

1                   **Phylogenetic and biogeographic history of the Snooks (Centropomidae:**  
2                   **Carangiformes) spanning the closure of the Isthmus of Panama**

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18  
19                  **Abstract**

20                  Amphiamerican New World fishes provide a unique opportunity to explore the impact of  
21                  geological processes and the formation of geographic barriers on biological diversification across  
22                  both spatial and temporal dimensions. We employed phylogenetic and biogeographic methods to  
23                  assess the impact of the emergence of the isthmus of Panama on the evolutionary history of  
24                  Snooks. Bayesian methods were used for phylogenetic inference and divergence time estimation,  
25                  incorporating the fossil record of Carangidae, Centropomidae, Istiophoriformes, Latidae, and

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26 Sphyraenidae to establish a timeline using methods of stratigraphic intervals. Biogeographic  
27 models were explored to test the hypothesis that trans-Isthmian vicariant events are coeval with  
28 the Isthmus closure. Our results suggest a sister relationship between Centropomidae and  
29 Sphyraenidae with a common ancestor that originated in the Upper Cretaceous (~78.18 Ma). The  
30 biogeographic model DEC+j indicated within-area speciation and dispersal (founder effect) as  
31 the primary modes of speciation in the genera *Centropomus*, *Lates*, and *Sphyraena*. The  
32 dispersion in the family Centropomidae was estimated from the Tropical Eastern Pacific to the  
33 Tropical Western Atlantic during the emergence of the isthmus of Panama. The alignment of  
34 divergence times with ancestral species distributions suggests a possible synchrony between the  
35 current distribution in *Centropomus* species and the gradual processes involved in the formation  
36 of the Isthmus of Panama during the Miocene. Furthermore, recent speciation events within each  
37 basin imply an influence of post-closure environmental conditions on the evolution of this group  
38 of fishes.

39

40 **Keywords:** allopatry, sympatry, speciation, phylogeny, geographic barriers.

41

## 42 **Introduction**

43 Geographic isolation plays a crucial role in speciation in different ways, such as  
44 reproductive isolation, adaptation to new environments, and other processes that either foster  
45 differentiation or restrict gene flow (Worsham et al. 2017). While the occurrence of speciation  
46 through geographic isolation is relatively rare in open systems like marine ecosystems, various  
47 ocean barriers exist, each exerting differing degrees of isolation. Soft barriers arise from  
48 oceanographic conditions or hydrobiological processes disrupting the interaction between

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49 conspecific individuals. Hard barriers are generally restrictions of terrestrial origin that  
50 physically separate marine populations (Cowman and Bellwood 2013), being the emergence of  
51 the Isthmus of Panama (IP) is one of its iconic examples. The rise of a terrestrial landscape  
52 separating the Eastern Pacific and the Western Atlantic led to the disappearance of the Central  
53 America Seaway (CAS), the creation of the Caribbean Sea, the modification of ocean dynamics,  
54 and therefore, an enormous impact on the Earth climate (Jaramillo 2018). This barrier acted as a  
55 bridge for terrestrial fauna and flora between South and North America and a barrier isolating the  
56 marine biota on both sides (Birkerland 1990; Duque-Caro 1990; Bartoli et al. 2005; Lessios  
57 2008; Montes et al. 2012; Coates and Stallard 2013; Bacon et al. 2015; O’Dea et al. 2016).

58

59 *Centropomidae sensu stricto* is a monogeneric New World family of marine fish,  
60 consisting of 13 species all in the genus *Centropomus* Lacepède, 1802, that inhabit marine,  
61 estuarine, and mangrove ecosystems with sandy and rocky bottoms. Given its presence on both  
62 sides of the IP, the family *Centropomidae* provides an excellent opportunity to test the effects of  
63 a hard barrier on divergence times and biogeographic patterns. They are commonly known as  
64 snooks or *robalos* in various regions of Central and South America where they have great  
65 commercial importance (Vergara-Chen 2014). Snooks have a high tolerance to low salinity but  
66 are vulnerable to temperature extremes (Tringali et al. 1999; Anderson and Williford 2020). The  
67 morphology of centropomid species is conservative, with strong similarities among species.  
68 Jordan (1908) suggested three pairs of sister species of the family *Centropomidae* based on  
69 morphological similarities, all living under essentially the same environmental conditions but  
70 separated since the end of the Miocene by the rise of the IP.

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71 Snooks belong to the series Carangaria, order Carangiformes, alongside the families  
72 Latidae and Sphyraenidae all of which share some morphological similarities (Betancur et al.  
73 2017; Girard et al. 2020; Thacker and Near 2023). The phylogenetic relationship between these  
74 families is still a subject of debate. Centropomidae has been proposed to be sister to Latidae  
75 (Tringali et al. 1999; Li et al. 2011; Betancur-R. et al. 2013, 2017; Carvalho - Filho et al. 2019;  
76 Anderson and Williford 2020; Figueiredo-Filho et al. 2021), or Sphyraenidae (Near et al. 2013;  
77 Mirande 2017; Rabosky et al. 2018; Girard et al. 2020). Latidae, with three extant genera, is  
78 distributed in Indo-West Pacific and African freshwater basins, often exhibiting endemism to  
79 specific lakes (Otero et al. 2014). Sphyraenidae comprises 29 extant species known as  
80 barracudas, that are found in tropical and subtropical regions of the Atlantic, Indian, and Pacific  
81 Oceans (Fricke et al. 2023). Our understanding of the biogeographic patterns in this group of  
82 families remains unexplored. The influence of geographic barriers, such as the IP, on the  
83 ancestral distribution of these species is still uncertain. If the Isthmus closure played any role in  
84 speciation in this group, we would expect to find a common area with pre-closure ages and  
85 younger, post-closure distributions of ages. Here, we constructed a time-calibrated phylogeny  
86 focusing on Centropomidae, Latidae, and Sphyraenidae. We used probabilistic modeling of  
87 biogeographic events on the phylogeny to test the association of the closure of the IP in 1) the  
88 divergence time of the species and, 2) the ancestral distribution of the species to assess the role  
89 of the isolation and large-scale barriers in shaping the current species geographical distribution.

90

## 91 **Methods**

### 92 **Sample collection**

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93           We collected specimens at local fish markets and landing areas across Caribbean and  
94 Pacific localities. All specimens collected were preserved and stored at the fish collection of  
95 Universidad del Valle (CIR-UV). Fishes were photographed, and a small fragment of the right  
96 pectoral fin was preserved in 96% ethanol and stored at -20 °C. We performed analyses using  
97 sequences generated in the present study and additional sequences obtained from GenBank. A  
98 total of 182 sequences (70 from this study and 112 from GenBank; Supplementary Table S1)  
99 from 13 species of Centropomidae, 22 species of Sphyraenidae, eight species of Latidae, two  
100 species of Carangidae, one species each of Coryphaenidae, Echeneidae, Nematistidae, Xiphiidae,  
101 and three species of Istiophoridae were used to estimate divergence times and infer phylogenetic  
102 relationships.

103

### 104 **DNA extraction, PCR amplification, and sequencing**

105           We extracted DNA following the Salting Out protocol (Sambrook et al. 1989). Four  
106 mitochondrial genes (12SrRNA, 16SrRNA, Cytochrome oxidase subunit I - COI, and  
107 cytochrome b -CYB) and one nuclear marker, a single-copy locus TMO-4c4 were amplified. The  
108 PCR amplification reactions were conducted in a final volume of 15µl containing 1 µl of DNA  
109 of stock concentration, 1.5 µl 10X reaction buffer BD (0.8M Tris -HCL, 0.2 M(NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>; Solis  
110 Bio Dyne), 1.2 µl of 2.0 mM MgCl<sub>2</sub>, 0.4 mM premixed deoxynucleotide triphosphates, 0.1 µl of  
111 5Uml *Taq* FIREPOL DNA polymerase (Solis Bio Dyne), and 0.2 µl of each oligonucleotide  
112 primer, each at 20mM concentration. PCR cycle parameters used to amplify all the genes  
113 included an initial denaturation step at 94 °C for 3min, followed by 35 cycles at 94 °C for 45 s,  
114 48 °C – 60°C (see supplementary Table S2 for details of the primers sequences and annealing  
115 temperature used for each gene) for 45 s, and extension at 72 °C for 45 s, and a final extension

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116 step at 72°C for 10min. All PCR products were loaded and run in agarose gels at 1% to verify  
117 the correct amplification. Macrogen Inc. (Seoul, Korea) performed the standard sequencing  
118 service.

### 119 **Phylogenetics analysis: Bayesian inference**

120 Sequences were edited using Geneious (Kearse et al. 2012) and aligned using MAFFT  
121 algorithm (Kato et al. 2013). The matrix concatenation was carried out using phyx (Brown et al.  
122 2017). The substitution model for each gene was selected based on the Akaike information  
123 criterion corrected for small sample sizes (AICc) using jModelTest 2 (Darriba et al. 2012). The  
124 substitution models that best fitted each locus were GTR + I + G (12SrRNA, 16SrRNA, COI,  
125 CYB), and HKY+I + G (TMO4c4).

126

127 Parallel-tempering Metropolis-Hastings MCMC (Metropolis et al. 1953; Hastings 1970)  
128 was used for sampling from the posterior distributions of the phylogenetic model. Sampling was  
129 carried out in Mr. Bayes (Ronquist et al. 2012) using parallelism (Altekar et al. 2004). We ran  
130 four independent analyses, each with eight chains (one cold and seven hot) for 40,000,000  
131 generations, sampling every 4,000th generation. A summary of posterior distributions was  
132 carried out after applying a burn-in of 50% while combining the remainder of the four analyses.  
133 Inter-chain parameter convergence was assessed using the potential scale reduction factor which  
134 approached 1.0 for all parameters. Intra-chain parameter convergence was assessed using the  
135 effective sample size, which was >1,000 for all parameters. The average standard deviation of  
136 split frequencies was used for assessing topological convergence, which reached a value of 0.02  
137 at the end of the analysis. The posterior tree distribution was summarized using a majority-rule

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138 consensus tree with average branch lengths. Branch support values are posterior probabilities  
139 summarized from the posterior tree distribution.

140

### 141 **Fossil calibrations and stratigraphic intervals**

142 Node calibrations based on the fossil record are often problematic because they represent  
143 a single constraint on the age of the node, which results in an improper distribution [e.g.,  
144 Uniform (minimum age, Infinite)] which does not integrate to 1.0 and often leads to convergence  
145 issues (Yang 2014). However, it is also difficult (and sometimes impossible) to set a maximum  
146 that does not depend for instance on a general constraint (e.g., the root age) that will define all  
147 the node calibrations in the tree. This issue does not apply only to hard bounds: It is also  
148 impossible to define a distribution with soft bounds unless we set at least two quantiles so that  
149 we can fit parameters that define a distribution matching these values. When we use a single  
150 constraint, we have only a single quantile and no proper distribution.

151 It is possible to estimate both the origination and extinction times for a given lineage  
152 using stratigraphic intervals, which are models that describe these times as parameters that are a  
153 function of the pattern of fossil occurrences in time (Strauss and Sadler 1989). Multiple methods  
154 exist and are based on different assumptions about the pattern or process that generates the fossil  
155 occurrences (Marshall 2010). One of these methods is the Beta-adaptive model (Wang et al.  
156 2016) which can be used when the preservation potential is unknown given a sample of  
157 occurrences in time for a given lineage. The advantage of these methods is that we can define a  
158 proper statistical distribution for the origination time of a series of occurrences, and therefore use  
159 the known fossil record of a given lineage as a sample for estimating the origination parameter as  
160 a distribution. Here, we are equating the origination time of a lineage with its most recent

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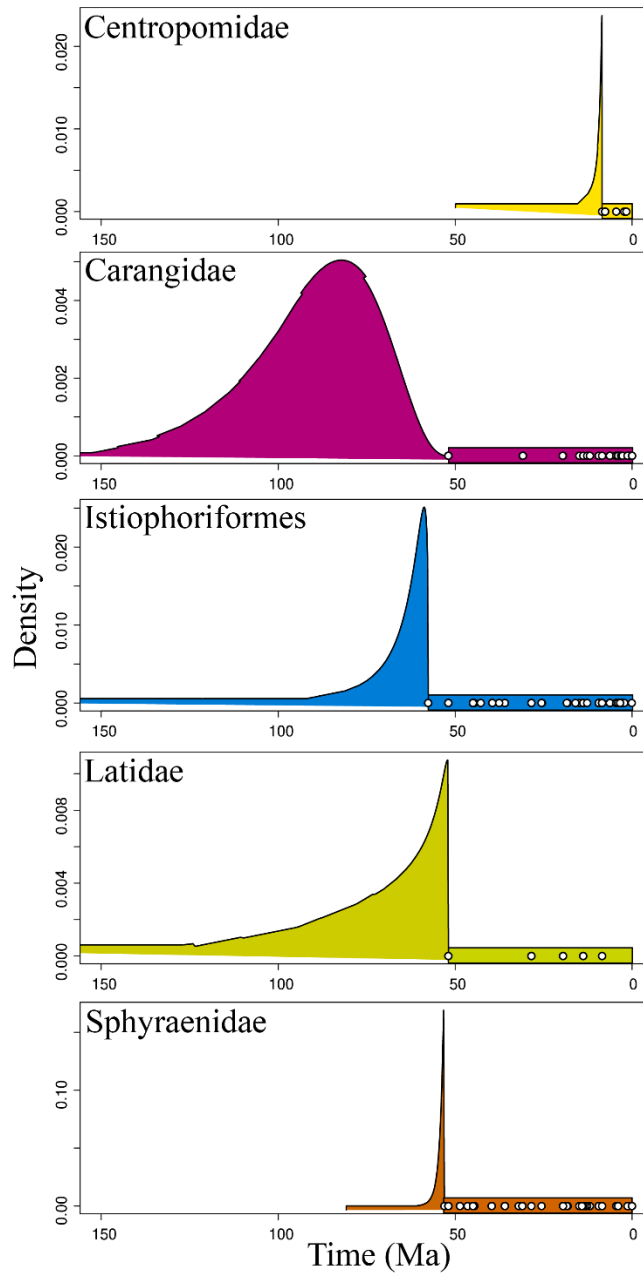
161 common ancestor. Thus, we can specify node time distributions using the fossil record,  
162 regardless of its completeness.

