Tursiops truncatus nuuanu, a new subspecies of the common bottlenose dolphin from the eastern tropical Pacific

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Abstract

In the eastern Pacific Ocean, three distinct forms of common bottlenose dolphin (*Tursiops truncatus*) have been identified, with suggestion they may be different species: a southern California/Mexico coastal, a northern temperate offshore, and an eastern tropical Pacific (ETP) offshore form. Currently, only one species (*T. truncatus*) is recognized in the region, with the first two forms described as distinct ecotypes. The goal of this study was to improve our understanding of the taxonomic status of these previously described forms through a re-examination of their morphological differentiation. We analyzed 135 skulls from the eastern and western Pacific, including the two nominal species, *T. gillii* and *T. nuuanu*, previously described for the eastern North Pacific and ETP, respectively. Additionally, we examined the holotypes of two currently recognized species in the genus, *T. truncatus* and *T. aduncus*. Our results showed significant morphological differentiation among bottlenose dolphins in the Pacific Ocean. The ETP offshore bottlenose dolphins were smaller in skull and body size and diagnostically distinct from dolphins in the western North Pacific and other regions in the eastern Pacific. Our results also indicated that while other bottlenose dolphins in the Pacific were more similar to the globally distributed *T. truncatus*, the ETP offshore dolphins shared similarities with a previously described species in that region. The distinct environmental conditions in the ETP may be driving the evolutionary differentiation of these bottlenose dolphins. Given these results, we here recommend the recognition of ETP offshore bottlenose dolphins as a distinct subspecies, *Tursiops truncatus nuuanu*.

Keywords: cetaceans, divergence, environment, speciation, tropical

Introduction

Environmental conditions and biological interactions can promote ecological divergence in highly mobile predators even in the absence of physical barriers to dispersal (Pilot et al. 2012; Wolf et al. 2008; Teske et al. 2019; Costa et al. 2021). Water temperature and competition for prey, for example, can lead to morphological and genetic differentiation, splitting populations into different ecological groups with evolving traits that will allow an efficient exploitation of the space and/or specific resources (Smith and Skúlason 1996; Ackermann and Doebeli 2004; Ruffler et al. 2007; Keller and Seehausen 2012). This divergent adaptation may even lead to reproductive isolation and result in ecological speciation (Schluter 2001).

Although most marine mammal species have the potential for large geographic dispersal, many exhibit local adaptations and distinct ecological groups with differential habitat preferences and foraging behaviors between conspecific populations even within short geographic distances (e.g., Heyning and Perrin 1994; Ford et al. 1998; Perrin et al. 2011; Costa et al. 2016). For example, distinct ecological preferences may be contributing to the differentiation of delphinids in the eastern Pacific Ocean, which in turn may be leading to speciation. Based primarily on morphological differences, subspecies of spinner (*Stenella longirostris longirostris, S. l. orientalis,* and *S. l. centroamericana*), pantropical spotted (*S. attenuata attenuata* and *S. a. graffmani*), and common (*Delphinus delphis delphis* and *D. d. bairdii*) dolphins have been recognized in the eastern Pacific (Perrin et al. 1982; Perrin 1990; Dizon et al. 1994; Committee on Taxonomy 2022). Interestingly three of the *Stenella* subspecies (*S. l. orientalis, S. l. centroamericana,* and *S. a. graffmani*) are endemic to the eastern tropical Pacific (ETP), each one with a different habitat range (Perrin et al. 1982; Perrin 1990; Dizon et al. 1994).

Morphological differentiation within bottlenose dolphins (genus *Tursiops*) has also been suggested for the region (e.g., Walker 1981; Perrin et al. 2011; Esteves-Ponte et al. 2022). Bottlenose dolphins are regularly sighted throughout the eastern Pacific (from Canada to Chile) and the Gulf of California (GoC) (e.g., May-Collado et al. 2005; Segura et al. 2006; Palacios et al. 2012; Hwang et al. 2014; Van Waerebeek et al. 2017; Halpin et al. 2018; Segura-García et al. 2018; Carretta et al. 2021; Esteves-Ponte et al. 2022) and currently only the species *T. truncatus* (the common bottlenose dolphin) is believed to occur throughout this geographic area (Committee on Taxonomy 2022). However, two nominal species of bottlenose dolphins have previously been described from the eastern Pacific. The first was collected in Monterey (California) in 1871 by Captain C. H. Scammon and then described in 1873 as *T. gillii* Dall, 1873 based solely on the lower mandible. Its distribution was described as being off the coasts of California and Baja California (Scammon 1874; Townsend 1916; Anthony 1928; Hershkovitz 1963; Huey 1964), with records in the GoC as far north as La Choya (Punta la Cholla; ca. 31º N, 113º W), Sonora, Mexico (Mayer 1950). The second was collected in the offshore waters of the ETP (12° N, 120° W; estimated as less than 2,000 km from the Mexican coast) on 6 December 1906 during the voyage of the Nuuanu and later described as *T. nuuanu* Andrews, 1911 based on its skull. Its distribution was identified as along the Pacific coast of Central America, extending southwards from Panama, with its southernmost record in waters off the Galapagos (Andrews 1911; Mayer 1950). Skulls assigned to *T. nuuanu* were also found in the lower GoC, in Santa Catalina Island (ca. 33º N, 118º W) (Andrews 1911; Townsend 1916; Anthony 1928), with a northerly record at Coronado Island (Isla Coronado; ca. 29º N, 113º W) (Van Gelder 1960). Such records suggest the GoC as an area of possible overlap between the two nominal species *T. gillii* and *T. nuuanu* (Andrews 1911; Mayer 1950; Van Gelder 1960). These nominal species were differentiated from each other and *T. truncatus* based on differences in tooth size, size of the

