantly, it was demonstrated that it is also possible to construct synthetic character matrices  
415 from semantic phenotypes of multiple different studies, as obtained for characid fishes (Figure 7). This  
416 opens up opportunities for ‘phenomic-scale’ studies with synthetic matrices (*e.g.*, Dececchi et al., 2015)  
417 exploring all the semantic phenotypes of teleost fishes available at Phenoscape KB and provides a model  
418 for future knowledgebases focused on other groups of organisms.

### 419 4.3 Current limitations

420 Although *rphenoscape* offers some tools for working with external ontologies (*i.e.*, other than UBERON)  
421 and NEXUS files associated with ontology annotations, other tools are specifically for working with  
422 the semantic phenotypes from the Phenoscape KB in synergy with *rphenoscape*. Furthermore, a major  
423 limitation in both cases—external character matrices or Phenoscape KB data—is that annotation of  
424 phylogenetic characters with ontology terms has to be done manually. In the case of external ontologies,  
425 semi-automatic annotations can be performed using *ontoFAST* and post-processing with *rphenoscape*, but  
426 those are limited to the anatomy terms only (*i.e.*, thus not including quality terms describing character  
427 states) and the final decision still requires expert judgment. One additional limitation is the number of  
428 models currently implemented to account for dependencies using ontology information (ED-ap, ED-ql,  
429 and SMM) and the automatic setting up option being restricted to only linear chains of dependencies and

430 a few hierarchical levels (*e.g.*, entity A *depends\_on* entity B; or entity A *depends\_on* entity B *depends\_on*  
431 entity C).

#### 432 4.4 Semantic phenotypes and new approaches to morphological data

433 Ontologies can provide a new framework for representing and studying organismal anatomy. As suggested  
434 in Vogt (2018a,b), alternative formalizations of morphological data, other than free-text descriptions in  
435 natural language or standard character matrices, offer several new opportunities but also challenges.  
436 Some advantages of working with semantically-enriched representations of morphological information  
437 (*e.g.*, Balhoff et al., 2010, 2014; Dececchi et al., 2015; Deans et al., 2015; Thessen et al., 2020; Stefen  
438 et al., 2022) include the possibility of automatically assembling synthetic character matrices for phy-  
439logenetic inference, as demonstrated here; integrating anatomical information at phenomic scale across  
440 databases and domains of knowledge; and developing graph-based phylogenetic algorithms for compara-  
441 tive analyses (Ramírez and Michalik, 2014; Vogt, 2018a,b). *rphenoscate* represents an important step in  
442 these directions.

443 In a broader context, working with ontologies and semantic representations of organismal anatomy  
444 have utilities and advantages beyond the few ones presented here. It is a fundamental and necessary step  
445 for fully exploiting morphological data in this new era of ‘Phenomics’ (Braun et al., 2018). It allows data  
446 from different sources and domains of knowledge to be easily integrated and summarized, making it easily  
447 findable, accessible, interoperable, and reusable by humans and machines, thus compliant with the FAIR  
448 principles in data science (Wilkinson et al., 2016). In this study, we showed that semantic phenotypes  
449 can be automatically converted into reasonable synthetic character matrices for downstream analysis.  
450 Thus, computer-assisted phenomic-scale research can be made possible in evolutionary biology. We hope  
451 that our new package will offer some useful tools in this direction encouraging interested researchers and  
452 prompting advances in the fields of comparative morphology, phylogenetics, and ontologies.

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#### 457 Conflict of Interest

458 The authors declare no conflict of interest.

## 459 Author's Contributions

460 D.S.P., S.T., and J.U. conceived the package. D.S.P., S.T., H.L., C.C., and J.U. designed the package,  
461 tested the package, and wrote the documentation. All authors wrote the first draft of the manuscript  
462 and revised the final version of the paper.

## 463 Data Availability Statement

464 The code of *rphenoscate*, tutorials and data sets are available on GitHub at <https://github.com/>  
465 [uyedaj/rphenoscate](https://github.com/uyedaj/rphenoscate) and [https://github.com/diegosasso/rphenoscate\\_tutorials](https://github.com/diegosasso/rphenoscate_tutorials), and Zenodo at  
466 XXXX.

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Table 1: Glossary of some important concepts and their definitions.