163 We used the Beta-adaptive method and the known fossil record of the families  
164 Carangidae (35 occurrences), Centropomidae (5 occurrences), Istiophoridae (52 occurrences),  
165 Latidae (11 occurrences), and Sphyraenidae (76 occurrences) (Fig. 1). A survey of published  
166 records was used to construct the sample of time occurrences for the families Carangidae,  
167 Istiophoridae, and Latidae (Uhen et al. 2023; website: <https://paleobiodb.org/>). Time occurrences  
168 of the family Sphyraenidae are based on Ballen (2020) and direct examination of museum  
169 specimens. The time occurrences of the family Centropomidae are herein published for the first  
170 time from a review of the literature as well as new fossil occurrences (Supplementary material).

171 All the information associated with these records can be found on the website  
172 <https://www.floridamuseum.ufl.edu/vertpaleo-search/>. The resulting distribution for the  
173 origination time of each family was used to generate the posterior credible interval, which in turn  
174 was approximated by the quantiles 0.025 and 0.975 of a truncated Cauchy distribution (Inoue et  
175 al. 2010) which is implemented for defining node calibrations in MCMCTree.



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176

177 Figure 1. Stratigraphic series for the families Centropomidae, Carangidae, Latidae, Sphyraenidae

178 and some families in the order Istiophoriformes. Circles represent fossil occurrences in geologic

179 time, and shaded areas represent the posterior density on the origination age of each stratigraphic

180 series. Note that all the series are constrained to be extant, and therefore  $\theta_2$  is fixed to 0.0

181 (present time). The extent of the posterior on origination time depends on the number of

182 observations as well as on the temporal pattern of occurrences: If they become less frequent

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183 towards the origination time, the density has higher variance, on the other hand, if occurrences  
184 are more frequent towards the origination time, the posterior has lower variance. The vertical  
185 axis (density) is not scaled across panels, whereas the horizontal (time) axis is shared across  
186 panels. The posterior densities on the origination time  $\theta_1$  are used as node calibration  
187 densities in the divergence time estimation analysis.

188

### 189 **Divergence time estimation**

190 We used divergence time estimation to put the phylogenetic hypothesis in a temporal  
191 context. We used a summary maximum credibility tree, that is, the topology with the maximum  
192 sum of branch posterior probabilities as the target tree. We calculated that tree with logcombiner  
193 (Bouckaert et al. 2019). The analysis was carried out in MCMCTree of the PAML suite (Yang  
194 2007). We used the method of approximate likelihood of dos Reis and Yang (2011) under the  
195 HKY substitution model to speed up the analysis runtime.

196 The clock model is important for the estimation of node ages (dos Reis et al. 2018), and  
197 therefore we used Bayesian model selection via marginal likelihood calculation using stepping  
198 stones for choosing the best relaxed-clock model for this dataset. We used the stepping stones  
199 procedure implemented in the mcmc3r package (dos Reis et al. 2018) R package (R Core Team  
200 2021) and the block bootstrap calculation of the standard error proposed by Álvarez-Carretero et  
201 al. (2022).

202 We used two clock models (independent and autocorrelated), and 64 stones. Each stone  
203 was sampled with a burn-in of 4,000 generations, and then sampling every two until 10,000  
204 samples were reached. The large number of stones compensates for the shorter chains when  
205 marginalizing the likelihood over the model parameters. The relaxed clock model was set to

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206 independent rates from a lognormal distribution following the results of the model selection  
207 analysis (Model Posterior Probability = 1.0; Supplementary Table S3).

208 We used a birth-death tree model setting the birth and death rates to 1.0, and the sampling  
209 fraction to 0.1. We used a gamma-Dirichlet (2,20) prior to the rates and the gamma-Dirichlet  
210 (1,10) prior to the  $\sigma^2$  parameter of the relaxed clock model. We set a gamma (2,0.2) prior to  
211 the kappa and a gamma (2,4) prior to the alpha parameters of the substitution model.

212 Five node calibrations and an age constraint on the root were used to generate the time  
213 prior: The nodes corresponding to the most recent common ancestor of the families Carangidae,  
214 Centropomidae, Latidae, and Sphyraenidae, and the order Istiophoriformes. Node calibrations  
215 were specified as truncated Cauchy distributions as described in the previous section. A soft-  
216 bound maximum on the root age was set to 120 Ma. Four independent analyses were run and  
217 compared to assess across-chain convergence. Effective sample size (ESS) values larger than  
218 500 were found and suggest adequate mixing inside each chain. All the analyses were run on the  
219 *Brycon* server at IBB/UNESP Botucatu.

220

### 221 **Biogeographic modeling and ancestral range estimation**

222 Ancestral areas of the families Centropomidae, Latidae, and Sphyraenidae were estimated  
223 on the time-calibrated phylogeny using BioGeoBEARS (Matzke 2013). Three models were  
224 tested: Dispersal-Extinction-Cladogenesis (DEC, Ree and Smith 2008), a likelihood version of  
225 the parsimony-based Dispersal Vicariance analysis (DIVALIKE, Ronquist 1997), and a  
226 likelihood version of the range evolution model implemented in BayArea (BAYAreaLIKE,  
227 Landis et al. 2013). In each model, an additional “j” parameter (founder event/jump speciation)  
228 was added, which allows descendant lineages to have a different area from the direct ancestor

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229 (Matzke 2013). Thus, a total of six models were tested and compared using statistical fit with the  
230 corrected Akaike Information Criterion (AICc). Species distribution data were obtained from  
231 Robertson and Allen (2015), Froese and Pauly (2017), and Robertson and Van Tassell (2023).  
232 Six marine bioregions were used based on Kocsis et al. (2018): Tr. EP: Tropical Eastern Pacific,  
233 Tr. WA: Tropical Western Atlantic, Tr. EA: Tropical Eastern Atlantic, Tr. IP: Tropical Indo-  
234 Pacific, Af: African; Au: Temperate Australian. Thus, we set six as the maximum number of  
235 areas in the ancestral area reconstruction analyses.

236

### 237 **Biogeographic stochastic mapping**

238 We estimated the number of each type of biogeographic event in the phylogeny using the  
239 Biogeographical Stochastic Mapping (BSM) implemented in BioGeoBEARS (Matzke 2015;  
240 Dupin et al. 2016). Six types of biogeographic events possible under the models, within-area  
241 speciation (sympatry), vicariance, and dispersal events (founder events) were tested. We  
242 conducted BSM using the MCC tree and the DEC +  $j$  that produced a significantly better fit to  
243 the data compared with other tested models. We generated 50 stochastic maps, and the event  
244 frequencies were estimated by taking the mean and standard deviation of event counts from 50  
245 BSM.

246

### 247 **Code and data**

248 All the code and data necessary for reproducing the results are available on Zenodo (DOI  
249 <https://doi.org/10.5281/zenodo.10535162>) as well as on  
250 [https://github.com/gaballench/centropomidae\\_divtime](https://github.com/gaballench/centropomidae_divtime).

251

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### 252 **RESULTS**

#### 253 **New fossil occurrences of the Centropomidae**

254           We reviewed the fossil specimens of the family Centropomidae deposited at the Florida  
255 Museum of Natural History (FM). A total of 26 bones were analyzed through the pictures  
256 processed by the museum (Supplementary material). The photographs from FM were compared  
257 with literature referent at the family Centropomidae (Fraser 1968; Potthoff and Tellock 1993)  
258 and with the same bones in extant species. The oldest record dates to the upper Late Miocene  
259 (5.33 - 11.63 Ma) and the earliest to Pleistocene (Calabrian 0.774 - 1.80 Ma). Fossils were  
260 collected in the Hawthorn Formation (15 occurrences) in Polk, Florida, the Tamiami Formation  
261 (three occurrences) in Southwest Florida, the Alachua Formation (four occurrences) north of  
262 Newberry, western Alachua County, and the Bermont Formation (four occurrences)  
263 Hillsborough County, Florida. The material corresponds to the head and mandible bones mainly.

264

#### 265 ***Phylogenetic inference***

266           In the concatenated analysis, a total of 3234 base pairs (bp) from combined genes  
267 (12SrRNA - 832 bp, 16SrRNA – 569 bp, COI – 614 bp, CYTB– 782 bp, TMO4c4 – 437 bp)  
268 were used to reconstruct the phylogeny of three families: Centropomidae (snooks), Latidae  
269 (perches), and Sphyraenidae (barracudas). Our findings indicate the monophyly of each family,  
270 supported by a posterior probability of 1.0. Centropomidae and Sphyraenidae were recovered as  
271 sister clades with a posterior probability 0.91, while Latidae was recovered near the base of the  
272 tree (Fig. 2).

273

274

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275 ***Divergence time estimation***

276           The estimated crown age for the family was 58.47 Ma (95% highest posterior density  
277 interval, HPDi= 50.65 - 72.69). The genus *Lates* displayed an estimated divergence age of 26.23  
278 Ma (95% HPDi= 17.27 - 34.77) while the genera *Psammoperca* and *Hypopterus* exhibited an  
279 estimated divergence age of 26.83 Ma (95% HPDi= 6.34 - 55.9). Two pairs of sister species were  
280 recovered: *L. calcarifer* – *L. japonicus* with a divergence time of 22.16 Ma (95% HPDi= 13.43 -  
281 31.02) and *L. angustifrons* – *L. microlepis* with a more recent divergence time of 310 Ka (95%  
282 HPDi= 0 - 0.92).

283           The estimated crown age for the family Centropomidae was 32.91 Ma (95% HPDi=  
284 24.59 - 40.47). Two main clades encompassing the 13 species of the family were identified. The  
285 first one with a high support (0.99 PP) and an age of 26.69 Ma (95% HPDi= 24.59 - 40.47)  
286 comprised ((*C. medius*, *C. pectinatus*), (*C. mexicanus*, *C. parallelus* (*C. nigrescens*, (*C. viridis*,  
287 (*C. poeyi* (*C. irae*, *C. undecimalis*)))))). Noteworthy in this clade are three sister species pairs: a  
288 transisthmian pair (*C. pectinatus* – *C. medius*) with a divergence age estimated of 6.2 Ma (95%  
289 HPDi= 2.95 - 9.74), a sympatric pair found in the Western Atlantic (WA) (*C. mexicanus*, *C.*  
290 *parallelus*) with a recent divergence time (estimate= 1.18 Ma, 95% HPDi=0.27 – 2.26), and an  
291 allopatric pair, *C. irae* restricted to Amapa, Brazil, and *C. undecimalis* with broad distribution in  
292 the WA with a divergence time estimated at 5.51 Ma (95% HPDi=2.97 - 8.48). The second clade  
293 supported by one PP includes the species (*C. ensiferus*, (*C. unionensis*, (*C. robalito*, and *C.*  
294 *armatus*))). Within this clade, the sister species *C. armatus* and *C. robalito* are both present in the  
295 EP, and represent a sympatric pair with the most recent time of divergence, estimated age of 210  
296 Ka (95% HPDi=0 - 0.51).