101 temporal fossae (and its proportion to the overall length of the skull), and width of the vomer
102 posteriorly (Andrews 1911; Mayer 1950; Van Gelder 1960). However, the previous studies
103 were based on small sample sizes ($n < 10$) and showed some degree of overlap between the
104 characters used to distinguish the three species.

105 Later, in an effort to better characterize *Tursiops* in the eastern Pacific (Northern
106 Hemisphere), Walker (1981) suggested that at least three forms of *T. truncatus* with distinct
107 habitat preferences, diets, parasite loads, and morphological traits exist in the region: (1) a
108 southern California and Mexico coastal form, distributed in coastal waters of California and
109 the Pacific side of the Baja California peninsula and throughout the GoC, with a southernmost
110 record possibly around San Blas, Nayarit, along the Mexican mainland (21º30' N)
111 (corresponding to the previously described *T. gillii*); (2) a northern temperate offshore form,
112 mainly distributed in offshore waters off the California coast, with possible southern records
113 offshore off northern Baja California; and (3) an ETP offshore form, distributed in offshore
114 waters off southern Baja California, in the lower GoC, and in offshore waters of the ETP,
115 with a southernmost record possibly in waters around the Galapagos Islands (corresponding
116 to the previously described *T. nuuanu*). Although Walker (1981) recognized the southern
117 California/Mexico coastal form and the ETP offshore form as "at least modally distinct", he
118 avoided any taxonomic proposal, considering it "premature and beyond the scope" of his
119 work. He also proposed that the northern temperate offshore form was more morphologically
120 similar to the ETP offshore form than the southern California/Mexico coastal form, although
121 this suggestion was based on a very limited sample size.

122 Using a larger sample size, Perrin et al. (2011) also investigated differences in skull
123 morphology between the coastal and offshore dolphins found along the California coast (i.e.,
124 southern California/Mexico coastal and northern temperate offshore forms). Their results
125 indicated that the two forms have cranial differences that reflect distinct habitat use and prey

preferences; however, this study did not include specimens from the ETP or other areas in the eastern Pacific outside of California. Adding evidence of genetic differentiation (Segura et al. 2006; Lowther-Thieleking et al. 2015; Segura-García et al. 2018) to differences in feeding ecology (Hanson and Defran 1993; Segura-García et al. 2018) and distribution (Guevara-Aguirre and Gallo-Reynoso 2016; Carretta et al. 2021), the California/Mexico coastal form and northern temperate offshore form are now recognized as separate coastal and offshore ecotypes, respectively, without reference to the nominal species (Perrin et al. 2011; Lowther-Thieleking et al. 2015; Carretta et al. 2021).

The coastal ecotype (i.e., previous southern California/Mexico coastal form) occurs within 1 km of shore from northern California south to the Pacific side of northern Baja California (Defran et al. 2015; Lowther-Thieleking et al. 2015; Carretta et al. 2021). The offshore ecotype (i.e., previous northern temperate offshore form) is found in deeper waters (> 4 km from shore) between California and Washington (Barlow 2003), and may also be occasionally found in northern offshore waters off Canada (Halpin et al. 2018). The southern limit of the offshore ecotype is less well defined but might extend at least along the deeper waters off the Baja California Peninsula (Carretta et al. 2021), and may overlap with ETP offshore bottlenose dolphins (see below).