Concept	Definition and example	Reference
Anatomical entity	Any identifiable morphological characteristic of an organism. It is usually represented in an ontology by a class accompanied by a formal definition. <i>e.g.</i> , ‘maxilla’, ‘mandible’, ‘femur’, ‘tibia’.	Dececchi et al. (2015); Vogt (2017)
Phylogenetic character	Evidential unit of putative phylogenetic significance. Can be any variable characteristic of organisms that seems relevant for phylogenetic inference and/or identification of evolutionary unities ( <i>e.g.</i> , different shapes of a bone in different organisms).	Sereno (2007); Vogt (2017)
Semantic phenotype	Structured annotation describing a characteristic of the anatomy of organisms. It is constructed using terms referring to concepts in an ontology and employs a formal descriptive model, for example, the entity-quality (EQ) syntax. In this work, a single semantic phenotype is usually referred to as “semantic statement” and “semantic pattern” is applied to any observable pattern associated with ontology term annotations of the data.	Deans et al. (2012)
Biological dependency	Covariation among characters resultant from non-independent evolution due to shared selective pressures on groups of traits, pleiotropy and/or functional integration. <i>e.g.</i> , reduction or loss of multiple bones in miniature fishes.	Vogt (2018a)
Ontological (or Anatomical) dependency	When two or more characters refer to structurally non-independent anatomical entities. Ex.: (character 1) presence of digits and (character 2) presence of arms; digits can only present if (=depends on) an arm is present as well.	Vogt (2018a)

Table 2: Anatomical entities and phylogenetic characters studied from the Porto and Almeida (2021) data set and corresponding terms from the HAO ontology. C1-20 denote the phylogenetic characters.

HAO	entity	Phylogenetic character
HAO:0000212	clypeus	C1. Clypeus
HAO:0000212	clypeus	C2. Lateral margin of ventral portion of clypeus
HAO:0000690	paraocular carina	C3. Paraocular carina
HAO:0001454	anterior tentorial arm	C4. Spur produced laterad from the dorsal sheet of anterior tentorial arm towards mesal margin of compound eye margin at level of antennal foramen
HAO:0001454	anterior tentorial arm	C5. Lateral spur of the dorsal sheet of anterior tentorial arm
HAO:0001343	posterior tentorial arm	C6. Fan-shaped sheet of posterior tentorial arm
HAO:0001565	hypopharyngeal lobe	C7. Shape of hypopharyngeal lobe
HAO:0000456	labrum	C8. Median tubercle or transversal ridge on distal portion of anterior surface of labrum
HAO:0000081	acetabular groove	C9. Acetabular groove of mandible of female
HAO:0000676	outer groove	C10. Outer groove of mandible of female
HAO:0000219	condylar groove	C11. Condylar groove of mandible of female
HAO:0000958	stipes	C12. Comb on an emargination at distal portion of posterior margin of stipes
HAO:0000958	stipes	C13. Setae of the stipital comb
HAO:0000457	lacinial lobe	C14. Shape of lacinia
HAO:0002149	postarticular portion of the postmentum	C15. Mentum
HAO:0000686	paraglossa	C16. Paraglossa
HAO:0002498	furcula	C17. Furcula
HAO:0002498	furcula	C18. Dorsal arm of furcula
HAO:0000707	penisvalva	C19. Dorsal bridge of penis valves
HAO:0000395	harpe	C20. Gonostylus

Table 3: Anatomical entities studied for 420 species in the characid data set and corresponding terms from the UBERON ontology. Coverage and percentage represent respectively the number and proportion of species with absence/presence data available. Average indicates the mean presence (state 1) of anatomical entities across all species with data available.

