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

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

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.

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**

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$(NH_4)_2SO_4$; Solis

110   Bio Dyne), 1.2 µl of 2.0 mM $MgCl_2$, 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

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 (Katoh 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

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

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.

176
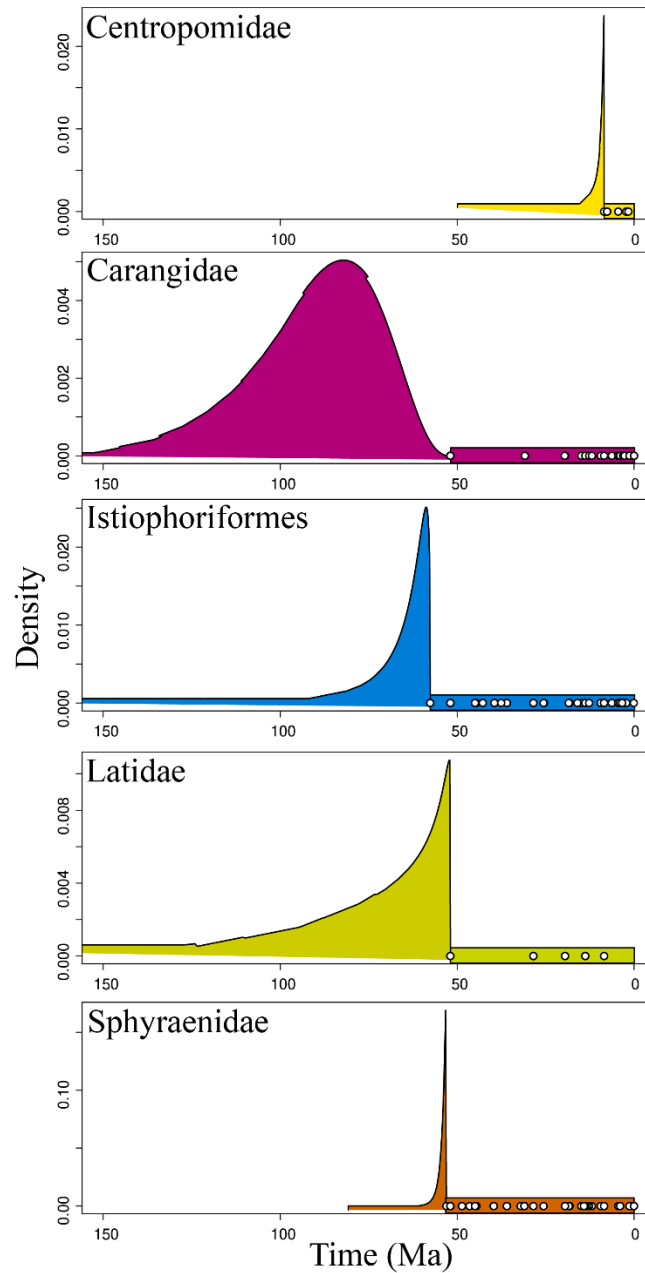
Figure 1. Stratigraphic series for the families Centropomidae, Carangidae, Latidae, Sphyraenidae and some families in the order Istiophoriformes. Circles represent fossil occurrences in geologic time, and shaded areas represent the posterior density on the origination age of each stratigraphic series. Note that all the series are constrained to be extant, and therefore theta2 is fixed to 0.0 (present time). The extent of the posterior on origination time depends on the number of observations as well as on the temporal pattern of occurrences: If they become less frequent

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 theta1 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

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

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.

251

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

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).

297

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    *viridens, S. argentea), (S. helleri, (S. novaehollandiae, (S. africana, (S. japonica, (S.*

303    *acutippinis, 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. viridens* (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).