Coastal and offshore ecotypes are recognized within the GoC where they exhibit a more latitudinal than longitudinal distribution, with some overlap. Coastal dolphins are more commonly found towards the upper GoC, whereas offshore dolphins are found towards the lower GoC (Segura et al. 2006; Segura-García et al. 2018). Although Walker (1981) suggested the California/Mexico coastal form was also found throughout the GoC, recent findings (Segura-García et al. 2018) have identified genetic and ecological differences between coastal bottlenose dolphins on either side of the Baja Peninsula, suggesting that the GoC coastal dolphins are different from the coastal dolphins found in California waters and

151 the Pacific side of the Baja California. Lowther-Thieleking et al. (2015) also suggested (based
152 on mitochondrial DNA) that California (CA) coastal and GoC coastal dolphins are genetically
153 differentiated, while the CA offshore ecotype was more genetically similar to both GoC
154 ecotypes than to the CA coastal dolphins.

155 Little is known about the ETP offshore bottlenose dolphin form and their degree of
156 differentiation from the offshore ecotype found along the Baja California Peninsula. The ETP
157 dolphins are described as occurring in deeper waters off southern Baja California, the Pacific
158 coast of Central America and Colombia and Ecuador, out to approximately 120º W (Walker
159 1981; Hamilton et al. 2009). Their northern range limit is suggested to be between Magdalena
160 Bay (ca. 24º N) on the Pacific side of Baja California, and Santa Catalina Island, Mexico (ca.
161 25º N) within the Gulf of California, whereas their southern limit might extend to at least the
162 Galapagos Islands, ca. 2º S (Walker 1981).

163 Although previous studies have revealed differentiation between bottlenose dolphins
164 throughout the eastern Pacific, there is still a need to understand the level of divergence
165 between the bottlenose dolphins in the area. In this study, we re-examine morphological
166 differentiation among the three previously recognized forms of bottlenose dolphins in the
167 eastern Pacific (Northern Hemisphere) with an attempt to clarify their taxonomic status and
168 distribution.

169

170 **Material and Methods**

171 **Samples**

172 We examined 135 physically mature skulls of common bottlenose dolphins (*Tursiops*
173 *truncatus*) collected in the Pacific Ocean, which we divided into five geographic groups based
174 on the region from which the skulls were originally obtained (Fig. 1; Online Resource 1). This

175 data set comprised 75 skulls collected along the west coast of California (CA)[1] (ca. 40º N to
176 32º N), four from the Gulf of California (GoC), including two from the upper GoC (ca. 31º N)
177 and two from the lower GoC (ca. 27º N; Santa Catalina Island), 30 from the eastern tropical
178 Pacific (ETP), which included 28 from the tuna purse seine fishery collected between Mexico
179 and Panama (ca. 7º N to 19º N) more than 200 km from shore, one from the waters around
180 San Juanito Island (ca. 21º N; approximately 100 km from shore) and one sample from the
181 Galapagos archipelago (approximately 1,000 km from the continental shore of Ecuador), four
182 samples from the eastern South Pacific (ESP) south of 10º S, and 19 skulls collected from a
183 drive fishery off Taiji, Japan in the western North Pacific (WNP). Three skulls were
184 unassignable to a geographic group as two had original collection location information listed
185 only as “Baja California, Mexico”, and the other as “Mexico”.
186 All the skulls from the CA group were previously used in a study by Perrin et al.
187 (2011) for an examination of morphological differentiation between offshore and coastal
188 ecotypes from California waters. A total of 61 of the CA samples had also been sequenced for
189 the mitochondrial DNA (mtDNA) control region and the ecotype defined whenever possible
190 according to the mtDNA haplotype for 47 of these samples (offshore: n = 14; coastal: n = 33)
191 following data in Perrin et al. (2011) (see also Online Resource 1 in the current study). Our
192 data set also includes 30 skulls previously used in Walker (1981): 17 classified as "Eastern
193 Tropical Pacific offshore form" (15 ETP skulls and two lower GoC skulls); one as "northern
194 temperate offshore form" (a CA offshore skull); and 12 as "southern California and Mexico
195 coastal form" (ten CA coastal skulls and two upper GoC skulls) (Online Resource 1).
196 Included in the data set above are the two eastern Pacific type specimens: the holotype
197 of *Tursiops nuuanu* Andrews, 1911 (deposited in the American Museum of Natural History

[1] A majority of the CA samples (n = 61) were strandings, 11 were captured in offshore waters (around Santa Catalina and St. Miguel Islands) and three captured in coastal waters (around San Diego).

under the accession number AMNH 35045), for which the skull was available, and the holotype of *T. gillii* Dall, 1873 (deposited in the Smithsonian National Museum of Natural History under the accession number USNM A13022), which comprises only the lower jaw. Finally, we also measured the skull of the holotype of *T. truncatus* (Montagu, 1821) collected in the River Dart in southwestern England (deposited in the Natural History Museum, London under the accession number NHMUK 353a), and also used the cranial measurements from Perrin et al. (2007) for the holotype of *T. aduncus* (Ehrenberg, 1832) collected in the Dahlak Archipelago of Ethiopia in the Red Sea (deposited in the Zoologisches Museum Berlin under the accession number ZMB66400). Thus, a total of 137 specimens were used in this study (Online Resource 1).