UBERON	entity	coverage	percentage	average
UBERON:2000223	infraorbital 1	361	0.86	0.99
UBERON:2001407	infraorbital 2	361	0.86	0.99
UBERON:2001409	infraorbital 4	360	0.85	0.95
UBERON:2001674	infraorbital 6	334	0.79	0.95
UBERON:2001408	infraorbital 3	325	0.77	0.99
UBERON:0006849	scapula	298	0.71	0.99
UBERON:2000495	infraorbital 5	292	0.69	0.94
UBERON:0004743	coracoid bone	289	0.68	0.99
UBERON:2001737	coracoid foramen	269	0.64	0.04
UBERON:2002064	uroneural 1	246	0.58	0.98
UBERON:2002109	uroneural 2	243	0.58	0.25
UBERON:4200123	scapular process	226	0.54	0.99
UBERON:2001192	supraneural 3 bone	19	0.05	0.28
UBERON:2002007	supraneural 4 bone	13	0.03	0.08
UBERON:2001165	supraneural 5 bone	7	0.02	0.14

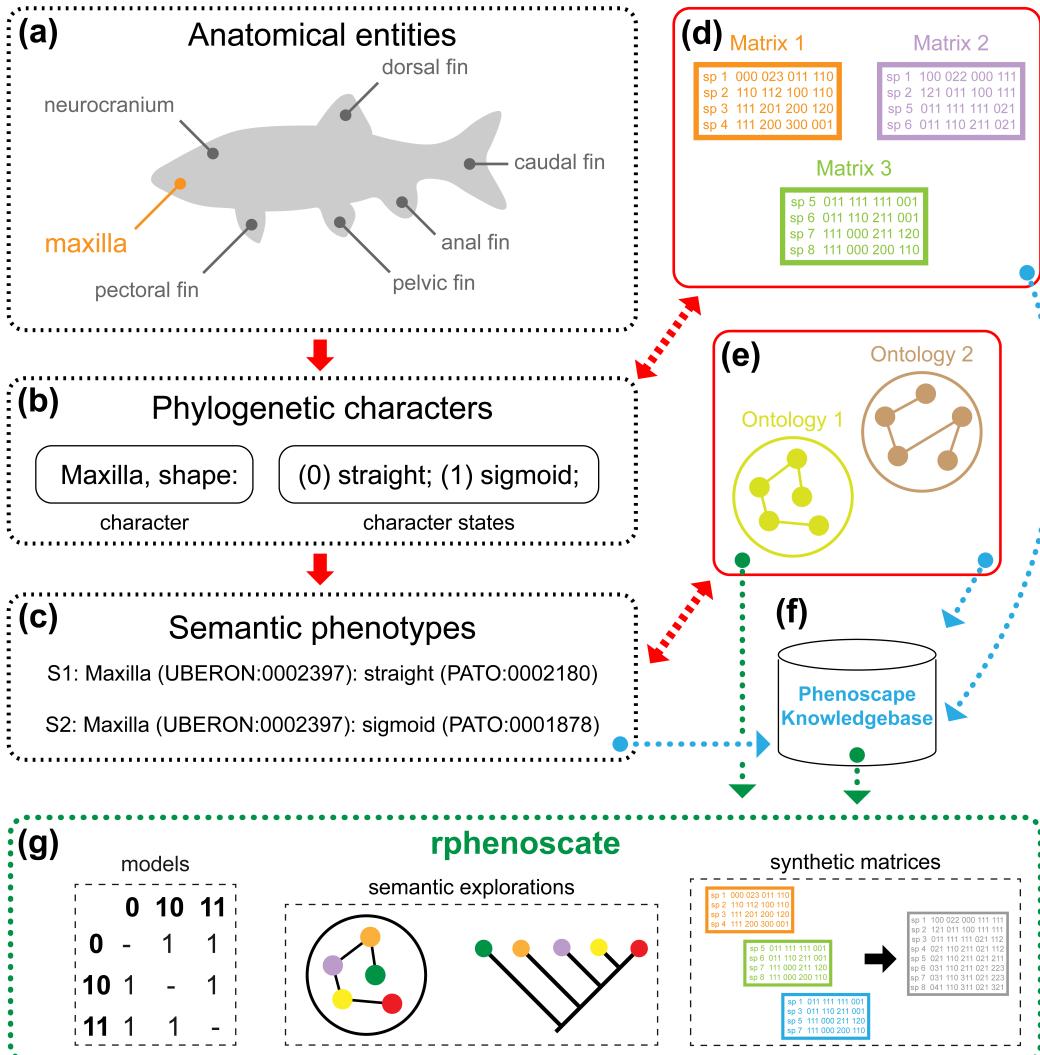


Figure 1: Scheme of the main concepts and components in *rphenoscape*. (a) Organismal anatomy can be conceptualized and described through anatomical entities; all of which are valuable for phylogenetic inference at a particular phylogenetic level (e.g., ‘maxilla’). (b) A systematist can thus propose a phylogenetic character formalizing the putative phylogenetic evidence; multiple phylogenetic characters evaluated for multiple taxa are usually organized in a character matrix (d). (c) An expert can further enrich the phylogenetic character with semantic information, thus proposing a semantic phenotype, by linking the anatomical entities and qualities to concepts in an anatomy ontology (e). (f) The Phenoscape Knowledgebase contains expert-curated annotations of semantic phenotypes from multiple phylogenetic studies of teleost fishes and integrates multiple ontologies (e.g., PATO, UBERON). (g) The *rphenoscape* package allows integrating knowledge from ontologies and accessing semantic phenotypes available at the Phenoscape KB (f) to automate model specification for dependent traits, perform semantic explorations of data, and assemble synthetic character matrices with the aid of the *rphenoscape*.

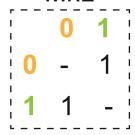
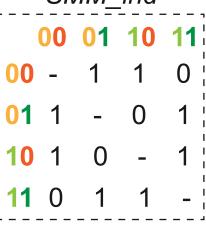
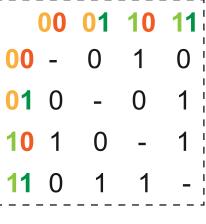