312

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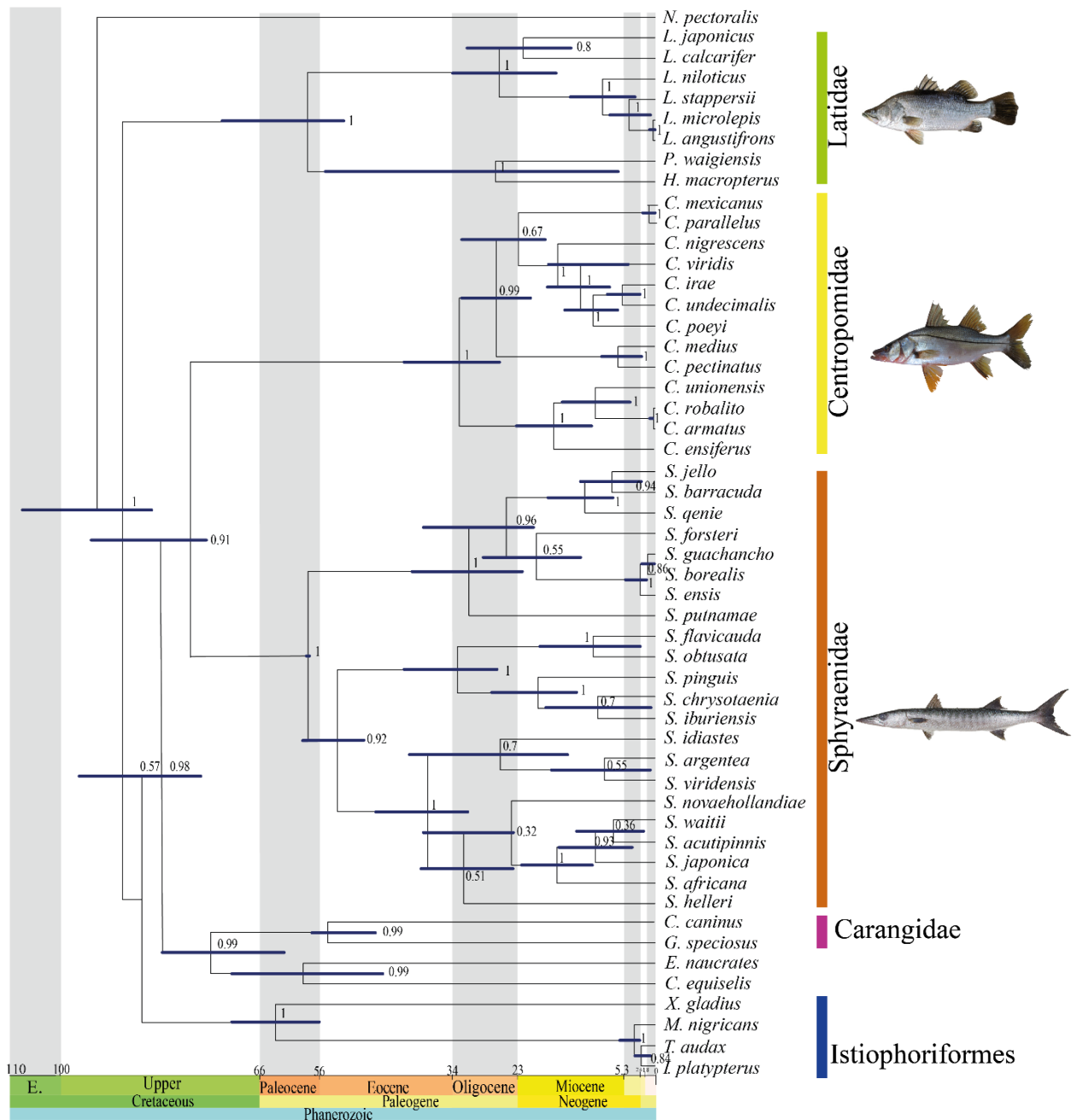
Figure 2- Time-calibrated maximum credibility tree of the family Centropomidae, Latidae, and

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

ages. Node labels represent the posterior probability.