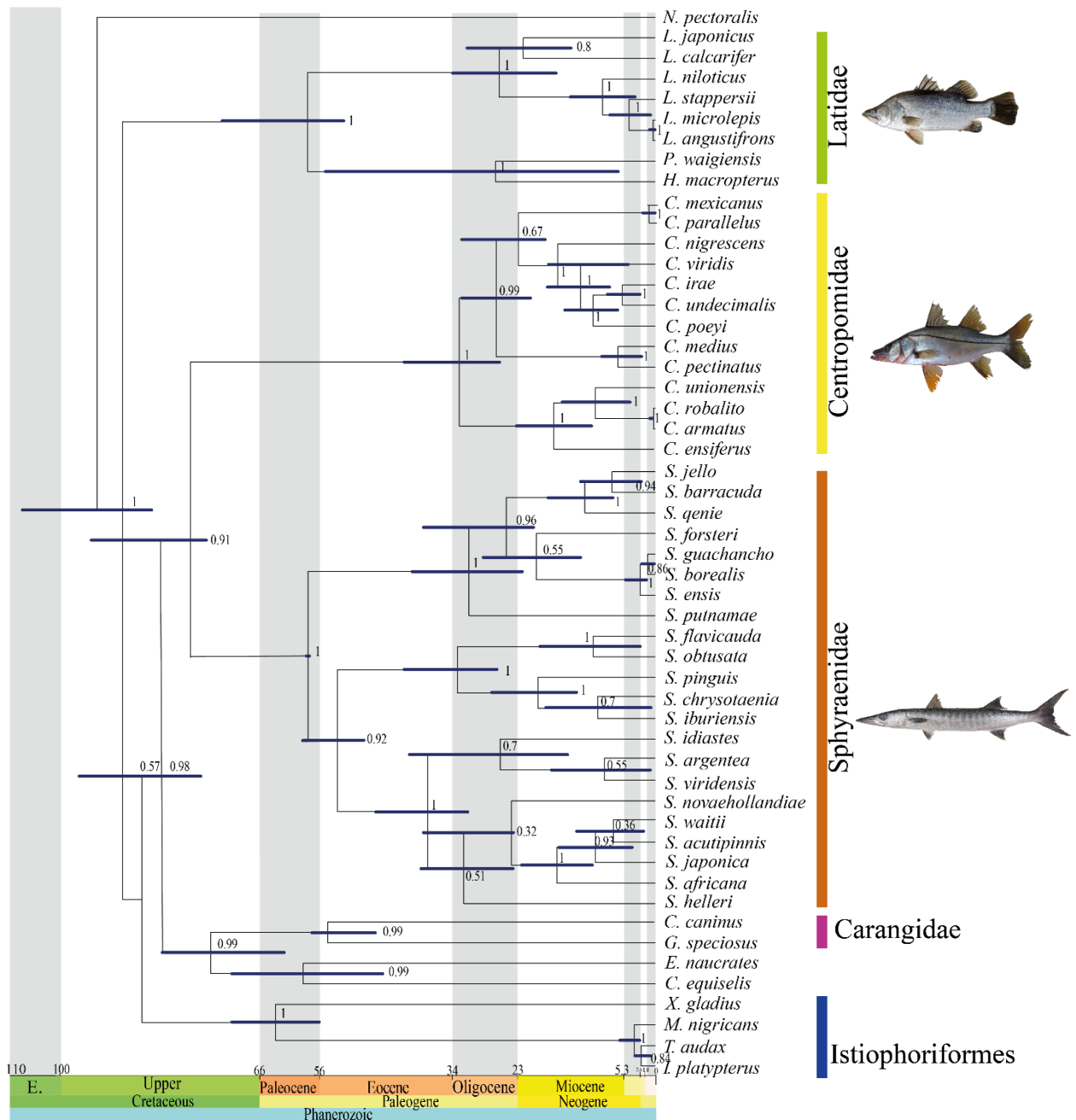
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298           The crown age for the family Sphyraenidae was estimated to be 58.39 Ma (95% HPDi=  
299 58.34 - 58.36). Two main clades can be identified. The first one was supported by a posterior  
300 probability of 0.92 with an age of 53.47 Ma (95% HPDi= 48.9 - 57.18) which included the  
301 species ((*S. obtusata*, *S. flavicauda*), (*S. pinguis*, (*S. iburiensis*, *S. chrysotaenia*), (*S. idiastes*, (*S.*  
302 *viridensis*, *S. argentea*), (*S. helleri*, (*S. novaehollandiae*, (*S. africana*, (*S. japonica*, (*S.*  
303 *acutipinnis*, *S. waitii*)))))))). The second one is supported by a posterior probability of 1.0 and  
304 has an age of 31.31 Ma (95% HPDi= 22.26 - 40.92) including the species (*S. putname*, (*S. qenie*,  
305 (*S. barracuda*, *S. jello*), (*S. forsteri*, (*S. ensis*, (*S. borealis*, *S. guachancho*)))))). Six sister-species  
306 pairs were identified. The divergence time in sister pairs ranges between 1.2 to 9.66 Ma. *S.*  
307 *guachancho* – *S. borealis* (estimate= 1.2, 95% HPDi=0.22 - 2.37); *S. waitii* – *S. acutipinnis*  
308 (estimate= 6.98, 95% HPDi=1.68 - 12.99); *S. jello* – *S. barracuda* (estimate= 7.23, 95%  
309 HPDi=2.45 - 12.72); *S. argentea* – *S. viridensis* (estimate= 8.5, 95% HPDi=1.34 - 18.05); *S.*  
310 *chrysotaenia* – *S. iburiensis* (estimate= 9.66, 95% HPDi=1.18 – 18.97) and, *S. flavicauda* – *S.*  
311 *obtusata* (estimate= 10.37, 95% HPDi=2.56 - 19.52).

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313

314 Figure 2- Time-calibrated maximum credibility tree of the family Centropomidae, Latidae, and

315 Sphyraenidae. Blue bars represent 95% highest posterior density interval (HPDi) of the node

316 ages. Node labels represent the posterior probability.

317

318



## PHYLOGENY AND BIOGEOGRAPHIC HISTORY OF SNOOKS

### 319 *Biogeographic analysis*

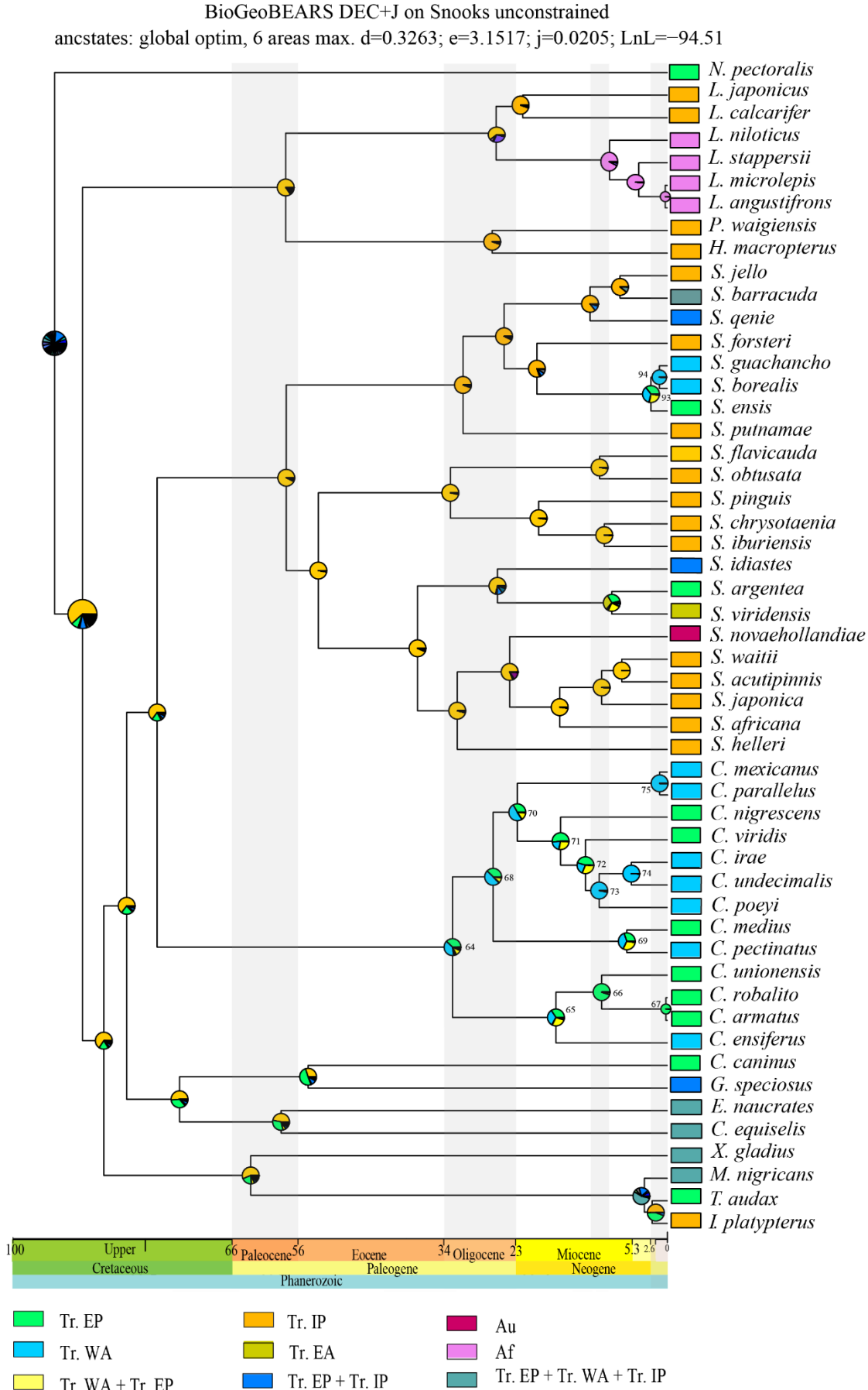
320 Historical range optimization using BioGeoBEARS indicates that the biogeographic  
321 model DEC+*j* was the best one, based on the Akaike information criterion (weight 1.0;  
322 Supplementary Table S4). The founder event speciation parameter (*j*) was favored in all models  
323 tested, indicating that this mode of dispersal was significant in forming the broad-scale  
324 biogeographic pattern in these families (Supplementary Table S4).

325

326 The time-calibrated phylogeny suggests that the common ancestor of the clade  
327 Centropomidae + Sphyraenidae arose during the upper Cretaceous from approximately 88.49 Ma  
328 to 69.01 Ma (Fig. 3). Ancestral range estimations under this best-fitting model (DEC+*j*) showed  
329 that the most probable ancestral area for extant species of Sphyraenidae + Centropomidae was  
330 the Tr. IP  $P = 0.25$ , (with  $P = 0.26$  for Tr. EP and  $P = 0.21$  for the combination Tr. EP + Tr. WA)  
331 (Fig. 3). The node containing all species of the family Sphyraenidae has the Tr. IP ( $P = 0.57$ ) as  
332 the more probable estimated ancestral range. Other deep nodes in the family Sphyraenidae also  
333 have Tr. IP as the estimated ancestral range. During the Oligocene (26 Ma) the estimated  
334 ancestral area showed a clade in the Tr. IP + Tr. EP ( $P = 0.66$ ) and another one in the Tr. EP  
335 ( $P = 0.92$ ). Ancestral areas in the family Centropomidae have the Tr. EP + Tr. WA as the  
336 estimated range ( $P = 0.58$ ) (Fig. 3). Two clades with three species each, diverged during the  
337 Miocene (10 Ma) with the first having an estimated ancestral area in the Tr. EP ( $P = 0.97$ ) and the  
338 other in the Tr. WA ( $P = 0.98$ ). The root node of the family Latidae has an ancestral area in the  
339 Tropical Indo Pacific during the Paleocene (58.47 Ma), and during the Miocene one clade has an  
340 estimated ancestral in the freshwaters of Africa ( $P = 0.97$ ).

341

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343 Figure 3- Biogeographic history based on the BioGeoBEARS optimization of the time-calibrated  
344 phylogeny. Colored boxes at the terminals of the phylogeny show the extant geographic distribution of  
345 species. Operational areas, according to Kocsis et al. (2018) are Tr. IP: Tropical Indo-Pacific; Tr. WA:  
346 Tropical Western Atlantic; Te. Au: Temperate Australian; Tr. EP: Tropical Eastern Pacific; Tr. EA:  
347 Tropical East Atlantic; Af: African. Other biogeographic areas are based on combinations of those  
348 defined a priori. The numbered nodes are the ones with estimated ancestral area in Tr. EP, Tr. WA,  
349 and Tr. EP or Tr. WA. Shaded areas represent periods of major divergence events of target families.  
350

### 351 **Estimation of the number, type, and directionality of biogeographical events**

352 A summary of our Biogeographical Stochastic Models (BSMs) revealed that most  
353 biogeographical events across the species included in the present study were within–area  
354 speciation (58%), followed by dispersal (38%), and a few vicariant events (4%) (Table 1). The  
355 largest number of events of within–area speciation occurred 53% in Tr. IP, 21 in % Tr. EP, and  
356 16% in the Tr. WA. Twelve nodes were examined in detail in the family Centropomidae finding  
357 that 68% of the events correspond to within-area speciation, 24% to dispersal, and 8% to  
358 vicariance. Dispersal events were estimated at 60% from the Tr. EP to Tr. WA during the  
359 Miocene. Twenty-one nodes were examined in the family Sphyraenidae finding that 85% of the  
360 events correspond to within-area speciation, 13% to dispersal, and 2% to vicariance. Seven nodes  
361 in the Latidae clade showed that 85% of the events correspond to within-area speciation, 13% to  
362 dispersal, and 2% to vicariance (Table 1).

363

364 **Table 1** - Summary of biogeographical stochastic mapping counts using the DEC+ *j* model.

365 Mean numbers of the different types of events estimated are shown here along with standard

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366 deviations. No range contractions were estimated because the relevant model parameter (e) was  
 367 not required in the best-fitting model.