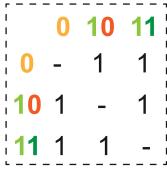
(a) Models	States	Examples
<b>individual</b> <i>Mk2</i>		<b>Characters\Anatomical entities:</b> Fishes: [C1] Antorbital: (0) absent; (1) present
	C1 0 (absent) 1 (present)	Bees: [C1] Paraocular carina: (0) absent; (1) present
<b>(b) independent</b> <i>SMM_ind</i>		<b>Characters\Anatomical entities:</b> Fishes: [C1] Uroneural 1: (0) absent; (1) present [C2] Uroneural 2: (0) absent; (1) present
	C1/C2 00 (state A1/state B1) 01 (state A1/state B2) 10 (state A2/state B1) 11 (state A2/state B2)	Bees: [C1] Clypeus: (0) flat; (1) convex [C2] Clypeus, lateral margin: (0) slightly deflected; (1) strongly deflected
<b>(c) dependent</b> <i>SMM_sw</i>		<b>Characters\Anatomical entities:</b> Fishes: [C1] Scapula: (0) absent; (1) present [C2] Scapular process: (0) absent; (1) present
	C1/C2 00 (absent/state B1) 01 (absent/state B2) 10 (present/state B1) 11 (present/state B2)	
<i>ED_ql (2)</i>		<b>Characters\Anatomical entities:</b> Bees: [C1] Anterior tentorial arm, lateral spur: (0) absent; (1) present [C2] Anterior tentorial arm, lateral spur (0) long; (1) short
	C1/C2 0 (absent) 10 (present/state B2) 11 (present/state B1)	

Figure 2: Types of models automatically set-up by *rphenoscate*. (a) Standard Markov models with variable number of states for individual characters (Mk), in this case, a binary character. (b) Structured Markov models for groups of independent characters (SMM-ind), in this case, a pair of binary characters. (c) Two types of models that account for character dependencies: Structured Markov models of the switch-on type (SMM-sw) and embedded dependency Markov models of the quality type (ED-ql). In both cases, the example is for a pair of binary characters. Note that SMM-sw and ED-ql treat absences differently (state 0); as two combinations of hidden states (only one observable) in the former and only one observable state in the latter. C1 and C2 indicate characters 1 and 2 respectively. Color codes are used to facilitate character state visualization for characters.