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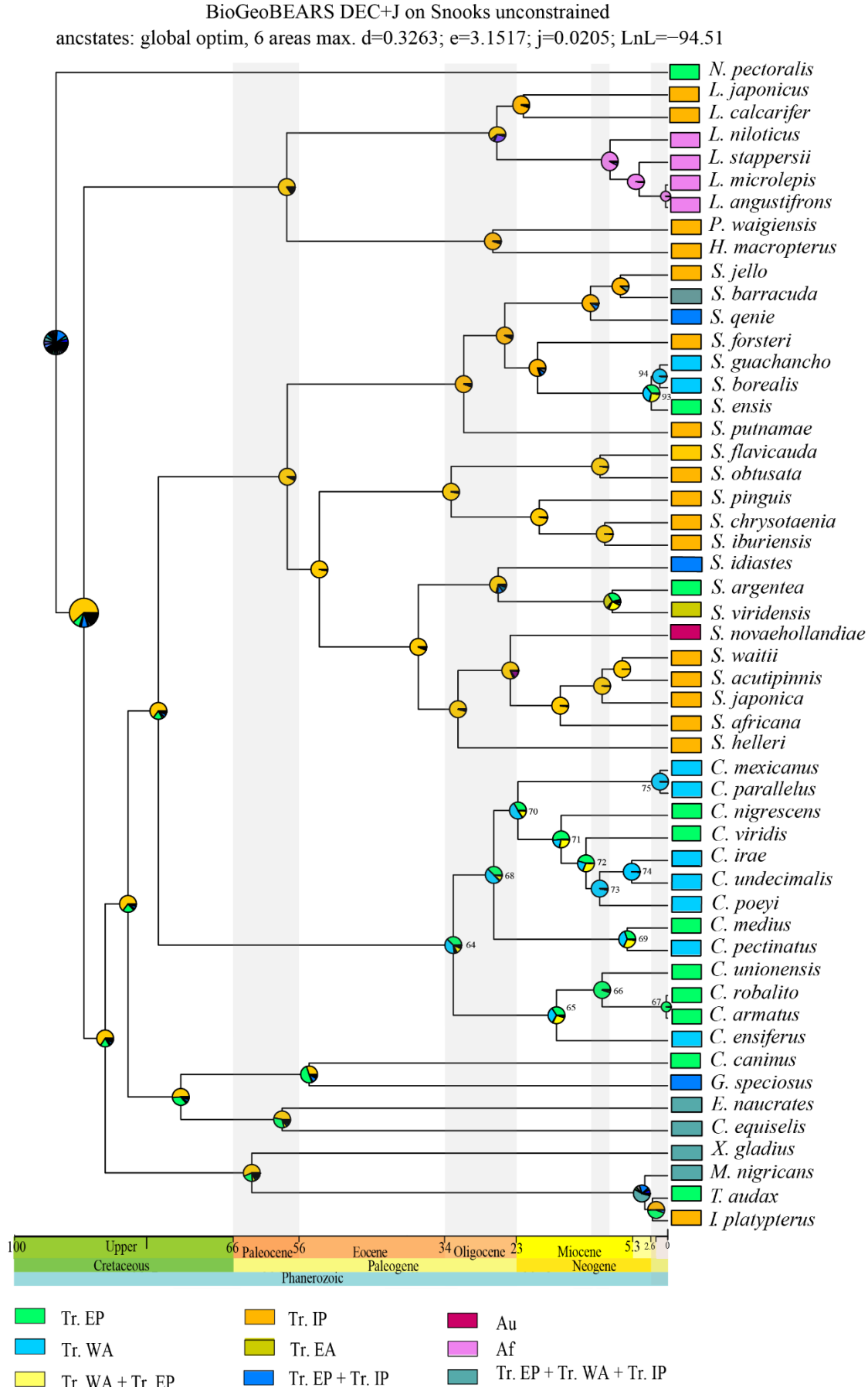319    *Biogeographic analysis*

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

BioGeoBEARS DEC+J on Snooks unconstrained
ancstates: global optim, 6 areas max. d=0.3263; e=3.1517; j=0.0205; LnL=−94.51

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

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) | % |
|---|---|---|---|---|---|---|---|---|---|
| **Within-area speciation** | 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 |
| **Dispersal** | Founder events | 10.3 (1.79) | 38 | 20.9 (16.43) | 24 | 12.8 (17.95) | 13 | 18.5 (21.92) | 10 |
| **Vicariance** | Vicariance | 2.8 (1.56) | 4 | 9.4 (5.73) | 8 | 2.7 (1.97) | 2 | 9 (9.90) | 5 |
| **Total** | | 65.5 (1.56) | 100 | 150.0 (150.41) | 100 | 237.5 (303.32) | 100 | 87.5 (134.94) | 100 |