Skull Measurements

For each skull, where available, a total of 20 measurements (Online Resource 2) were taken with dial and digital calipers and anthropometers by APBC, FIA, and WFP as in Perrin (1975a). Measurements made by FIA and WFP were calibrated to those made by APBC with linear regressions fit to sets of skulls measured by both pairs of authors (n = 6 for FIA and APBC; n = 23 for WFP and APBC). We only measured skulls defined as physically mature following the definition in Perrin and Heyning (1993). For the holotype *T. gillii*, only LORO, RAML, and RAMH were collected since the specimen is only represented by the lower mandible. Each measurement was also paired with each of the other 19 measurements, resulting in 190 unique pairs of measurements. The ratio was then computed for all 190 unique combinations and used in the analyses of sexual dimorphism and geographical variation described below. All analyses and summaries described in the methods were conducted using R version 4.1.0 (R Core Team 2021).

223 **Sexual Dimorphism**

224 We investigated the presence of sexual dimorphism in order to determine whether
225 analyses of geographical variation would be influenced by differences between the sexes. We
226 conducted Kolmogorov-Smirnov (KS) tests of differentiation between sexes for each of the
227 original measurements. Tests were conducted using the R *ks.test* function for all samples and
228 within each group that contained more than 10 samples (CA, ETP, and WNP). We also
229 created Random Forest models using the *randomForest* package (Liaw and Wiener 2002) to
230 quantify the degree to which sex could be classified as a function of the original
231 measurements and the measurement ratios. We first created one model using data from all
232 skulls with sex information available, followed by a separate model for each group as in the
233 KS tests. Within the CA group, we also evaluated sexual dimorphism within the coastal and
234 offshore ecotypes separately. CA samples were classified to an ecotype based on the findings
235 of Perrin et al. (2011) using the mtDNA data (coastal: 33; offshore: 14; unassigned: 28). In
236 order to create balanced models, the same number of samples was randomly selected for each
237 sex without replacement for each tree in the Random Forest as described in Archer et al.
238 (2017). For each model, 10,000 trees were run and the number of measurements sampled at
239 each node (the *mtry* parameter) was left at the *randomForest* default of the square root of the
240 total number of measurements.

241

242 **Geographical Variation**

243 The morphological distinctiveness of each geographic group was evaluated with
244 another set of Random Forest models. As with the models for sexual dimorphism described
245 above, these models classified groups as a function of the original measurements and the
246 measurement ratios. Only the three groups with a sufficient number of samples for statistical
247 power were examined (CA, ETP, WNP). Random Forest models were constructed with the

CA coastal and offshore ecotypes considered together as a single CA group as well as separate groups. Additionally, a Random Forest model was also conducted to classify just the CA coastal and offshore ecotypes alone. All of these models were also balanced as described above. A total of 10,000 trees were run for each model. The relative importance of measurements and measurement ratios to the classification accuracy of a model was assessed using the Mean Decrease in Accuracy metric (Liaw and Wiener 2002). We identified measurements that were significantly more important than a randomly distributed measurement with the permutation test implemented in the *rfPermute* R package (Archer 2020). A total of 1,000 permutation replicates were run for each Random Forest model to create a null distribution of importance scores from which p-values were estimated. These models were also used to assign skulls that could not be stratified due to low sample sizes (GoC and ESP) as well as the three skulls that had ambiguous collection localities.

Unsupervised Clustering

We also identified distinct clusters of skulls in the Pacific Ocean using the unsupervised Density Clustering algorithm of Rodrigues and Laio (2014) as implemented in the *densityClust* R package (Pedersen et al. 2017). This method first identifies peaks of clusters by computing the local density (ρ) of each individual and its distance (δ) to the nearest individual of higher density. Other individuals are then assigned to the cluster belonging to the nearest peak of higher density (Rodrigues and Laio 2014). The input for Density Clustering is a matrix of pairwise distances between samples based on the original measurements. In order to avoid having this distance overly influenced by differences in the absolute values measurements, all of the original measurements were first scaled and centered such that they each had a mean of zero and standard deviation of one. A matrix of pairwise Euclidean distances among skulls was then computed from these scaled measurements.

Ordination of the same scaled original skull measurements was also performed with a Principal Component Analysis (PCA) as implemented in the R *prcomp* function, and the distributions of clusters identified by Density Clustering and *a priori* defined groups were visualized along the first two components.