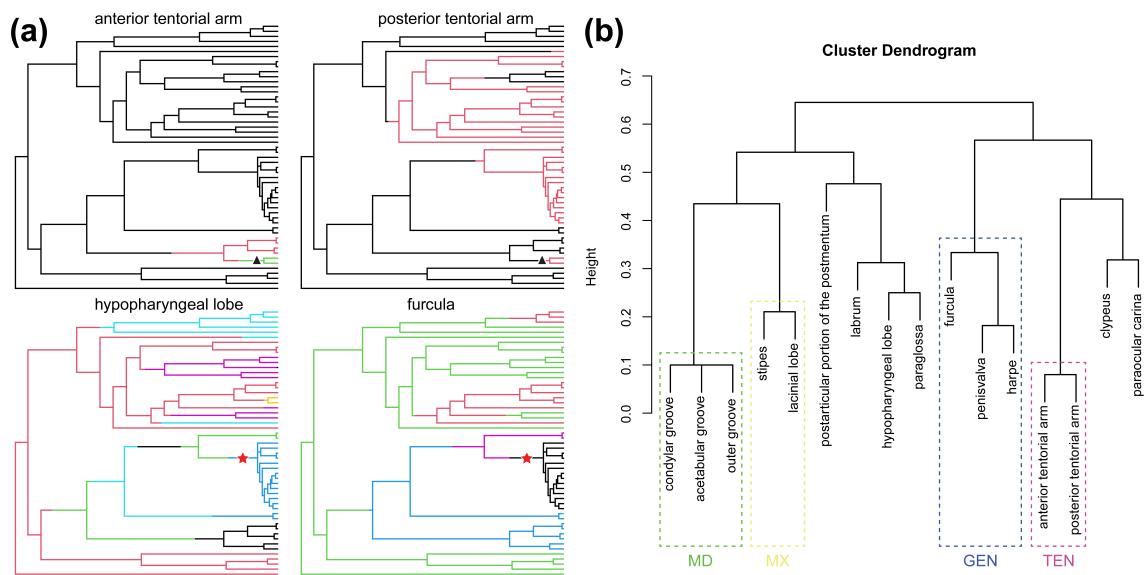


Figure 3: Exploration of the bee data set of Porto and Almeida (2021). (a) Sample of stochastic character maps obtained from four different anatomical entities. Branches in different colors indicate different ancestral character states. The red stars and black triangles indicate some clades with congruent patterns of reconstructed character states. (b) Clustering dendrogram showing the relationships among HAO terms referring to the anatomical entities of this data set based on the Jaccard semantic similarity. Dashed boxes indicate some clusters based on parthood relations known for the Hymenoptera anatomy. Abbreviations: GEN, genitalia; MD, mandible; MX, maxilla; TEN, tentorium.