369

370

371   ***Summary of estimated ancestral area over time in the Tropical Eastern Pacific and Tropical***

372   ***Western Atlantic during the Neogene.***
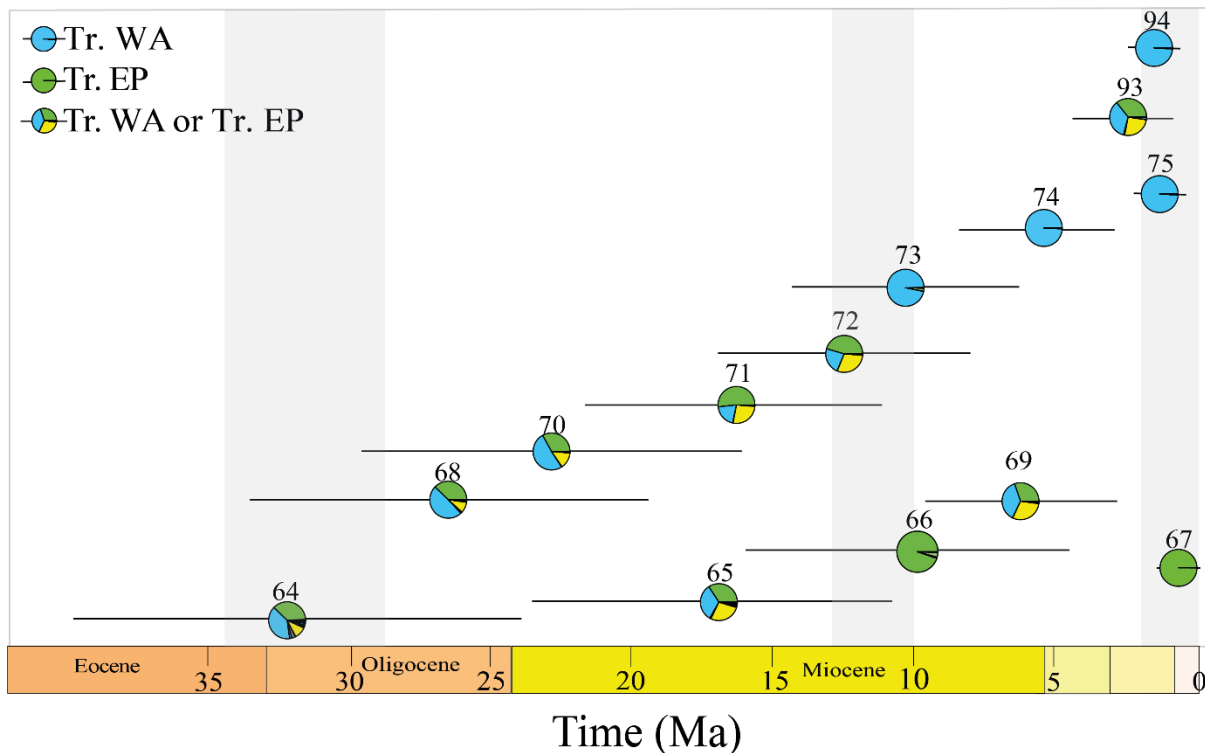
373         A total the 14 nodes in the phylogenetic inferences showed estimated ancestral areas in

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

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.*

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 Oliviera 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.