368

Mode	Type	Total mean (SD)	%	Centropomidae Mean (SD)	%	Sphyraenidae Mean (SD)	%	Latidae Mean (SD)	%
<b>Within-area speciation</b>	Speciation	30.4 (2.15)	47	40.4 (13.13)	61	40.4 (12.53)	72	48.2 (4.49)	83
	Speciation subset	7.4 (2.83)	11	10.8 (2.22)	7	13.3 (7.50)	13	6	2
<b>Dispersal</b>	Founder events	10.3 (1.79)	38	20.9 (16.43)	24	12.8 (17.95)	13	18.5 (21.92)	10
<b>Vicariance</b>	Vicariance	2.8 (1.56)	4	9.4 (5.73)	8	2.7 (1.97)	2	9 (9.90)	5
<b>Total</b>		65.5 (1.56)	100	150.0 (150.41)	10	237.5 (303.32)	10	87.5 (134.94)	10

369

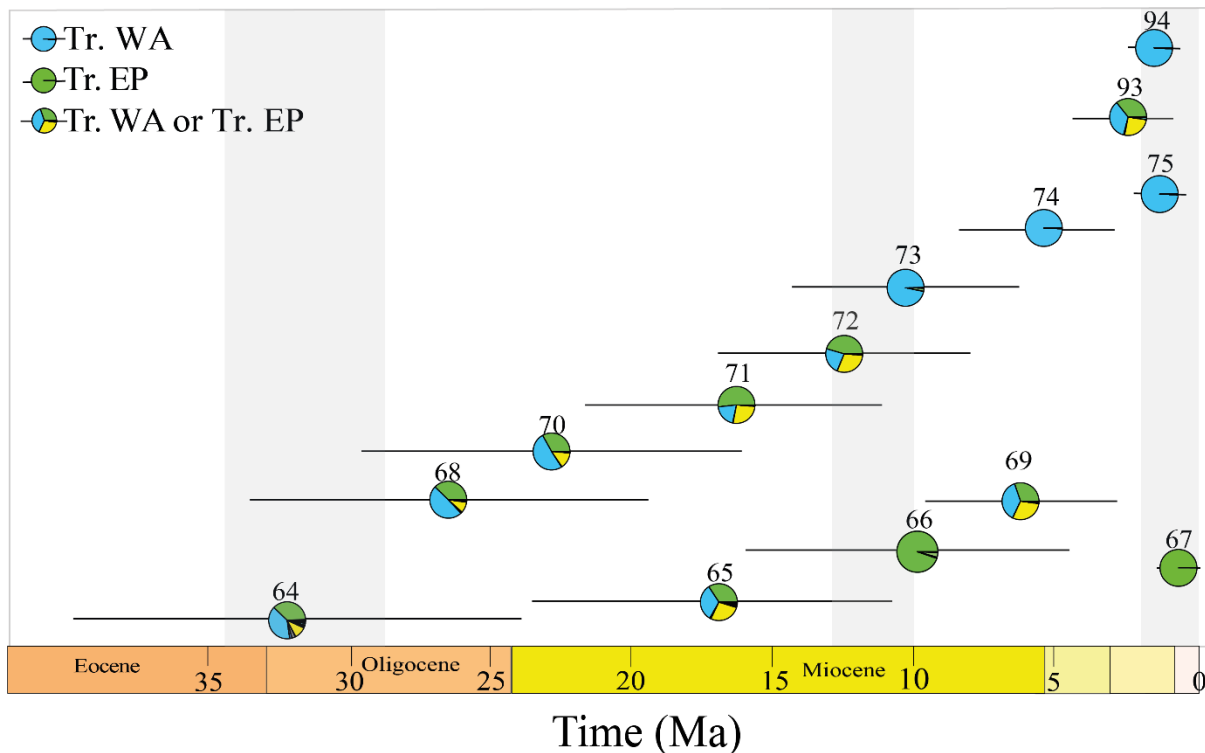
370

371 *Summary of estimated ancestral area over time in the Tropical Eastern Pacific and Tropical*  
 372 *Western Atlantic during the Neogene.*

373 A total the 14 nodes in the phylogenetic inferences showed estimated ancestral areas in  
 374 Tr. EP (2), Tr. WA (4), and Tr. EP or Tr. WA (8) as the estimated ancestral range during the  
 375 Neogene. We extracted the age of each node with distribution in these areas and plotted this data.  
 376 We observed that the distribution of areas is aligned with the final gradual process of emergence  
 377 of the Isthmus of Panama where the Pacific and the Atlantic Oceans were separated. The nodes  
 378 number 64 – 75 correspond to the family Centropomidae, where those nodes had an ancestral  
 379 area in the Tr. EP + Tr. WA, Tr. EP, and Tr. WA with divergence times in the Oligocene (33.9  
 380 Ma - 23.03 Ma) to the Upper Miocene (11.63 Ma - 5.33 Ma) (Fig. 4), and the nodes with an

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381 estimated distribution either in the Tr. EP or in the Tr. WA has ages ranging between the  
382 Pliocene (5.33 Ma- 2.58 Ma) to the Pleistocene (2.58 Ma- 0.774 Ma) (Fig. 4). The nodes number  
383 93-94 correspond to the family Sphyraenidae, where there is one node with ancestral areas in Tr.  
384 EP or Tr. WA with divergence during the early Pleistocene (~2.49 Ma).  
385  
386



387  
388 Figure 4- Forest-plot of value to High Posterior Density interval (HPDi) of the age of the 14  
389 nodes in the phylogenetic inferences with estimated ancestral area in Tr. EP, Tr. WA, and Tr. EP  
390 or Tr. WA. Pie represents the estimated median age, and the length of the line represents the 95%  
391 HPDi. Gray shading as in Figure 3.

392

### 393 Discussion

394 *Phylogenetic interrelationships between Centropomidae, Latidae, and Sphyraenidae.*

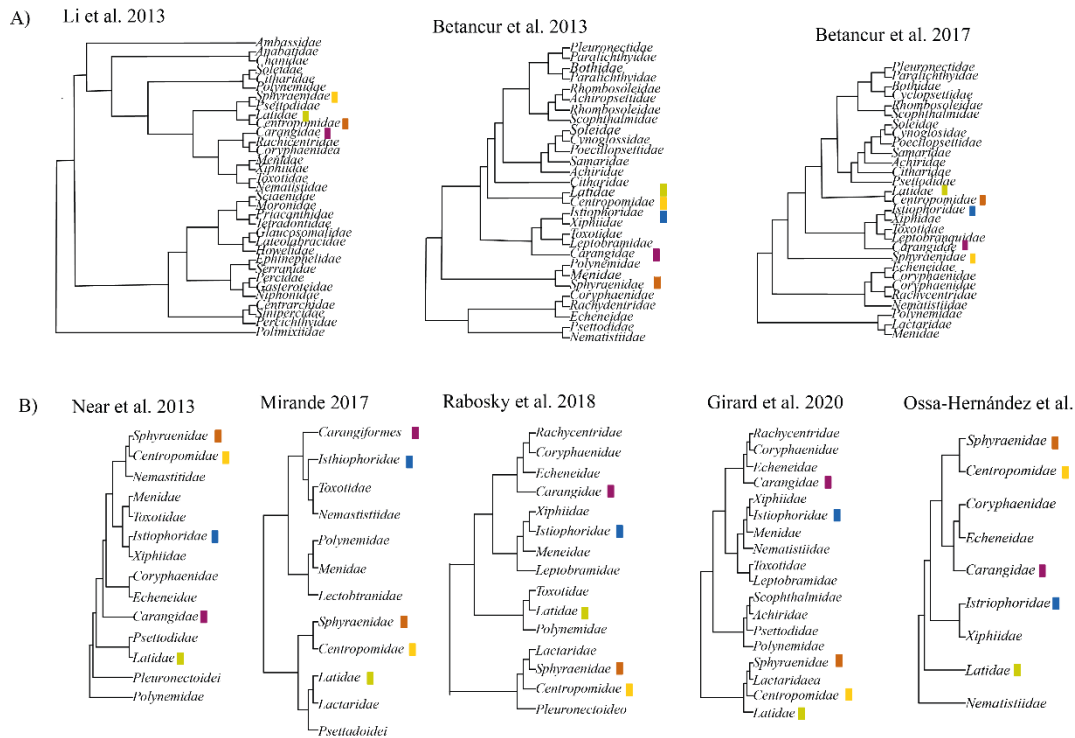
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395           The historical debate and subsequent modifications regarding the interrelationship of the  
396 Centropomidae with the family Latidae have a long history. At the beginning of phylogenetic  
397 studies, Centropomidae comprised two subfamilies, Centropominae and Latinae (Greenwood  
398 1976). A taxonomic and phylogenetic revision redefined the family Latidae as monophyletic,  
399 encompassing the genera *Lates*, *Psammoperca*, and *Eolates* (fossil), while the genus  
400 *Centropomus* was assigned to the family Centropomidae (Otero 2004).

401           Subsequently, the monophyly of the Centropomidae and Latidae clade was proposed by  
402 Li et al. (2011), although with weak support (0.74 PP), and only four species representing these  
403 two families were used. Betancur et al. (2013, 2017) recovered Latidae as the sister clade of  
404 Centropomidae with weak support (0.61 PP) and placed them as *incertae sedis* at the ordinal  
405 level as a part of Carangaria together with the family Sphyraenidae. Girard et al. (2020)  
406 recovered Centropomidae as a sister clade of Sphyraenidae and included them together with  
407 Latidae in the order Carangiformes.

408           After the designation of Centropomidae *sensu stricto*, little attention was directed to the  
409 interrelationships among these families. Interestingly, the family Sphyraenidae is related to the  
410 family Centropomidae in some studies (Near et al. 2013; Mirande 2017; Rabosky et al. 2018;  
411 Girard et al. 2020) (Fig. 5-A). We found that Centropomidae and Sphyraenidae are sister clades  
412 (0.91PP), while Latidae emerged as a basal unrelated clade, sister to all families included in our  
413 phylogeny. The phylogenetic hypotheses previously presented for the family Centropomidae had  
414 suggested Latidae as a sister family (Tringali et al. 1999; de Oliveira et al. 2014; Carvalho-Filho  
415 et al. 2019). In the same way, in a phylogenetic hypothesis of the Latidae, Centropomidae was  
416 used as an outgroup (Koblmuller et al. 2021). However, Santini et al. (2015) used  
417 Centropomidae as an outgroup in the Sphyraenidae phylogeny, being congruent with our results.

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418

419 Figure 5- Hypotheses of relationships among ray-finned fishes where the closest relationship A)

420 Centropomidae and Latidae are sister clade according to molecular studies (Li et al. 2011;

421 Betancur 2013, 2017). B) Centropomidae and Sphyracnidae are recovered as sister clades based

422 on the following molecular studies: Near et al. (2013); Mirande (2017); Rabosky et al. (2018);

423 Girard et al. (2020). The color boxes indicate the families used in the present study.

424

425 *Hypotheses of the relationship among centropomid species.*

426 This study represents the first attempt at estimating the divergence times among species

427 of the Centropomidae by using information derived from the fossil record. De Oliveira et al.

428 (2014) recovered an age for the Centropomidae family during the Miocene (~23 Ma), whereas

429 our findings place the family's origin in the Oligocene (~32.91 million years ago). Additionally,

430 the divergence times for sister species pairs do not align with De Oliveira et al. (2014).

431

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432           We have identified two main clades congruent with the findings of Tringali et al. (1999);  
433 however, there are discrepancies in the relationships within each clade. It is important to note  
434 that Tringali et al. (1999) based their phylogenetic inferences on one locus. In the first clade ((*C.*  
435 *medius*, *C. pectinatus*), (*C. mexicanus*, *C. parallelus* (*C. nigrescens*, (*C. viridis*, (*C. poeyi* (*C.*  
436 *irae*, *C. undecimalis*))))), our topologies align with Tringali et al. (1999). Nonetheless, we  
437 include *C. irae*, a species described after Tringali and collaborators published their hypothesis. In  
438 our phylogeny, this species is retrieved as a sister to *C. undecimalis*—a sister pair also identified  
439 by Oliveira et al. (2014). In the second clade (*C. ensiferus*, (*C. unionensis*, (*C. robalito*, and *C.*  
440 *armatus*))), we report *C. armatus* and *C. robalito* with PP 1.0. While Tringali et al. (1999)  
441 recovered *C. robalito* and *C. ensiferus* with 78% bootstrap support and *C. armatus* and *C.*  
442 *unionensis* with 98% bootstrap. Oliveira et al. (2014) also identified *C. robalito* as a sister  
443 species to *C. ensiferus*. Figueiredo-Filho et al. (2021) suggest that *C. robalito* and *C. armatus* are  
444 the same species based on the gene COI; however, our findings based on five molecular markers  
445 suggest that both are distinct species, yet with a very recent divergence time. Figueiredo-Filho et  
446 al. (2021) carried out a phylogenetic and taxonomic revision of the genus *Centropomus* with an  
447 emphasis on Atlantic species. Their inferences based on COI led them to propose taxonomic  
448 modifications that do not align with our results. For example, they suggest *C. mexicanus* is a  
449 junior synonym of *C. parallelus*; however, our findings indicate that both are distinct species  
450 with a recent divergence time, a hypothesis supported also by Seyoum et al. (2023), which  
451 indeed proposed the existence of three lineages in the *C. mexicanus* and *C. parallelus* complex.  
452 Figueiredo-Filho et al. (2021) suggest that *Centropomus nigrescens* and *C. viridis* may be the  
453 same species, but our results indicate that these two species are distinct, lacking a close  
454 phylogenetic relationship and possessing different ages—*C. viridis* ~12.54 Ma and *C. nigrescens*



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455 ~16.35 Ma. Results are supported by Martínez-Brown et al. (2021), who conducted a  
456 morphological review, identifying diagnostic characteristics that differentiate these two species  
457 as distinct entities.