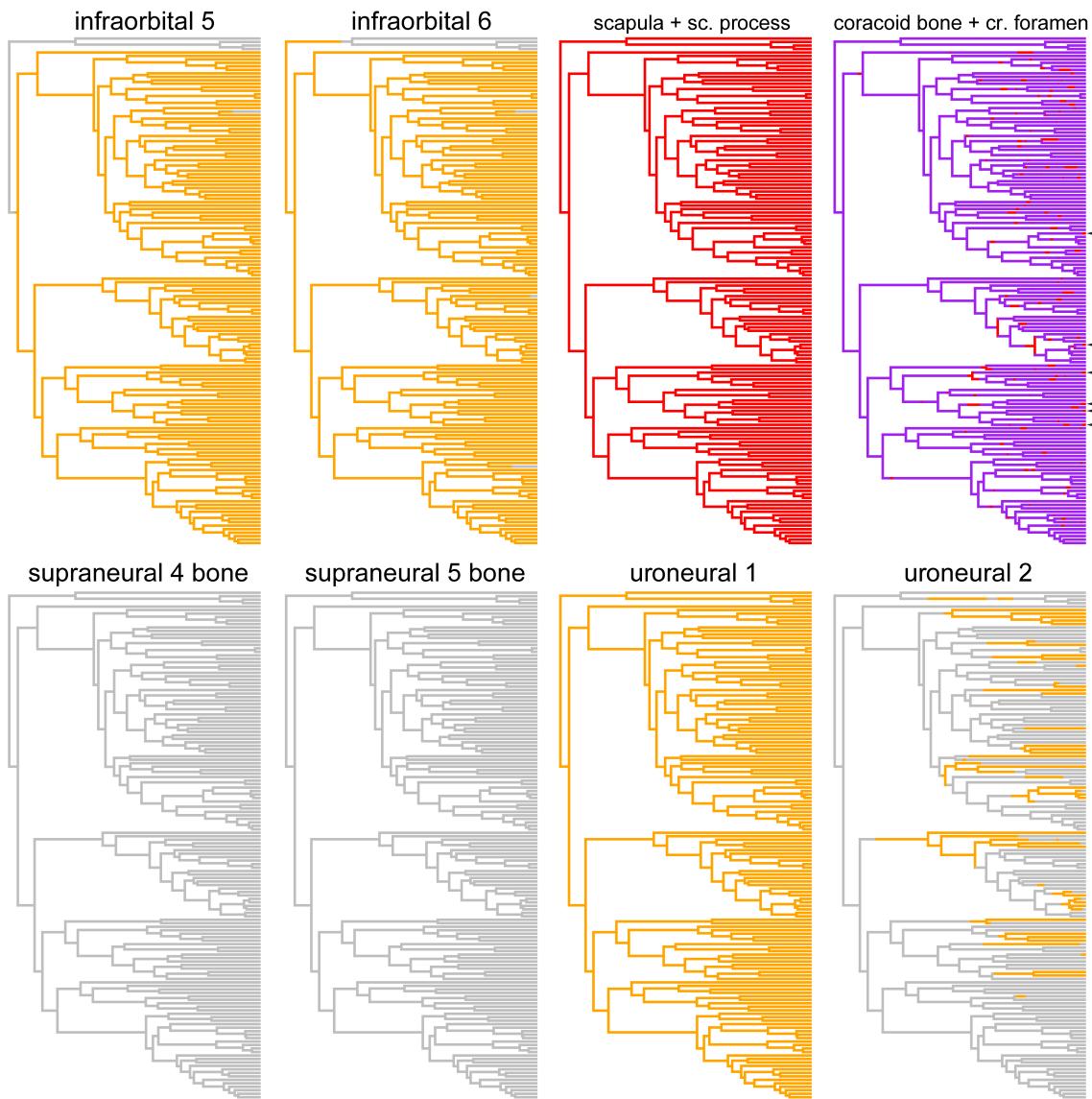


Figure 4: Sample of stochastic character maps obtained from ten different anatomical entities of the Characidae data set. Branches in orange indicate inferred presence of the respective anatomical entity and those in grey indicate absence; for pairs of entities, red color indicates the presence of both, as indicated with arrowheads for the pair 'coracoid bone + coracoid foramen' and purple indicates the presence of the first entity but the absence of the second.