418
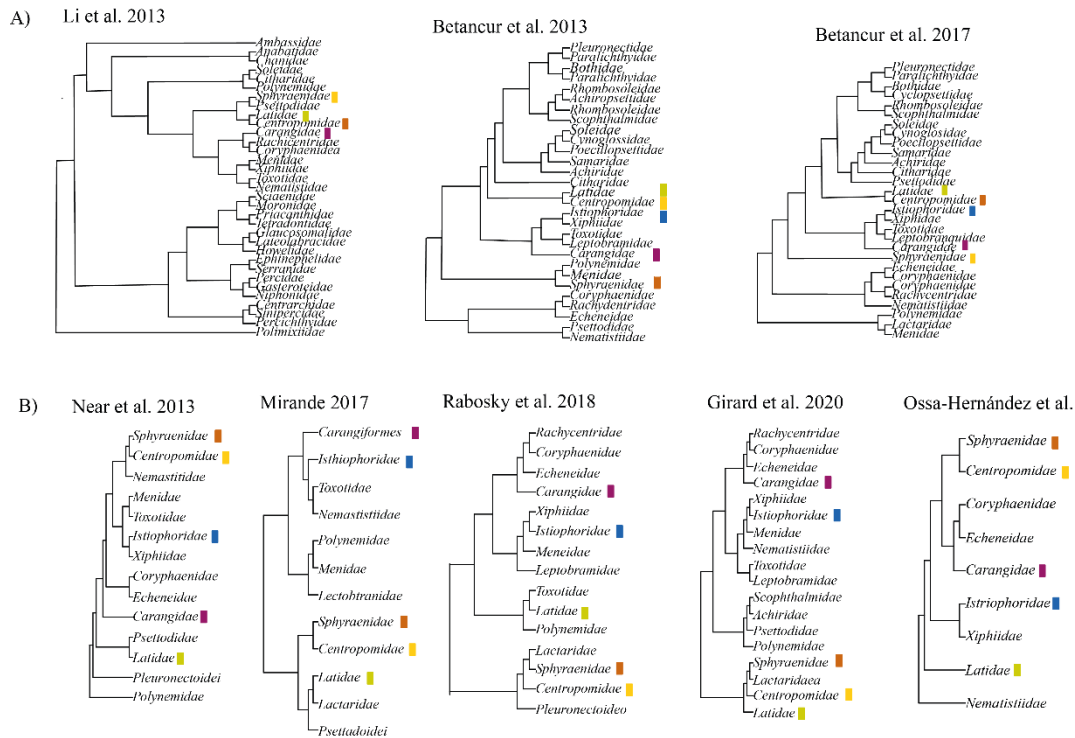
Figure 5- Hypotheses of relationships among ray-fin fishes where the closest relationship A) Centropomidae and Latidae are sister clade according to molecular studies (Li et al. 2011; Betancur 2013, 2017). B) Centropomidae and Sphyraenidae are recovered as sister clades based on the following molecular studies: Near et al. (2013); Mirande (2017); Rabosky et al. (2018); Girard et al. (2020). The color boxes indicate the families used in the present study.

424

*Hypotheses of the relationship among centropomid species.*

This study represents the first attempt at estimating the divergence times among species of the Centropomidae by using information derived from the fossil record. De Oliviera et al. (2014) recovered an age for the Centropomidae family during the Miocene (~23 Ma), whereas our findings place the family's origin in the Oligocene (~32.91 million years ago). Additionally, the divergence times for sister species pairs do not align with De Oliviera et al. (2014).

431

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*

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.

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

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 to 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