458

459 *Hypotheses of the relationship between sphyraenid species.*

460 The relationship between the different species of the family Sphyraenidae has been  
461 published previously. Santini et al. (2015) presented a phylogenetic hypothesis based on two  
462 mitochondrial genes (COI, CytB) of the family recovering three main groups. The same clades  
463 are recovered in our hypothesis (using five molecular markers), with some different relationships  
464 between species. The inclusion of *S. qenie* and *S. waitii* modified the interrelationship between  
465 the *S. barracuda* group and the *S. sphyraena* group reported by Santini et al. (2005). We  
466 recovered *S. jello* -*S. barracuda* as a sister species, this pair was previously reported by Betancur  
467 et al. (2017) in their ray-finned fish phylogenetic study.

468

469 *Ancestral range estimations*

470 Our estimation of biogeographic history showed a similar pattern to the current  
471 distribution of the extant species. The families Latidae and Sphyraenidae are mostly distributed  
472 in the Eastern Hemisphere; species of the family Latidae are distributed in the Indo-Pacific and  
473 Africa; while species of the family Sphyraenidae are mainly distributed in the Indo-Pacific, with  
474 some species distributed in the Eastern Pacific and Western Atlantic and one species in  
475 Australia. On the other hand, in the Western Hemisphere, we have the family Centropomidae  
476 which is a New World endemic family.

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477 Tropical IP was estimated as the ancestral area of the family Latidae and Sphyraenidae  
478 during the Paleocene, approximately ~ 58 million years ago. However, when these families  
479 originated, the configuration of the Indo-Pacific differed from its present state. At that time, the  
480 Tethys Sea (TS) occupied the region currently comprised of the Mediterranean Sea and the Indo-  
481 Pacific Ocean. The TS exerted a substantial influence on the Earth's ecological dynamics and  
482 supported a diverse array of marine and freshwater species (Hou and Li 2018, Zhao et al. 2022).  
483 The Indian Ocean had taken on its present configuration since 36 million years ago. During the  
484 Eocene–Oligocene boundary (~33.9 Ma), when the southern Mediterranean was created, the  
485 connection between the TS and the Indian Ocean was reduced (Hou and Li 2018), until the  
486 complete closing of the Tethys during the Miocene (~20). The closure of the TS during the  
487 Miocene (~20 million years ago) was coeval with significant events of divergence in Latidae and  
488 Sphyraenidae. During that period the estimated ancestral area for the genus *Lates* was Africa,  
489 and for some species of the genus *Sphyraena*, it was the Tr. EP, Tr. EA, and Tr. WA. More  
490 recent divergence events were estimated in Sphyraenidae (~2.49 Ma) in the Tr. EP + Tr. WA,  
491 this divergence occurred after the interruption of water exchange between the Pacific and  
492 Atlantic Oceans, following the complete formation of the Isthmus of Panama (~3.5 Ma).

493 In the Western Hemisphere, the emergence of the Isthmus of Panama stands out as a  
494 pivotal geological event. Throughout the Oligocene to the Miocene, spanning from 33.9 to 15.98  
495 million years ago, North and South America remained separated by one or more extensive and  
496 deep seaways that connected the Atlantic and Pacific Oceans (Jaramillo 2018). The snook family  
497 most probably originated in the Oligocene (~32.91) in waters that divided North and South  
498 America in the absence of any geographical barriers. The events of diversification during the  
499 Oligocene to the early Miocene in the family Centropomidae overlap with terrestrial landscape

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500 development in the IP (Montes et al. 2012, Coates and Stallard 2013, Jaramillo 2018). The nodes  
501 with estimated ancestral area in Tr. EP or Tr. WA occurred in a range between 22.99 Ma to  
502 12.54 Ma. The events of divergence with species restricted to either the Pacific or the Caribbean  
503 occurred ~10 Ma. During this time (~10 Ma), the closure of the CAS significantly affected the  
504 oceanic exchange between the Pacific and the Caribbean, decreasing the flow of intermediate  
505 and deep waters from the Pacific to the Caribbean along the CAS (Sepulcre et al. 2014; Montes  
506 et al. 2015; Jaramillo 2018). The temporal separation of transisthmian sister species among  
507 snooks (~6.2 Ma), aligns with the distribution of vicariance events linked to the Isthmus of  
508 Panama. Bacon et al. (2015) proposed the events of divergence separating marine organisms to  
509 intensify during the 10 to 4.2 Ma interval. O’Dea et al. (2016) report a divergence timeframe  
510 ranging from 10 Ma to 5 Ma for sister taxa within Teleostei. Additionally, various families of  
511 marine fishes, including Serranidae (Craig et al. 2004), Haemulidae (Tavera et al. 2012),  
512 Labridae and Chaetodontidae (Cowman and Bellwood 2013), Eleotridae and Apogonidae  
513 (Thacker 2017), exhibit a predominant vicariance pattern during the Late Miocene to Early  
514 Pliocene.

515

516 An allopatric event of speciation occurred ~5.51 Ma in the snooks *Centropomus irae* and  
517 *C. undecimalis*; some authors suggest that the divergence in these species was induced by the  
518 influence of the Amazon River (Malcher et al. 2023). We believe that other mechanisms must be  
519 involved in the separation of this pair of species. *Centropomus undecimalis* is a widely  
520 distributed species in the Caribbean and the Atlantic, and it has a high tolerance to salinity (e.g. it  
521 has been reported from Lake Gatún in Panama). Rather, the separation of these species may be  
522 due to environmental and ecological factors. Even more recent speciation events within the

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523 family Centropomidae occurred within the same basin as in the sympatric Caribbean species *C.*  
524 *mexicanus* and *C. parallelus* (~1.8 Ma), and the Pacific *C. armatus* and *C. robalito* (~210 Ka).

525

526 Thus, speciation events in Centropomidae are found pre- and post-final closure of the  
527 Isthmus of Panama. This pattern aligns with observations in other studies focusing on diverse  
528 families of marine fishes, where divergence times have been detected before and after the uplift  
529 of the Isthmus of Panama. Some examples include the genus *Holacanthus* within the angelfish  
530 family Pomacanthidae (Tariel et al. 2016), the genus *Cyclopsetta* within the flatfish family  
531 Paralichthyidae (Byrne et al. 2018), and the genus *Haemulon* in the grunt family Haemulidae  
532 (Tavera et al. 2019). In the same way, our results are congruent with those found in diverse  
533 groups of marine invertebrates (Lessios 1981; Weinberg and Starczak 1989; Knowlton and  
534 Weight 1998; Marko and Jackson 2001; Lessios 2008; Miura et al. 2010; Hiller and Lessios  
535 2019; Lima et al. 2020) where, after the closure of the Isthmus of Panama, climatic,  
536 oceanographic, and ecological conditions play important roles in sympatric speciation.

537

538

539 Supplementary material

540 **Fossil occurrences**

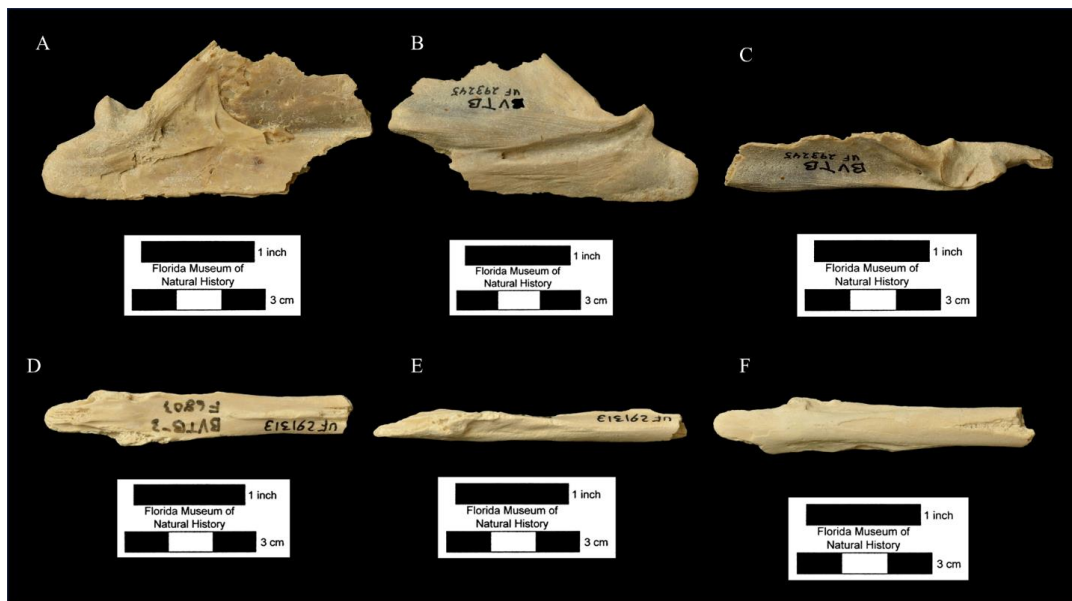
541 **Specie:** *Centropomus* sp.

542 **Material:** United States, Florida. Polk country, Tiger Bay Mine, Hawthorn group, Peace  
543 River formation, Bone Valley member, early Pliocene collected by Eric Kendrew, articular left  
544 UF 293245 (Fig 1- A-C), basioccipital and parasphenoid UF 293352(Fig 2- A-D). Collected by  
545 Timberlane Research Organization Crew Ceratohyal left UF/TRO 23210 (Fig 3- A-B), vomer

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546 UF/TRO 23211(Fig 3- C-D); collected by John S. Waldrop Parasphenoid UF 291313(Fig 1- D-  
547 F). Nichols Mine, Hawthorn group, Peace River formation, Bone Valley member, early Pliocene  
548 collected by Eric Kendrew Dentary right UF 113175 (Fig 4 A-C), Hyomandibular, left UF  
549 113209 (Fig 4 D-E), Premaxilla right UF 109998 (Fig 4 F-G) Palmetto Mine, Hawthorn group,  
550 Peace River formation, Bone Valley member Early Pliocene collected by John S. Waldrop  
551 Hypural UF 291601, vertebra atlas UF 293427, vertebra UF/TRO 23027 (Fig 5 A-D), UF  
552 291382 (Fig 5 E-I). They were photographed by Sean Moran.

553

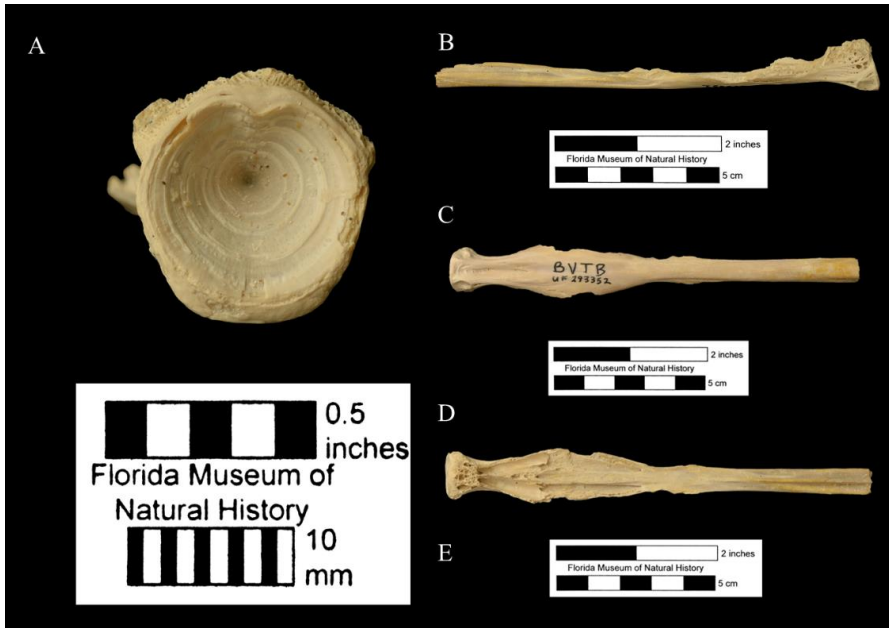


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555 (Figure 1 A-F)

556

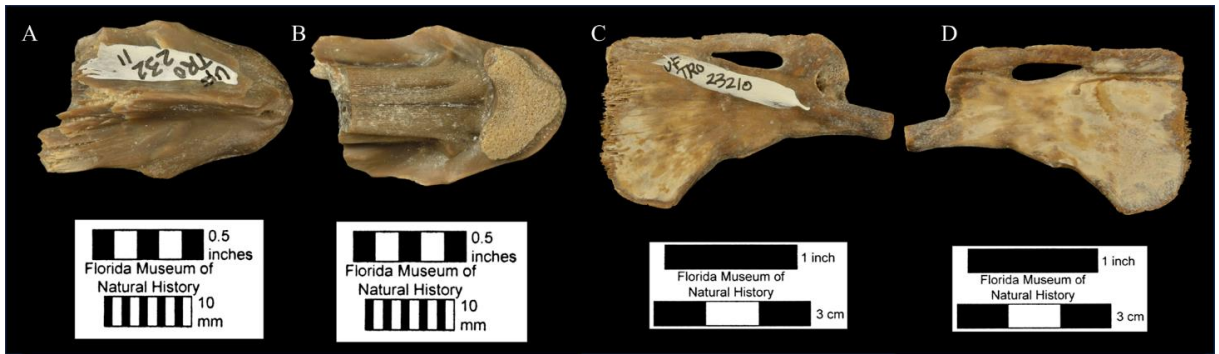
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(Figure 2 A-E)