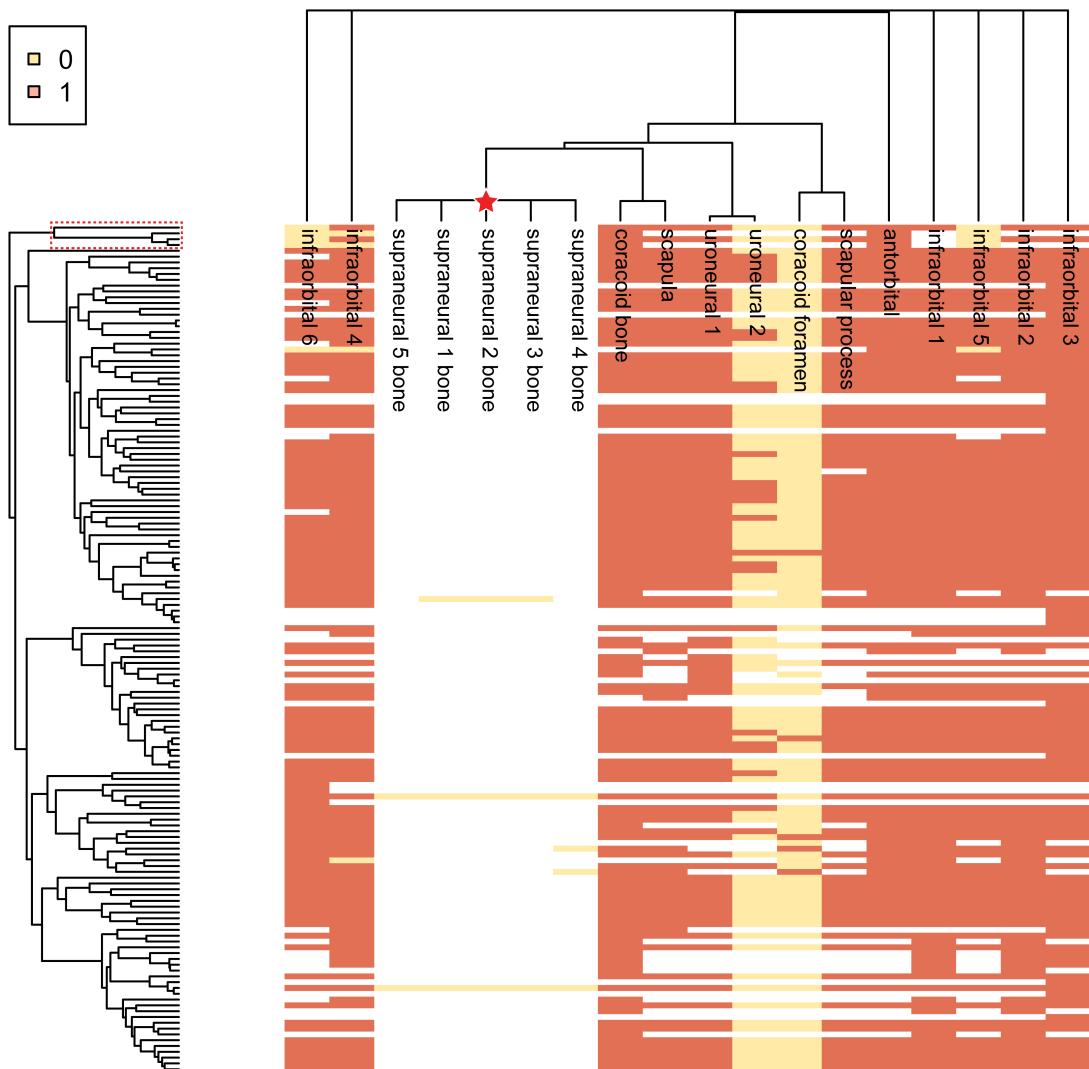


Figure 5: Visualization of phylogenetic and semantic patterns of the Characidae data set. The tree to the left is the dated species phylogeny obtained from the *fishtree* package. The clustering dendrogram at the top shows the relationships among UBERON terms referring to the anatomical entities of this data set based on the Jaccard semantic similarity. The heatmap shows absence (state 0, yellow) or presence (state 1, orange) for each anatomical entity in each species; empty cells indicate the absence of information. The dashed box at the top of the phylogeny indicates a clade of fishes supported by the absence of the bones 'infraorbital 5' and 'infraorbital 6'. The red star in the dendrogram indicates a cluster of related anatomical entities with a lack of information for this particular group of fishes.