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

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

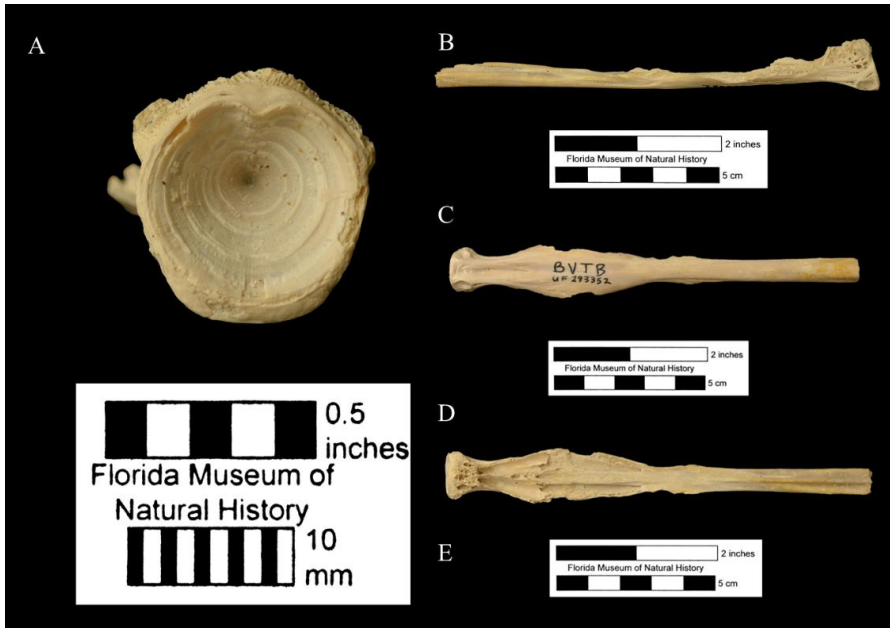552     291382 (Fig 5 E-I). They were photographed by Sean Moran.
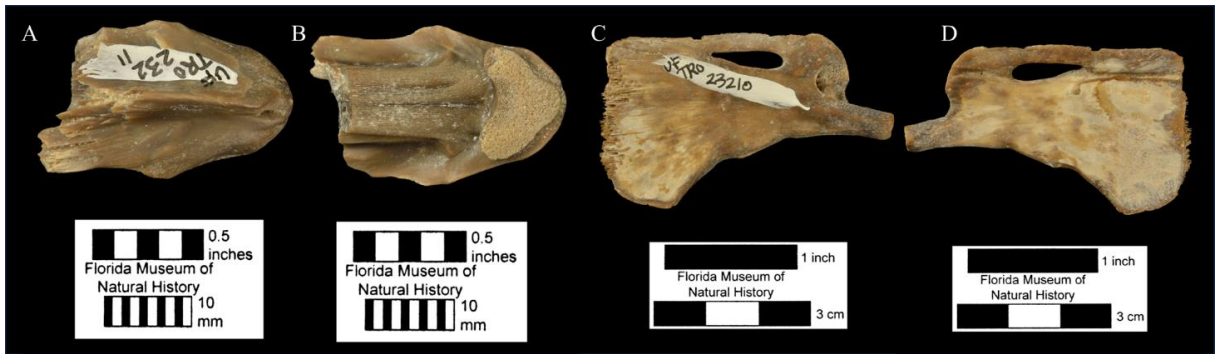
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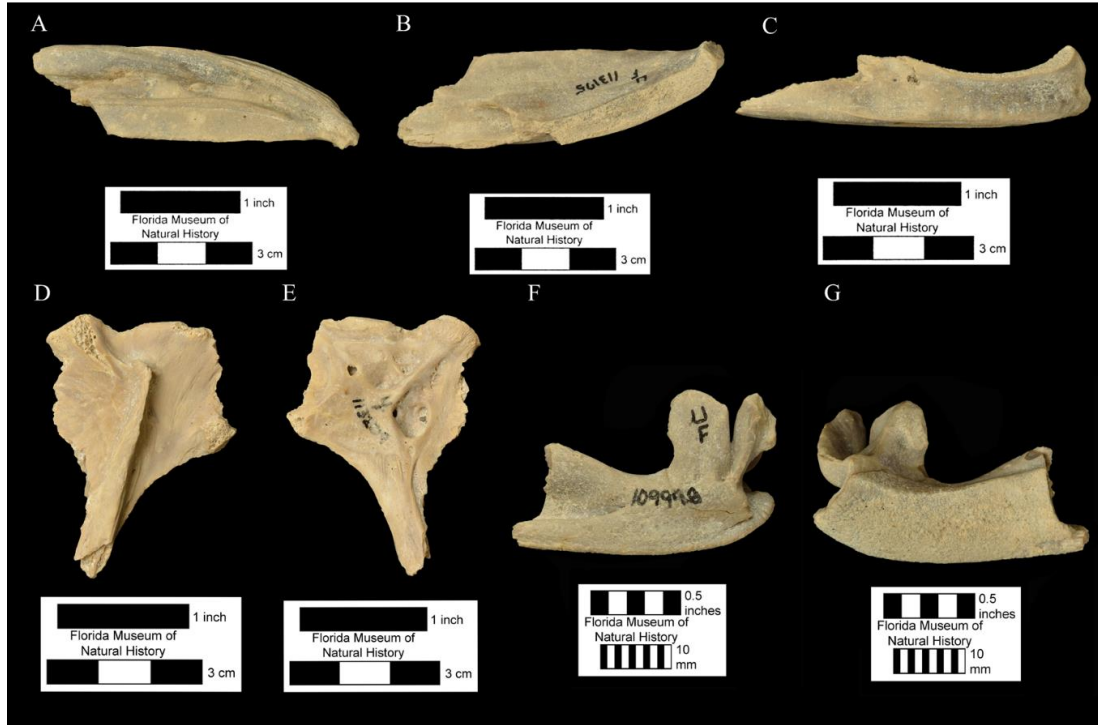
555     (Figure 1 A-F)