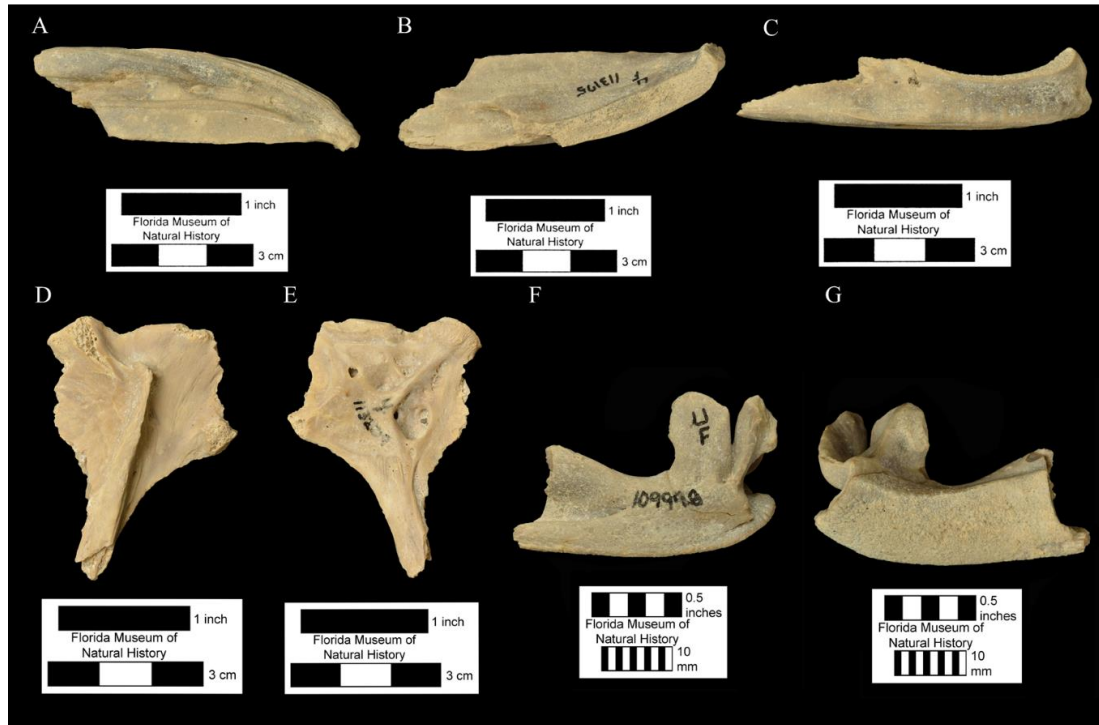


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(Figure 3 A-D)

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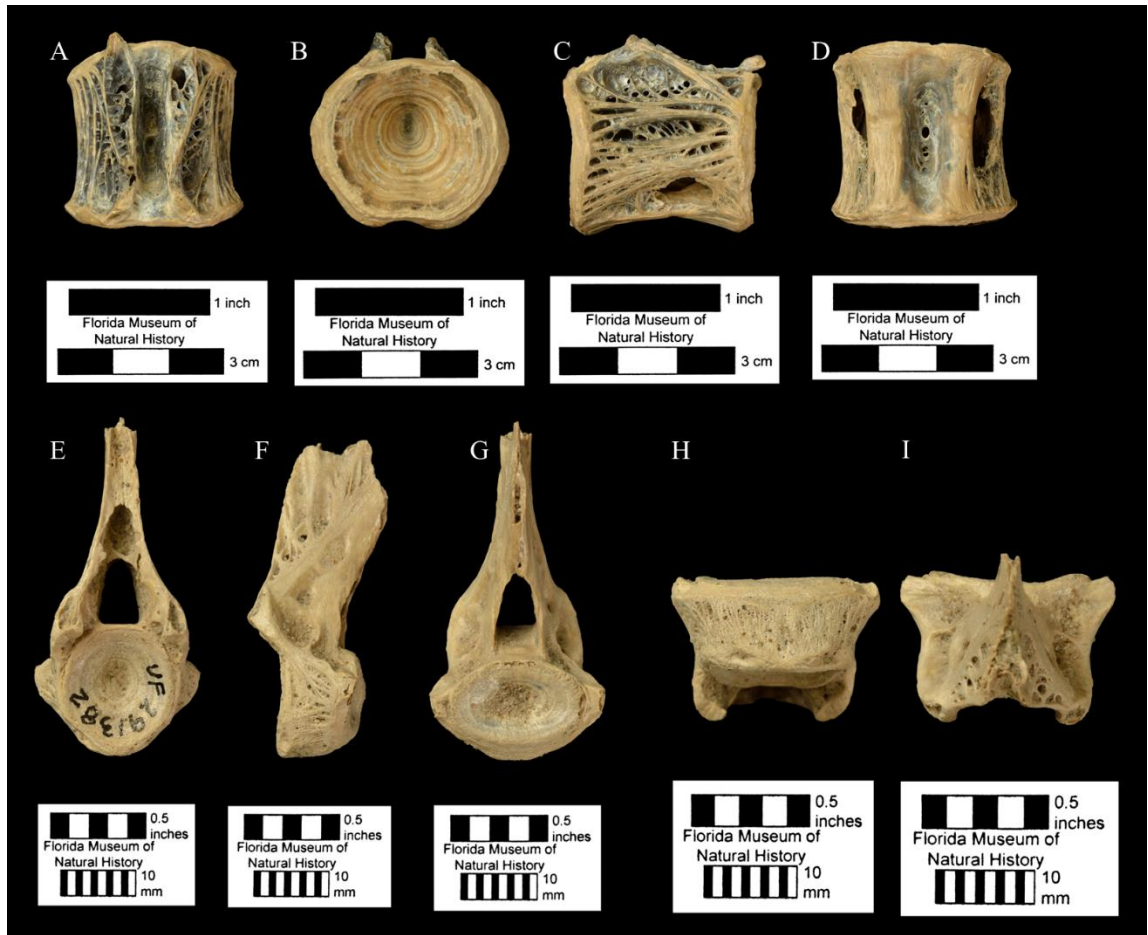


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(Figure 4 A-G)

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(Figure 5 A-I)

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574 Supplementary Table S1- Accession number in NCBI. \*Sequences obtained in this study;

575 \*\*Sequences obtained in collaboration with the Ecological and Evolutionary Genomics

576 Laboratory at STRI.

<i>Especies</i>	<b>Localidad</b>	<b>12S</b>	<b>16S</b>	<b>COI</b>	<b>CYTB</b>	<b>TMO</b>
<i>Centropomus armatus</i>	Colombia: Valle del cauca	OR805158*	OR805147*	OR825518*	OR829270*	OR8229617*
<i>Centropomus ensiferus</i>	Cabo de la Vela	OR805159*	OR805148*	OR825519*	OR829271*	OR8229618*
<i>Centropomus irae</i>			KJ641473.1	MW183548	KJ641490.1	
<i>Centropomus medius</i>	Colombia: Valle del cauca	OR805160*	OR805149*	OR825520*	OR829272*	OR8229619*
<i>Centropomus mexicanus</i>			U85015.3	MZ376960	AF018596.1	
<i>Centropomus nigrescens</i>	Panamá: Golfo de Panama	STRI**	STRI**	STRI**	OR829273*	OR8229620*
<i>Centropomus paralellus</i>			U85014.3	JQ365275.1	EU927346.1	
<i>Centropomus pectinatus</i>	Panamá: Colon	STRI**	STRI**	STRI**	OR829274*	OR8229621*
<i>Centropomus poeyi</i>			U85009.3		AF018599.1	
<i>Centropomus robalito</i>	Colombia: Choco	OR805161*	OR805150*	OR825521*	OR829275*	OR8229622*
<i>Centropomus undecimalis</i>	Cabo de la Vela	OR805162*	OR805151*	OR825522*	OR829276*	OR8229623*
<i>Centropomus unionensis</i>	Colombia: Valle del cauca	OR805163*	OR805152*	OR825523*		OR8229624*
<i>Centropomus viridis</i>	Panamá: Golfo de Panama	STRI**	STRI**	STRI**	OR829277*	
<i>Hypopterus macropterus</i>				LC269834.1		
<i>Lates angustifrons</i>	Lake Tanganyika	MN255593.1	MN255675.1	ISZA08021		
<i>Lates calcarifer</i>		AY141371	AY141441	JF919821	EU126588.1	
<i>Lates japonicus</i>		AP006788.1	AP006788.1	AP006788.1	AP006788.1	
<i>Lates niloticus</i>		MN255585	GU324156	KJ443712	AB117106.1	
<i>Lates stappersii</i>		MN255586.1	MN255679.1			
<i>Psammoperca waigiensis</i>		KM082972.1	KM198901.1	FJ237578.1	Y986971.1	
<i>Sphyraena acutipinnis</i>				HM902634.1		
<i>Sphyraena africana</i>		LC499574.1				
<i>Sphyraena argentea</i>			EU0099477.1	GU440525		DQ388071
<i>Sphyraena barracuda</i>	Colombia: Choco	OR805164*	OR805153*	OR825524*	OR829278*	OR8229625*
<i>Sphyraena borealis</i>	Venezuela: Isla Margarita	OR805165*	OR805154*	OR825525*		OR8229626*
<i>Sphyraena crysotaenia</i>			GQ485295.1	KY176643.1		
<i>Sphyraena ensis</i>	Colombia: Valle del cauca	OR805166*	OR805155*	OR825526*		OR8229627*
<i>Sphyraena flavicauda</i>			GQ485296.1	KY176644.1		
<i>Sphyraena forsteri</i>		LC385307.1		MK777495.1	AB264366.1	
<i>Sphyraena guachancho</i>	Colombia: Magdalena	OR805167*	OR805156*	OR825527*	OR829279*	OR8229628*
<i>Sphyraena helleri</i>		LC327187.1			AB264367.1	
<i>Sphyraena iburrensis</i>		LC499397.1			AB264361.1	
<i>Sphyraena idiaestes</i>			DQ532963.1			
<i>Sphyraena japonica</i>		AP012501.1.	AP012501.1.	AP012501.1.	AP012501.1.	
<i>Sphyraena jello</i>		KT445895.1.	KT445895.1.	KT445895.1.	KT445895.1.	

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<i>Sphyraena novaehollandiae</i>			KX234684.1			
<i>Sphyraena obtusata</i>		LC037054.1	KR153518.1	KU499681.1	AB264338.1.	
<i>Sphyraena pinguis</i>		LC506671.1		JF952863.1	AB264356.1	
<i>Sphyraena putnamae</i>		LC037053.1	JQ938993.1.	MZ329572.1	KR007749.1	
<i>Sphyraena qenie</i>	Colombia: Valle del cauca	OR805168*	OR805157*	OR825528*	OR829280*	
<i>Sphyraena sphyraena</i>		DQ533304.1	JQ939013.1.	KY176645.1	EF439597.1	
<i>Sphyraena viridensis</i>		KJ499108.1		KJ396640.1	DQ198006.1	
<i>Sphyraena waitii</i>				HM902624.1		
<b>Outgroup</b>						
<i>Caranx caninus</i>	Colombia: Valle del cauca	This study	This study	OR825517*	This study	
<i>Coryphaena equiselis</i>		MH576916.1	MH576916.1	MH576916.1	MH576916.1	
<i>Echeneis naucrates</i>		KF021242.1	KF021242.1	KF021242.1	KF021242.1	
<i>Gnathanodon speciosus</i>		NC_054367	NC_054367	NC_054367	NC_054367	
<i>Isthiophorus platypterus</i>		NC_012676.1	NC_012676.1	NC_012676.1	NC_012676.1	DQ3880772.1
<i>Makaira nigricans</i>		HQ611116.1	HQ592244.1	HQ611116.1	HQ611116.1	DQ388073.1
<i>Nematistius pectoralis</i>		ON838225.1	ON838225.1	ON838225.1	ON838225.1	
<i>Tetrapterus audax</i>		NC_012678.1	NC_012678.1	NC_012678.1	NC_012678.1	
<i>Xiphias gladius</i>		AB470301	AB470301.1	AB470301	AB470301	DQ388074.1

577

578 Supplementary Table S2- Primer sequences used for PCR amplifying this study's mitochondrial

579 and nuclear genes.