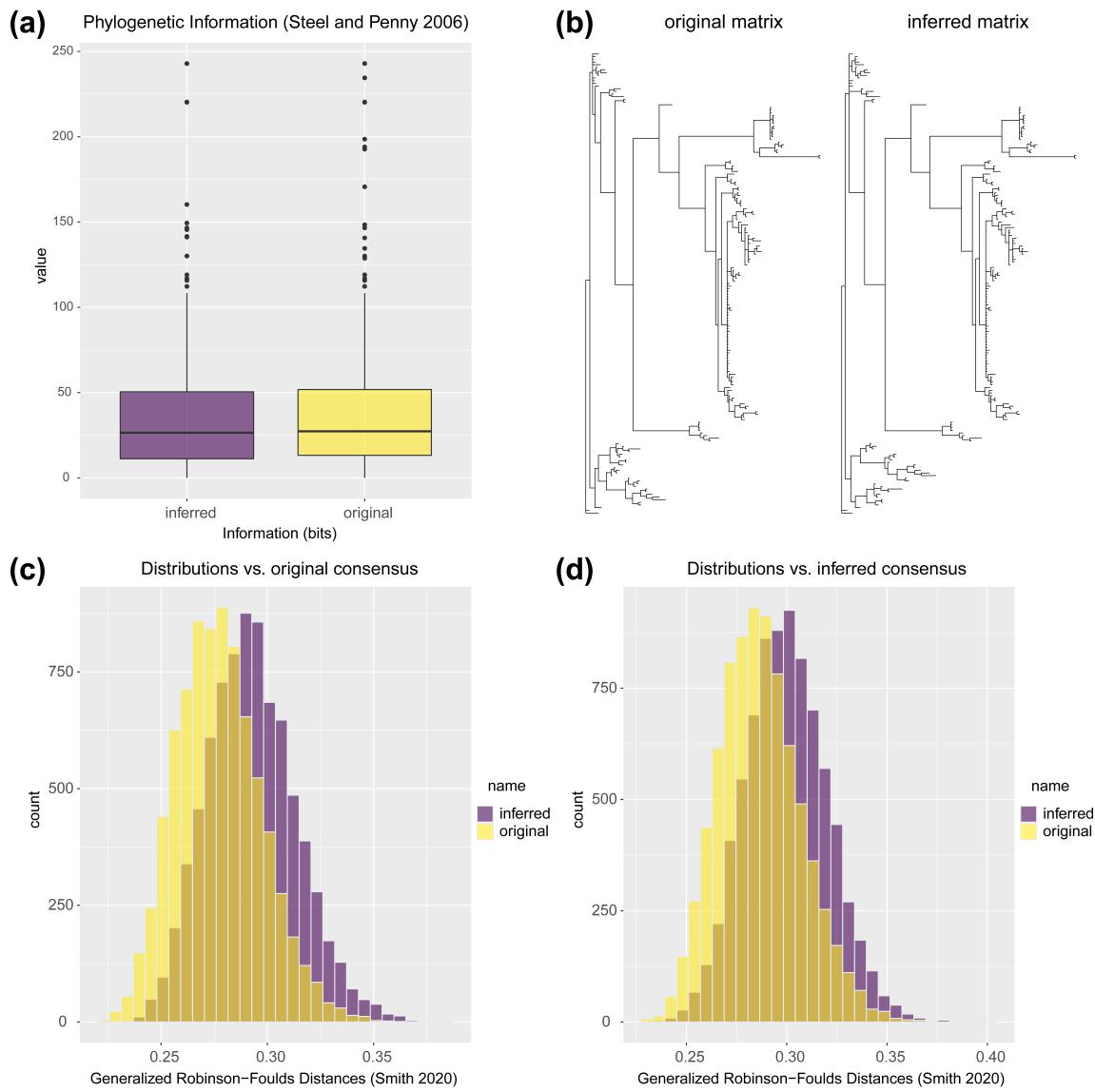


Figure 6: Assessments of the phylogenetic information of the original and inferred synthetic anostomoid data sets from Dillman et al. (2016). (a) Boxplots of cladistic information content (*sensu* Steel and Penny, 2005) for phylogenetic characters in both data sets. (b) Majority-rule consensus trees inferred from Bayesian analyses of both data sets. (c) Distribution of Generalized Robinson-Foulds distances for trees in the posterior obtained from the original and inferred synthetic data sets compared to the majority-rule consensus tree of the original data set. (d) Same as (c) but compared to the majority-rule consensus tree of the inferred data set.

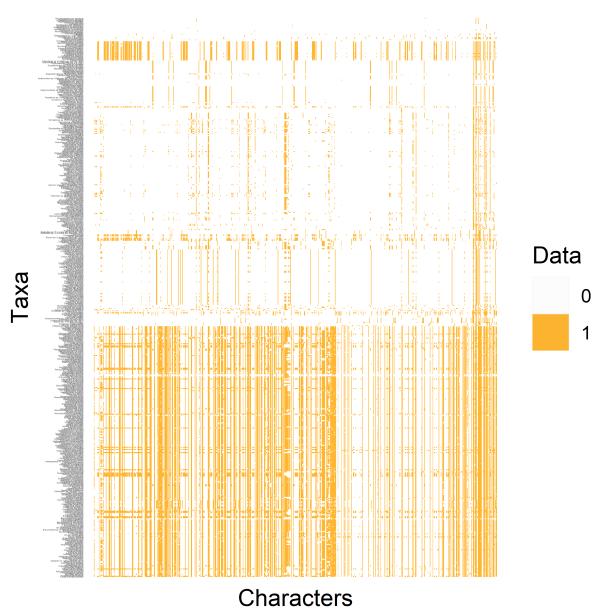


Figure 7: Heatmap representing the synthetic character matrix obtained from all semantic phenotypes of Characidae available at Phenoscape KB. Filled cells (state 1, orange color) indicate information available for a given taxon, irrespective of the actual character state.