556
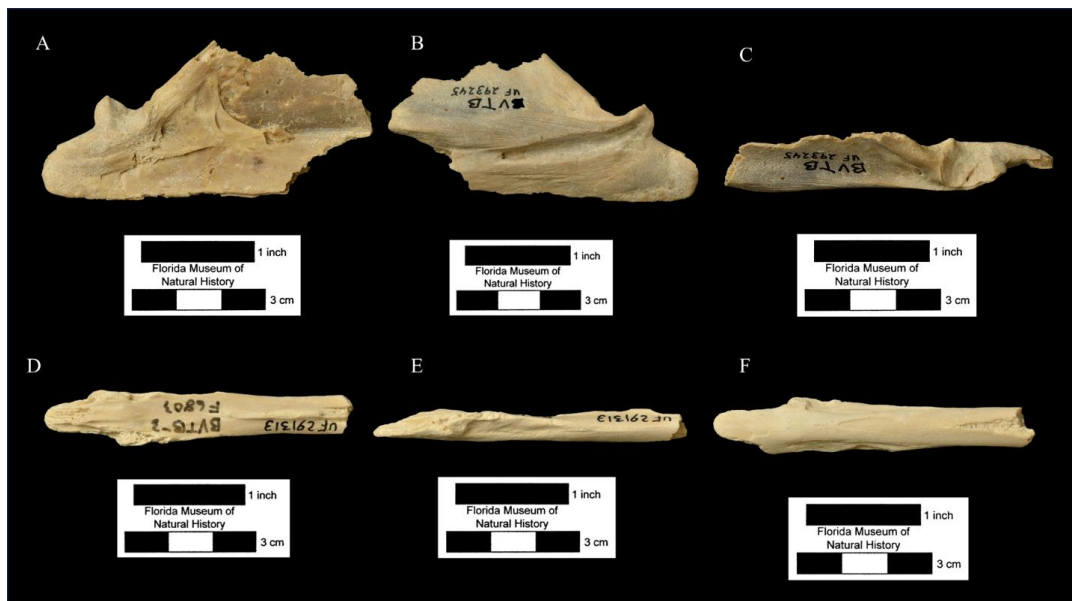
557



558    (Figure 2 A-E)

559



560    (Figure 3 A-D)