580

<b>Primer name</b>	<b>Primer Sequence</b>	<b>T<sub>m</sub> (°C)</b>	<b>Reference</b>
<b>12S229Fa</b> <b>12S954Ra</b>	5'- GYCGGTAAAAYTCGTGCCAG -3' 5'- YCCAAGYGCACCTTCCGGTA -3'	60	Palumbi 1996
<b>16SAR</b> <b>16SBR</b>	5'- CGCCTGTTTATCAAAAACAT -3' 5'- CCGGTCTGAACTCAGATCACG -3'	54	Palumbi 1996
<b>FishF1</b> <b>FishR1</b>	5'- TCAACCAACCACAAAGACATTGGCAC -3' 5'- TAGACTTCTGGGTGGCCAAAGAAT CA -3'	54	Ward <i>et al.</i> 2005
<b>Glud-GL</b> <b>CB3H</b>	5'- GAYGCAYTARTYGAYCTYCCR GC -3' 5'- GGGTCYCCIARIARRTTIGG-3'	48-52	Palumbi 1996
<b>Tmo4c4-F</b> <b>Tmo4c4-R</b>	5' CCTCCGGCCTTCCTAAAACCTCTC 3' 5' CATCGTGCTCCTGGGTGACAAAGT 3'	54	Westneat <i>et al.</i> 2005

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581 Supplementary Table S3. Bayesian relaxed clock model selection using marginal likelihood and  
 582 Bayes factors. The relaxed clock where independent rates follow a lognormal distribution was  
 583 strongly favored as the best for the current dataset.

584

Clock Model	Log (Marginal Likelihood)	Standard Error	Posterior Probability
Independent lognormal	-536.573980786701	0.475257291697664	0.999999999993294
Geometric Brownian Motion	-562.302019175086	0.551420967186908	0.0000000000670586641

585

586

587

588 Supplementary table S4. Comparison of four biogeographic model selections using the weight of  
 589 the Akaike Information Criterion (AICwt). The best model is highlighted in boldface.

590

	LnL	numparams	d	e	j	AICc	AICc_wt
DEC	-97.5	2	0.46	3.22	0	199.3	0.082
<b>DEC+J</b>	<b>-94.51</b>	<b>3</b>	<b>0.33</b>	<b>3.15</b>	<b>0.02</b>	<b>195.5</b>	<b>0.53</b>
DIVALIKE	-101.8	2	0.3	1.00E-12	0	207.9	0.0011
DIVALIKE+J	-95.06	3	0.19	1.00E-12	0.027	196.6	0.31
BAYAREALIKE	-118.4	2	0.075	1.42	0	241.99	7.00E-11
BAYAREALIKE+J	-96.44	3	0.057	0.31	0.032	199.4	0.077

591

592 **Conclusions**

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593           The family Centropomidae is the sister clade of the family Sphyraenidae, with a common  
594 ancestor in the Upper Cretaceous. The families Latidae and Sphyraenidae originated in the  
595 Paleocene in the region we know today as the Indo-Pacific. The family Centropomidae  
596 originated in the Western Atlantic and Eastern Pacific in the Oligocene. The transitions in the  
597 estimated ancestral area in this last family occurred from the Eastern Pacific to the Western  
598 Atlantic during the emergence of the isthmus of Panama. The divergence times and  
599 biogeographic patterns identified in the family Centropomidae are congruent with a gradual  
600 impact on the species diversification, rather than a single synchronous event during the formation  
601 process of the Isthmus of Panama. Both geographic isolation during and after the emergence of  
602 the Isthmus of Panama and the environmental and ecological changes created post-Isthmus of  
603 Panama shaped the diversification in this family.

604

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619

### 620 **References**

621 Altekar, G., Dwarkadas, S., Huelsenbeck, J. P., & Ronquist, F. (2004). Parallel  
622 metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic  
623 inference. *Bioinformatics*, 20(3), 407-415.

624

625 Álvarez-Carretero, S., Tamuri, A. U., Battini, M., Nascimento, F. F., Carlisle, E., Asher,  
626 R. J., ... & Dos Reis, M. (2022). A species-level timeline of mammal evolution integrating  
627 phylogenomic data. *Nature*, 602(7896), 263-267.

628

629 Anderson, J., Williford, D., González, A., Chapa, C., Martínez-Andrade, F., & Overath,  
630 R. D. (2020). Demographic, taxonomic, and genetic characterization of the snook species  
631 complex (*Centropomus* spp.) along the leading edge of its range in the northwestern Gulf of  
632 Mexico. *North American Journal of Fisheries Management*, 40(1), 190-208.

633

634 Bacon, C. D., Silvestro, D., Jaramillo, C., Smith, B. T., Chakrabarty, P., & Antonelli, A.  
635 (2015). Biological evidence supports an early and complex emergence of the Isthmus of  
636 Panama. *Proceedings of the National Academy of Sciences*, 112(19), 6110-6115.

637

OSSA-HERNANDEZ, BALLEEN, ACERO, TAVERA

638 Ballen, G. A. (2019). Nomenclature of the Sphyraenidae (Teleostei: Carangaria): A  
639 synthesis of fossil-and extant-based classification systems. *Zootaxa*, 4686(3), 397-408.

640

641 Ballen, G. A. (2020). New records of the genus *Sphyraena* (Teleostei: Sphyraenidae)  
642 from the Caribbean with comments on dental characters in the genus. *Journal of Vertebrate*  
643 *Paleontology*, 40(6), e1849246.

644

645 Bartoli, G., Sarnthein, M., Weinelt, M., Erlenkeuser, H., Garbe-Schönberg, D., & Lea, D.  
646 W. (2005). Final closure of Panama and the onset of northern hemisphere glaciation. *Earth and*  
647 *Planetary Science Letters*, 237(1-2), 33-44.

648

649 Betancur-R, R., Broughton, R. E., Wiley, E. O., Carpenter, K., López, J. A., Li, C., ... &  
650 Ortí, G. (2013). The tree of life and a new classification of bony fishes. *PLoS Currents*, 5.

651

652 Betancur-R, R., Wiley, E. O., Arratia, G., Acero, A., Bailly, N., Miya, M., ... & Orti, G.  
653 (2017). Phylogenetic classification of bony fishes. *BMC Evolutionary Biology*, 17, 1-40.

654

655 Birkeland, C. (1990). *Caribbean and Pacific coastal marine systems: similarities and*  
656 *differences*. Parthenon Publishing.

657

658 Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M.,  
659 Gavryushkina, A., ... & Drummond, A. J. (2019). BEAST 2.5: An advanced software platform  
660 for Bayesian evolutionary analysis. *PLoS Computational Biology*, 15(4), e1006650.

## PHYLOGENY AND BIOGEOGRAPHIC HISTORY OF SNOOKS

661

662           Brown, J. W., Walker, J. F., & Smith, S. A. (2017). Phyx: phylogenetic tools for  
663 Unix. *Bioinformatics*, 33(12), 1886-1888.

664

665           Byrne, L., Chapleau, F., & Aris-Brosou, S. (2018). How the Central American seaway  
666 and an ancient northern passage affected flatfish diversification. *Molecular Biology and*  
667 *Evolution*, 35(8), 1982-1989.

668

669           Carvalho-Filho, A., De Oliveira, J., Soares, C., & Araripe, J. (2019). A new species of  
670 snook, *Centropomus* (Teleostei: Centropomidae), from northern South America, with notes on  
671 the geographic distribution of other species of the genus. *Zootaxa*, 4671(1), 81-92.

672

673           Coates, A. G., & Stallard, R. F. (2013). How old is the Isthmus of Panama? *Bulletin of*  
674 *Marine Science*, 89(4), 801-813.

675

676           Cowman, P. F., & Bellwood, D. R. (2013). Vicariance across major marine  
677 biogeographic barriers: temporal concordance and the relative intensity of hard versus soft  
678 barriers. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768), 20131541.

679

680           Craig, M. T., Hastings, P. A., & Pondella, D. J. (2004). Speciation in the Central  
681 American Seaway: The importance of taxon sampling in the identification of trans-isthmian  
682 geminate pairs. *Journal of Biogeography*, 31(7), 1085-1091.

683

OSSA-HERNANDEZ, BALLEEN, ACERO, TAVERA

684 Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: more  
685 models, new heuristics, and high-performance computing. *Nature Methods*, 9(8), 772.

686

687 de Oliveira, J. N., Gomes, G., do Rêgo, P. S., Moreira, S., Sampaio, I., Schneider, H., &  
688 Araripe, J. (2014). Molecular data indicate the presence of a novel species of *Centropomus*  
689 (Centropomidae–Perciformes) in the western Atlantic. *Molecular Phylogenetics and*

690 *Evolution*, 77, 275-280.

691

692 dos Reis, M., & Yang, Z. (2011). Approximate likelihood calculation on a phylogeny for  
693 Bayesian estimation of divergence times. *Molecular biology and evolution*, 28(7), 2161-2172.

694

695 dos Reis, M., Gunnell, G.F., Barba-Montoya, J., Wilkins, A., Yang, Z., and Yoder, A.D.  
696 (2018). Using phylogenomic data to explore the effects of relaxed clocks and calibration  
697 strategies on divergence time estimation: Primates as a test case. *Systematic Biology*, 67(4), 594–  
698 615.

699

700 Dupin, J., Matzke, N. J., Särkinen, T., Knapp, S., Olmstead, R. G., Bohs, L., & Smith, S.  
701 D. (2017). Bayesian estimation of the global biogeographical history of the Solanaceae. *Journal*  
702 *of Biogeography*, 44(4), 887-899.

703

704 Duque-Caro, H. (1990). Neogene stratigraphy, paleoceanography, and  
705 paleobiogeography in northwest South America and the evolution of the Panama  
706 Seaway. *Paleogeography, Palaeoclimatology, Palaeoecology*, 77(3-4), 203-234.



## PHYLOGENY AND BIOGEOGRAPHIC HISTORY OF SNOOKS

707

708 Figueiredo-Filho, J. M. D., F., Marceniuk, A. P., Feijo, A., Siccha-Ramírez, R., Ribeiro,

709 G. S., Oliveira, C., & Rosa, R. S. (2021). Taxonomy of *Centropomus* Lacépède, 1802

710 (Perciformes: Centropomidae), with a focus on the Atlantic species of the

711 genus. *Zootaxa*, 4942(3), zootaxa-4942.

712

713 Fraser, T. H. (1968). Comparative osteology of the Atlantic snooks (Pisces,

714 *Centropomus*). *Copeia* 1968, 433-460.

715

716 Fricke, R., Eschmeyer, W. N. & Van der Laan, R. (eds) (2023). Eschmeyer's catalog of

717 fishes: Genera, species, references.

718 (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>).

719 Electronic version accessed 01 September 2023.

720

721 Froese, R. and Pauly, D. (2017) Fish Base. World Wide Web Electronic Publication.

722 ([www.fishbase.org](http://www.fishbase.org)).

723

724 Girard, M. G., Davis, M. P., & Smith, W. L. (2020). The phylogeny of Carangiformes

725 fishes: morphological and genomic investigations of a new fish clade. *Copeia*, 108(2), 265-298.

726

727 Greenwood, P. H. (1976). A review of the family Centropomidae (Pisces,

728 Perciformes). *Bull. British Mus. Nat. Hist., Zool Ser.*, 29, 1-81.

729

OSSA-HERNANDEZ, BALLEEN, ACERO, TAVERA

730 Hastings, W. K. (1970). Monte Carlo sampling methods using Markov chains and their  
731 applications. *Biometrika*, 57(1), 97–109.

732

733 Hiller, A., & Lessios, H. A. (2020). Marine species formation along the rise of Central  
734 America: The anomuran crab *Megalobrachium*. *Molecular Ecology*, 29(2), 413-428.

735

736 Hou, Z., & Li, S. (2018). Tethyan changes shaped aquatic diversification. *Biological*  
737 *Reviews*, 93(2), 874-896.

738

739 Inoue, J., Donoghue, P. C., & Yang, Z. (2010). The impact of the representation of fossil  
740 calibrations on Bayesian estimation of species divergence times. *Systematic Biology*, 59(1), 74-

741 89.

742

743 International Commission on Stratigraphy (ICS). International Stratigraphic Table, 2023.

744 In: <https://stratigraphy.org/chart#latest-version>. Accessed 24 April 2023.

745

746 Jaramillo, C. (2018). Evolution of the Isthmus of Panama: biological, paleoceanographic  
747 and paleoclimatological implications. In *Mountains, Climate, and Biodiversity*, Hoorn, C.,

748 Perrigo, A., & Antonelli, A. Ed. 323-338.

749

750 Jordan, D. S. (1908). The law of geminate species. *The American Naturalist*, 42(494), 73-

751 80.

752

## PHYLOGENY AND BIOGEOGRAPHIC HISTORY OF SNOOKS

753           Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software  
754 version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30(4),  
755 772-780.

756

757           Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., ... &  
758 Drummond, A. (2012). Geneious Basic: an integrated and extendable desktop software platform  
759 for the organization and analysis of sequence data. *Bioinformatics*, 28(12), 1647-1649.

760

761           Knowlton, N., & Weigt, L. A. (1998). New dates and new rates for divergence across the  
762 Isthmus of Panama. *Proceedings of the Royal Society of London. Series B: Biological*  
763 *Sciences*, 265(1412), 2257-2263.