Holotype Assignment

Random Forest classification models were also created for each of the four holotype specimens to evaluate the taxonomic affiliations of the CA, ETP, and WNP groups. In each model, only original measurements present in the holotype specimen under consideration were used (Online Resource 3) and all samples that did not have missing data for these measurements were used to train the model. The type specimens themselves were excluded from the training data for the model. Parameters for these Random Forest models followed descriptions above. The models were then used to compute the assignment probabilities of each holotype specimen to each of the three groups.

Total Body Length

We evaluated differences in the total external body length (TL) between male and female samples from the CA, ETP, and WNP groups. Of the four holotypes, only *T. nuuanu* had a TL available (7 ¼ feet – estimated as 221 cm) and it was included in this analysis. A non-parametric Kolmogorov-Smirnov test (KS-test) using the *ks.test* function was performed to evaluate whether body length varied among the three groups (CA, ETP, WNP). Distributions of body length (mean and standard deviation) were summarized for each group by sex.

Results

298 **Measurement Summaries**

299 A total of 121 skulls, including the holotypes of *Tursiops nuuanu* and *T. aduncus*, had
300 data available for all of the 20 original measurements. The three mandibular measurements
301 (LORO, RAML, RAMH) and the distance from the tip of the rostrum to the internal nares
302 (TIPP) were most frequently missing across skulls (varying from 7 to 12 individuals).
303 Therefore, these four measurements were excluded from the majority of the multivariate
304 analyses requiring complete data sets (with exception of the holotype assignment analyses –
305 see below). Furthermore, six individuals were missing data for at least one of the other 16
306 cranial measurements (Online Resource 4): two samples in the CA group (one missing
307 measurement each), two samples in the GoC group – collected at Santa Catalina Island, Baja
308 California (1-2 missing measurements), and the holotypes *T. gillii* and *T. truncatus*. For the
309 holotype *T. gillii*, only the three mandibular measurements were obtained (i.e., the holotype is
310 only the lower jaw). The holotype *T. truncatus* presented four missing measurements: the
311 three mandibular measurements (LORO, RAML, RAMH) and EXTN (a measurement
312 available for the majority of the samples). Therefore, these six specimens were excluded from
313 all multivariate analyses based on the 16 cranial measurements available for the majority of
314 the data set (i.e., with the exclusion of LORO, RAML, RAMH, and TIPP), resulting in a total
315 of 131 skulls with complete data for the 16 measurements. Summaries of measurements for
316 each group are provided in Online Resource 4.

317

318 **Sexual Dimorphism**

319 A total of 115 samples with complete data for the 16 measurements had sex
320 information available (females: 47; males: 68). Of these, two males belonged to GoC and ESP
321 groups, respectively, and the other 113 belonged to one of the three main groups (i.e., WNP,
322 CA, and ETP): 65 from CA (females: 27; males: 38), 29 from the ETP (females: 13; males:

16), and 19 from WNP (females: 7; males: 12). Within the CA group, 28 coastal (females: 13; males: 15) and 14 offshore (females: 5; males: 9) samples had sex information available and complete data for the 16 original measurements. No strong evidence of sexual dimorphism was observed when evaluating the differences in skull morphology based on sex using the full data set, within each group, or within each CA ecotype. A KS-test indicated that most width measurements (ROSH, PREO, POST, ZYGO, PMXM, FOSH, ANTO) were significantly ($p \leq 0.05$) greater for males than females, by an average of 6 mm in the CA group. Only ANTO was significantly larger for males in the ETP samples, and there were no differences in the WNP. In Random Forest models, the sex of fewer than 70% of the specimens could be correctly classified (Table 1). Thus, given the low absolute difference in measurements and lack of significant diagnosability, in further analyses of geographical variation, skulls were not separated by sex in order to maximize sample sizes of groups.

Geographical Variation

The Random Forest model based on skulls from CA (coastal and offshore ecotypes combined), ETP, and WNP correctly classified 103 of the 121 (85%) skulls from these three groups (Table 2). All of the ETP skulls (100%) were correctly classified, while only 57 of the 72 (79%) CA and 16 of the 19 (84%) WNP skulls were correctly classified. When the CA skulls were separated into coastal (n = 32; one coastal sample was excluded due to missing data) and offshore (n = 14) ecotypes in a separate model, 29 (96.7%) of the ETP skulls were correctly classified and one ETP skull was misclassified as CA offshore (Table 2). CA coastal and offshore had 81% and 43% of their skulls correctly classified, respectively. Only 15 of the 19 (79%) skulls from WNP were correctly classified in this model. In the model based only on the CA ecotypes, 84.4% of the coastal and 78.6% of the offshore skulls were correctly classified.