561

562        (Figure 4 A-G)
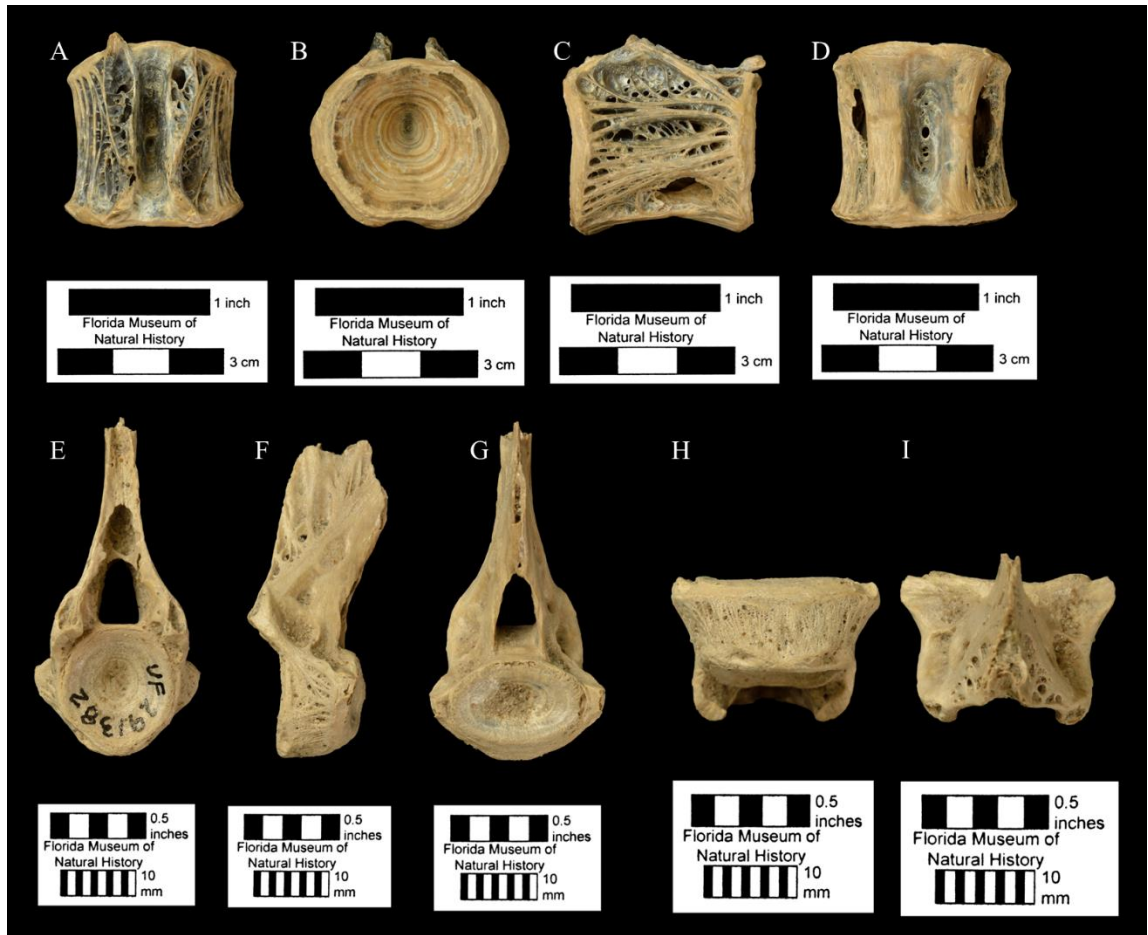
(Figure 5 A-I)

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.

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

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

| Primer name | Primer Sequence | Tm (•C) | Reference |
|---|---|---|---|
| *12S229Fa*<br>*12S954Ra* | 5'- GYCGGTAAAAYTCGTGCCAG -3'<br>5'- YCCAAGYGCACCTTCCGGTA -3' | 60 | Palumbi 1996 |
| *16SAR*<br>*16SBR* | 5'- CGCCTGTTTATCAAAAACAT -3'<br>5'- CCGGTCTGAACTCAGATCACG -3' | 54 | Palumbi 1996 |
| *FishF1*<br>*FishR1* | 5'- TCAACCAACCACAAAGACATTGGCAC -3'<br>5'- TAGACTTCTGGGTGGCCAAAGAAT CA -3' | 54 | Ward *et al.* 2005 |
| *Glud-GL*<br>*CB3H* | 5'- GAYGCAYTARTYGAYCTYCCR GC -3'<br>5'- GGGTCYCCIARIARRTTIGG-3' | 48-52 | Palumbi 1996 |
| *Tmo4c4-F*<br>*Tmo4c4-R* | 5' CCTCCGGCCTTCCTAAAACCTCTC 3'<br>5' CATCGTGCTCCTGGGTGACAAAGT 3' | 54 | Westneat *et al.* 2005 |

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 | 0.00000000000670586641 |

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 |
| **DEC+J** | **-94.51** | **3** | **0.33** | **3.15** | **0.02** | **195.5** | **0.53** |
| 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 | 7.00E-11 |
| BAYAREALIKE+J | -96.44 | 3 | 0.057 | 0.31 | 0.032 | 199.4 | 0.077 |

591

592 **Conclusions**

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

616    de las Ciencias del Mar (Cecimar), Universidad Nacional de Colombia sede Caribe. Carlos

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618    STRI Panamá, where this project could be completed.

619

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