764

765           Koblmüller, S., Schögl, C. A., Lorber, C. J., Van Steenberge, M., Kmentová, N.,  
766 Vanhove, M. P., & Zangl, L. (2021). African *Lates* perches (Teleostei, Latidae, *Lates*):  
767 Paraphyly of Nile perch and recent colonization of Lake Tanganyika. *Molecular Phylogenetics*  
768 *and Evolution*, 160, 107141.

769

770           Kocsis, Á. T., Reddin, C. J., & Kiessling, W. (2018). The stability of coastal benthic  
771 biogeography over the last 10 million years. *Global Ecology and Biogeography*, 27(9), 1106-  
772 1120.

773

774           Landis, M. J., Matzke, N. J., Moore, B. R., & Huelsenbeck, J. P. (2013). Bayesian  
775 analysis of biogeography when the number of areas is large. *Systematic Biology*, 62(6), 789-804.

OSSA-HERNANDEZ, BALLEEN, ACERO, TAVERA

776

777           Lessios, H. A. (1981). Divergence in allopatry: molecular and morphological  
778 differentiation between sea urchins separated by the Isthmus of Panama. *Evolution*, 618-634.

779

780           Lessios, H. A. (2008). The Great American Schism: divergence of marine organisms after  
781 the rise of the Central American Isthmus. *Annual Review of Ecology, Evolution, and*  
782 *Systematics*, 39, 63-91.

783

784           Li, C., Ricardo, B. R., Smith, W. L., & Ortí, G. (2011). Monophyly and interrelationships  
785 of snook and barramundi (Centropomidae sensu Greenwood) and five new markers for fish  
786 phylogenetics. *Molecular Phylogenetics and Evolution*, 60(3), 463-471.

787

788           Lima, F. D., Strugnell, J. M., Leite, T. S., & Lima, S. M. (2020). A biogeographic  
789 framework of octopod species diversification: the role of the Isthmus of Panama. *PeerJ*, 8,  
790 e8691.

791

792           Malcher, G., Amorim, A. L., Ferreira, P., Oliveira, T., Melo, L., Rêgo, P. S., & Araripe,  
793 J. (2023). First evaluation of the population genetics and aspects of the evolutionary history of  
794 the Amazonian snook, *Centropomus irae*, and its association with the Amazon  
795 plume. *Hydrobiologia*, 850(9), 2115-2125.

796

## PHYLOGENY AND BIOGEOGRAPHIC HISTORY OF SNOOKS

797 Marko, P. B., & Jackson, J. B. (2001). Patterns of morphological diversity among and  
798 within arcid bivalve species pairs separated by the Isthmus of Panama. *Journal of*  
799 *Paleontology*, 75(3), 590-606.

800

801 Marshall, C. R. (2010). Using confidence intervals to quantify the uncertainty in the end-  
802 points of stratigraphic ranges. *The Paleontological Society Papers*, 16, 291-316.

803

804 Martínez-Brown, J. M., Navarro-Flores, J., García-Rodríguez, F. J., Ibarra-Castro, L.,  
805 Vargas-Peralta, C. E., Del Río-Portilla, M. Á., & Martínez-Moreno, R. (2021). Revision of the  
806 diagnostic characters of two morphologically similar snook species, *Centropomus viridis* and *C.*  
807 *nigrescens* (Carangiformes: Centropomidae). *Zootaxa*, 4915(3), 326-338.

808

809 Matzke, N. J. (2013). *Probabilistic historical biogeography: new models for founder-*  
810 *event speciation, imperfect detection, and fossils allow improved accuracy and model testing.*  
811 University of California, Berkeley.

812

813 Matzke, N.J. (2015) Stochastic mapping under biogeographical models. Available at:  
814 [http://phylo.wikidot.com/biogeobears#stochastic\\_mapping](http://phylo.wikidot.com/biogeobears#stochastic_mapping) (accessed 1 October 2023).

815

816

817 Metropolis, N., Rosenbluth, A. W., Rosenbluth, M. N., Teller, A. H., & Teller, E. (1953).  
818 Equation of state calculations by fast computing machines. *The Journal of Chemical*  
819 *Physics*, 21(6), 1087-1092.

OSSA-HERNANDEZ, BALLEEN, ACERO, TAVERA

820

821           Mirande, J. M. (2017). Combined phylogeny of ray-finned fishes (Actinopterygii) and the  
822 use of morphological characters in large-scale analyses. *Cladistics*, 33(4), 333-350.

823

824           Miura, O., Torchin, M. E., & Bermingham, E. (2010). Molecular phylogenetics reveals  
825 differential divergence of coastal snails separated by the Isthmus of Panama. *Molecular*  
826 *Phylogenetics and Evolution*, 56(1), 40-48.

827

828           Montes, C., Cardona, A., McFadden, R., Morón, S. E., Silva, C. A., Restrepo-Moreno, S.,  
829 ... & Flores, J. A. (2012). Evidence for middle Eocene and younger land emergence in central  
830 Panama: Implications for Isthmus closure. *GSA Bulletin*, 124(5-6), 780-799.

831

832           Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J. C., Valencia, V., ... & Niño,  
833 H. (2015). Middle Miocene closure of the Central American seaway. *Science*, 348(6231), 226-  
834 229.

835

836           Near, T. J., & Thacker, C. E. (2023). Phylogenetic classification of living and fossil ray-  
837 finned fishes (Actinopterygii). *Bulletin of the Peabody Museum of Natural History*, 65.  
838 <https://doi.org/10.5281/zenodo.8352027>.

839

840           Near, T. J., Dornburg, A., Eytan, R. I., Keck, B. P., Smith, W. L., Kuhn, K. L., ... &  
841 Wainwright, P. C. (2013). Phylogeny and tempo of diversification in the superradiation of spiny-  
842 rayed fishes. *Proceedings of the National Academy of Sciences*, 110(31), 12738-12743.

## PHYLOGENY AND BIOGEOGRAPHIC HISTORY OF SNOOKS

843

844 O’Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A.

845 L., ... & Jackson, J. B. (2016). Formation of the Isthmus of Panama. *Science Advances*, 2(8),

846 e1600883.

847

848 Otero, O. (2004). Anatomy, systematics, and phylogeny of both recent and fossil latid

849 fishes (Teleostei, Perciformes, Latidae). *Zoological Journal of the Linnean Society*, 141(1), 81-

850 133.

851

852 Palumbi, S. R. (1996). Nucleic acids II: the polymerase chain reaction. In ‘Molecular

853 Systematics’. (Eds DM Hillis, C. Moritz, and BK Mable.) pp. 205–247.

854

855 Potthoff, T., & Tellock, J. A. (1993). Osteological development of the snook,

856 *Centropomus undecimalis* (Teleostei, Centropomidae). *Bulletin of Marine Science*, 52(2), 669-

857 716.

858

859 R Core Team (2021). R: A language and environment for statistical computing. R

860 Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

861

862 Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., ... &

863 Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine

864 fishes. *Nature*, 559(7714), 392-395.

865

OSSA-HERNANDEZ, BALLEEN, ACERO, TAVERA

866           Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range  
867 evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 57(1), 4-14.

868

869           Robertson, D. R., & Allen, G. R. (2015). *Shorefishes of the Tropical Eastern Pacific:*  
870 *online information system* (Vol. 2). Version.

871

872           Robertson, D. R., & Tassell, J. V. (2023). Shorefishes of the Greater Caribbean: online  
873 information system. Version 3.0. Smithsonian Tropical Research Institute, Balboa, Panamá.

874

875           Ronquist, F. (1997). Dispersal-vicariance analysis: a new approach to the quantification  
876 of historical biogeography. *Systematic Biology*, 46(1), 195-203.

877

878           Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., ... &  
879 MrBayes, J. H. (2012) 3.2: Efficient Bayesian phylogenetic inference and model choice across a  
880 large model space., 61. DOI: <https://doi.org/10.1093/sysbio/sys029>, 539-542.

881

882           Sambrook, J. Fritsch, E. F. y Maniatis, T. 1989. In: *Molecular Cloning: A Laboratory*  
883 *Manual*. Second Edition, vol. 2. Cold Spring Harbor: Cold Spring Harbor Laboratory Press.

884

885           Santini, F., Carnevale, G., & Sorenson, L. (2015). The first-time tree of Sphyraenidae  
886 (Percomorpha) reveals a Middle Eocene crown age and an Oligo–Miocene radiation of

887 barracudas. *Italian Journal of Zoology*, 82(1), 133-142.

888



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889 Sepulchre, P., Arsouze, T., Donnadieu, Y., Dutay, J. C., Jaramillo, C., Le Bras, J., ... &  
890 Waite, A. J. (2014). Consequences of shoaling of the Central American Seaway determined from  
891 modeling Nd isotopes. *Paleoceanography*, 29(3), 176-189.

892

893 Seyoum, S., Anderson, J., Williford, D., Hayes, M. C., Dutka-Gianelli, J., Figuerola-  
894 Hernández, M. G., ... & Tringali, M. D. (2022). A novel allopatric lineage within the fat snook  
895 species complex of the genus *Centropomus* (Perciformes: Centropomidae). *Bulletin of Marine*  
896 *Science*, 98(4), 471-492.

897

898 Strauss, D., & Sadler, P. M. (1989). Classical confidence intervals and Bayesian  
899 probability estimates for ends of local taxon ranges. *Mathematical Geology*, 21, 411-427.

900

901 Tariel, J., Longo, G. C., & Bernardi, G. (2016). Tempo and mode of speciation in  
902 *Holacanthus* angelfishes based on RADseq markers. *Molecular Phylogenetics and Evolution*, 98,  
903 84-88.

904

905 Tavera, J. J., & Wainwright, P. C. (2019). Geography of speciation affects the rate of trait  
906 divergence in haemulid fishes. *Proceedings of the Royal Society B*, 286(1896), 20182852.

907

908 Tavera, J. J., Acero P., A., Balart, E. F., & Bernardi, G. (2012). Molecular phylogeny of  
909 grunts (Teleostei, Haemulidae), with an emphasis on the ecology, evolution, and speciation  
910 history of New World species. *BMC Evolutionary Biology*, 12, 1-16.

911

OSSA-HERNANDEZ, BALLEEN, ACERO, TAVERA

912 Thacker, C. E. (2017). Patterns of divergence in fish species separated by the Isthmus of  
913 Panama. *BMC Evolutionary Biology*, 17(1), 1-14.

914

915 Tringali, M. D., Bert, T. M., Seyoum, S., Bermingham, E., & Bartolacci, D. (1999).

916 Molecular phylogenetics and ecological diversification of the transisthmian fish genus

917 *Centropomus* (Perciformes: Centropomidae). *Molecular Phylogenetics and Evolution*, 13(1),

918 193-207.

919

920 Uhen, M.D., B. Allen, N. Behboudi, M. E. Clapham, E. Dunne, A. Hendy, P. A. Holroyd,

921 M. Hopkins, P. Mannion, P. Novack-Gottshall, C. Pimiento, and P. Wagner. (2023).

922 Paleobiology Database User Guide Version 1.0. *PaleoBios* 40(11): 1-56.

923

924 Vergara-Chen, C. (2014). Los róbalo (Pisces, Centropomidae) del pacífico de Panamá:

925 desafíos emergentes en investigación y conservación. *Tecnociencia*, 16(1), 15-40.

926

927 Wang, S. C., Everson, P. J., Zhou, H. J., Park, D., & Chudzicki, D. J. (2016). Adaptive

928 credible intervals on stratigraphic ranges when recovery potential is

929 unknown. *Paleobiology*, 42(2), 240-256.

930

931 Ward, R. D., Zemlak, T. S., Innes, B. H., Last, P. R., & Hebert, P. D. (2005). DNA

932 barcoding Australia's fish species. *Philosophical Transactions of the Royal Society B: Biological*

933 *Sciences*, 360(1462), 1847-1857.

934

## PHYLOGENY AND BIOGEOGRAPHIC HISTORY OF SNOOKS

935 Weinberg, J. R., & Starczak, V. R. (1989). Morphological divergence of Eastern Pacific  
936 and Caribbean isopods: effects of a land barrier and the Panama Canal. *Marine Biology*, 103,  
937 143-152.

938

939 Westneat, M. W., Alfaro, M. E., Wainwright, P. C., Bellwood, D. R., Grubich, J. R.,  
940 Fessler, J. L., ... & Smith, L. L. (2005). Local phylogenetic divergence and global evolutionary  
941 convergence of skull function in reef fishes of the family Labridae. *Proceedings of the Royal*  
942 *Society B: Biological Sciences*, 272(1567), 993-1000.

943

944 Worsham, M. L., Julius, E. P., Nice, C. C., Diaz, P. H., & Huffman, D. G. (2017).  
945 Geographic isolation facilitates the evolution of reproductive isolation and morphological  
946 divergence. *Ecology and Evolution*, 7(23), 10278-10288.

947

948 Yang, Z. (2007). PAML 4: phylogenetic analysis by maximum likelihood. *Molecular*  
949 *biology and evolution*, 24(8), 1586-1591.

950

951 Yang, Z. (2014). *Molecular evolution: A statistical approach*. Oxford. University Press.

952

953 Zhao, Z., Hou, Z. E., & Li, S. Q. (2022). Cenozoic Tethyan changes dominated Eurasian  
954 animal evolution and diversity patterns. *Zoological Research*, 43(1), 3.