348 In the two Random Forest models classifying CA, ETP, and WNP skulls (with CA
349 ecotypes both combined and separated), there were eight measurements that best explained
350 the differentiation among groups based on Mean Decrease in Accuracy importance scores
351 (significant scores higher than 25.0; $p \leq 0.01$). The measurements reflected differences in the
352 overall length (CBLN) and width (ZYGO, POST, and PREO) of the skull, as well as in the
353 width of the rostrum (ROSW and ROSH), premaxillaries (PMXM) and internal nares (INTN)
354 (Online Resource 5).
355 Skulls of specimens collected in the ETP were significantly and diagnosably smaller
356 than those in other regions. For example, when considering overall length and width of the
357 skull, ETP skulls were relatively shorter (CBLN: 423-512 mm) and narrower (ZYGO: 225-
358 257 mm) than those from CA (CBLN: 470-572 mm; ZYGO: 239-304 mm) and WNP (CBLN:
359 496-578 mm; ZYGO: 263-301 mm) groups (Fig. 2). We also detected a narrower rostrum,
360 premaxillaries, and internal nares in the ETP skulls. Lastly, the Random Forest models
361 indicated that the skulls from the upper GoC (n = 2) and the ESP (n = 4) were more likely to
362 be classified to CA or WNP skulls than to the ETP (Table 3). Of the three unassigned skulls,
363 only one was more likely to be classified to the ETP (Table 3).
364
365 **Clustering and PCA**
366 We used all specimens collected in the Pacific Ocean (n = 130) with complete data for
367 the 16 cranial measurements in the Density Clustering analysis. The *densityClust* parameters
368 were set to $\delta = 3.032$ and $\rho = 8.151$ after evaluation of the decision graph, and two clusters
369 were identified (Fig. 3). As seen in Table 4, Cluster 1 (n = 98) was composed of a majority of
370 the CA skulls (n = 69), all of the skulls from the WNP (n = 19) and the ESP (n = 4), two
371 skulls from upper GoC, two samples collected in the ETP, and two unassigned samples.
372 Cluster 2 (n = 32) was composed of most of the ETP skulls (n = 28; and included the holotype

373 *T. nuuanu*), three skulls collected in CA waters (one CA coastal and two CA offshore), and
374 one unassigned skull. Thus, 96.9% of the specimens knowingly collected outside the ETP
375 composed Cluster 1, whereas 93.3% of the specimens collected in the ETP were in Cluster 2.
376 It is noteworthy that the three CA skulls assigned to Cluster 2 were among the smallest
377 samples in the CA data set based on overall length (CBLN: 479-491 mm) and width (ZYGO:
378 240-247 mm) of the skull, whereas the two ETP samples assigned to Cluster 1 were among
379 the biggest samples in the ETP data set (CBLN: 495-511.5 mm; ZYGO: 242-257 mm)
380 (Online Resource 4).

381 The first two components in the PCA accounted for 75.4% of the variance in the
382 measurements. The first component, which accounted for 65.2% of the variance, had negative
383 loadings on all measurements, indicating that it was related to variability in overall skull size.
384 The second component (10.2% of the variance) was mainly defined by measurements along
385 the length of the skull (CBLN, ROST, UPRO, and TIPN) and those describing the width of
386 the external nares (EXTN) and the shape of the temporal fossa (FOSH and FOSL) (Online
387 Resource 6). All of the Cluster 2 skulls had more positive values on the first component,
388 while the Cluster 1 skulls tended to be more negative on this component (Fig. 4). No visible
389 differences were detected between Cluster 1 and Cluster 2 on the second component,
390 suggesting that differences in size are the primary driver of the differentiation between the
391 clusters, with Cluster 1 skulls being larger than Cluster 2.

392

393 **Holotype Assignment**

394 Random Forest models were conducted using all ETP, CA, and WNP samples that had
395 complete sets of the measurements present in each of the four holotype skulls. The *T. nuuanu*
396 and *T. aduncus* holotypes had all 20 measurements so we were able to classify them in a
397 single model, while the other two specimens (*T. truncatus* and *T. gillii*) were only classifiable

based on models built with the measurements each had present. The holotypes of *T. truncatus* (16 measurements) and *T. gillii* (three mandibular measurements) were both assigned to the CA group with 73% and 88% probability, respectively. The *T. nuuanu* holotype was assigned to the ETP group with 80% probability. Of the three groups available (i.e., ETP, CA, WNP), *T. aduncus* was assigned to ETP with 69% probability. None of the holotypes strongly assigned to WNP, although *T. truncatus* was more similar to skulls in this group than the other three holotypes (Table 5).

Total Body Length

Total external body length (TL) was available for all 63 samples from CA (27 females, 34 males, 2 unknown sex), 28 from the ETP (13 females, 14 males, 1 unknown sex), and 19 from WNP (7 females, 12 males). The KS-tests between groups indicated that each had significantly different ($p \leq 0.001$) TL distributions. Samples from the ETP had the smallest total body length (mean ♀: 243.85 cm; mean ♂: 255.86 cm), followed by CA (mean ♀: 274.63 cm; mean ♂: 297.94 cm) and WNP (mean ♀: 297.86 cm; mean ♂: 305.42 cm) (Fig. 5). It is noteworthy that for the CA group, both coastal and offshore samples were grouped together, which might be contributing to the large range in size for this group in Fig. 5. There is also indication of sexual dimorphism within each group for TL, with males tending to be larger than females in all groups, by approximately 8-23 cm. Total length for the holotype *T. nuuanu* was 221 cm, being slightly smaller than the minimum size observed in the ETP group and suggesting that it is also more similar to the ETP samples for the total external body length.

Discussion

422 The results of our analyses demonstrate significant morphological differentiation
423 between bottlenose dolphins collected from various regions of the Pacific Ocean, with skulls
424 separating into two distinct clusters. The unsupervised clustering analysis placed 93.3% of the
425 ETP samples into a single cluster (Cluster 2), whereas 96.9% of the samples outside the ETP
426 (i.e., CA, ESP, GoC, and WNP) formed the other cluster (Cluster 1). The two samples from
427 the upper GoC that were assigned to the same cluster as the CA samples showed congruence
428 with previous findings: Walker (1981) classified these two samples as belonging to the
429 southern California/Mexico coastal form. Due to missing data, we were unable to evaluate if
430 the other two GoC samples, collected from Santa Catalina Island (lower GoC), were more
431 similar to the ETP group, as previously suggested by Andrews (1911) and Walker (1981).
432 Although the two CA ecotypes (offshore and coastal) were not diagnosably distinct
433 from each other, we observed slight cranial differences between them that together with the
434 analyses reported in Perrin et al. (2011) support the finding that the CA ecotypes are distinct
435 populations, possibly in an early stage of divergence, and should continue to be managed
436 separately to preserve local ecological adaptations. However, in our analysis, the degree of
437 differentiation between CA ecotypes was low in the context of an analysis of geographical
438 variation including skulls from WNP and the ETP. Thus, for the purposes of this analysis, we
439 consider these ecotypes to be a single group. Additionally, while Perrin et al. (2011) also
440 reported the presence of sexual dimorphism for some cranial variables in the CA coastal
441 ecotype, we did not detect sexual dimorphism in any of the three main groups examined to a
442 degree that is likely to bias our analysis of geographical variation.
443 ETP offshore bottlenose dolphins were found to be diagnosably distinct when
444 compared to dolphins from CA and the WNP, with the ETP samples being significantly
445 smaller than the other groups based on both skull and body size. In fact, with a CBLN ranging
446 from 423-512 mm and an observed maximum total body length of 287 cm, the ETP offshore

447 bottlenose dolphin is the smallest common bottlenose dolphin reported from the Atlantic and
448 Pacific coasts of the Americas, and of similar size range to Tamanend's bottlenose dolphin (*T.*
449 *erebennus*), a small coastal species described for the western North Atlantic (see Table 6 in
450 Costa et al. 2022).

451 In a variety of locations, morphological differentiation between parapatric coastal and
452 offshore dolphin ecotypes has been identified, for example long-beaked and short-beaked
453 common dolphins off California (Heyning and Perrin 1994), common bottlenose and
454 Lahille's bottlenose dolphins in the western South Atlantic (Costa et al. 2016), and common
455 and Tamanend's bottlenose dolphins in the western North Atlantic (Costa et al. 2022). In
456 these cases, the morphological differences in the skull have been primarily attributed to
457 differences in prey preference (Heyning and Perrin 1994; Costa et al. 2016, 2022). However,
458 the ETP offshore bottlenose dolphins, the CA offshore and WNP dolphins are all categorized
459 as offshore dolphins: the majority of the ETP dolphin samples were obtained through
460 incidental catch in oceanic waters, and, as previously reported by Walker (1981), the
461 bottlenose dolphins of this area seem to feed primarily on squids and small epipelagic and
462 mesopelagic fishes, differing from the feeding habits of the CA coastal ecotype, which mainly
463 feeds on nearshore fishes such as croakers (Sciaenidae) and surfperches (Embiotocidae)
464 (Walker 1981; Hanson and Defran 1993). Although no stomach contents have been examined
465 for the CA offshore ecotype to date, Perrin et al. (2011) suggested its diet might parallel the
466 ETP dolphins due to the similarity in habitat preference (i.e., oceanic waters). So why do the
467 ETP bottlenose dolphins differ morphologically from the other offshore bottlenose dolphins
468 in the eastern North Pacific? The answer may lie in the unique physical oceanographic

469 characteristics of the eastern tropical Pacific, which appear to have influenced the divergence
470 of several delphinids in the region (e.g., Au and Perryman 1985; Reilly 1990).

471 Comparable to the results obtained in our study of *Tursiops* skulls, significant
472 differences in the overall length and width of skulls were observed in two *Stenella* species in
473 the ETP – the spinner dolphin *S. longirostris* and the pantropical spotted dolphin, *S.*
474 *attenuata*. The differences in these characteristics, along with external morphology, and
475 differences in habitat, were considered important enough to distinguish spinner and
476 pantropical spotted dolphin subspecies (Perrin 1972a, 1972b, 1975a, 1975b, 1990). More
477 specifically, the offshore pantropical spotted subspecies (*S. a. attenuata*) exhibits both a
478 shorter and narrower skull than the coastal subspecies (*S. a. graffmani*) (Perrin 1975a), and
479 the eastern spinner dolphin subspecies (*S. l. orientalis*) found in ETP offshore waters has a
480 shorter and also narrower skull when compared to the large coastal spinner dolphin (*S. l.*
481 *centroamericana*), as well as a smaller skull than the globally distributed nominate subspecies
482 (Perrin 1990). Like the bottlenose dolphins of the ETP group, the two offshore subspecies (*S.*
483 *a. attenuata* and *S. l. orientalis*) found in the ETP were also considered the smaller form.

484 These *Stenella* subspecies are distributed in the ETP in a region of high productivity,
485 including the Costa Rica Dome, a biodiversity hotspot, influenced by warm and highly
486 stratified surface waters, with a shallow thermocline and oxygen minimum layer (Fiedler et
487 al. 2017). The distribution of the ETP offshore bottlenose dolphin overlaps at least in part
488 with this highly productive region of the ETP, suggesting the factors influencing divergence
489 in the *Stenella* species may also be driving evolutionary divergence in *Tursiops* in the ETP. It
490 has been suggested that adaptation to different thermal habitats can promote ecological
491 speciation, where the differentially adapted populations usually exhibit a parapatric

492 distribution along the thermal gradient with reproductive isolation sometimes evolving as a
493 result of this divergent adaptation (Keller and Seehausen 2012). While bottlenose dolphins in
494 the eastern North and South Pacific are under the influence of the cold California and Peru
495 Currents, respectively, ETP offshore bottlenose dolphins inhabit much warmer temperature
496 regimes (Perrin et al. 1976; Findler et al. 2017). Furthermore, these warmer waters may also
497 explain why ETP offshore bottlenose dolphins are smaller than their colder water
498 counterparts, following predictions of Bergmann's rule (Meiri and Dayan 2003).

499 Geographic varieties within species with sufficient diagnostic distinctness can be
500 considered different subspecies (see Winker 2010; Archer et al. 2017; Taylor et al. 2017). We
501 observed a small classification error rate (less than 5%) in the group assignment for the ETP
502 samples in all Random Forest models. The morphological differentiation observed suggests a
503 low level of gene flow between the ETP offshore bottlenose dolphins and the other groups,
504 indicating that they are likely to be on independent evolutionary trajectories. The ETP group
505 was morphologically similar to the holotype of *T. nuuanu*, a species previously described
506 from ETP waters. Although we also observed that *T. aduncus* was assigned to the ETP with
507 almost 69% probability, this is likely due to similarities in size based on cranial measurements
508 between both taxonomic groups. Jedensjö et al. (2020), who also examined the holotype *T.*
509 *aduncus*, has shown that the skulls of *T. aduncus* are overall smaller, with a longer and
510 narrower rostrum than *T. truncatus*. Furthermore, our ETP samples do not exhibit the
511 morphological characteristics that distinguish *T. aduncus* from *T. truncatus* (e.g., premaxillary
512 convexity from lateral view, premaxillary 'pinch' at approximately 1/3 rostral length from
513 dorsal view; see Wang et al. 2000), being therefore more similar to *T. truncatus* in this sense,
514 thereby ruling out the possibility that the ETP dolphins belong to *T. aduncus*.

In contrast, the holotype assignment indicated that the WNP and CA groups were more similar to the *Tursiops truncatus* holotype. A few of the WNP samples of this study (n = 4) were also used in the worldwide morphological analyses performed in Costa et al. (2022) showing that they cluster with other worldwide distributed *T. truncatus* samples, and separately from the ETP samples. Further studies with larger sample sizes are needed to better investigate the relationship of these WNP samples with other *T. truncatus* samples collected worldwide. The CA samples were highly assigned to the nominal species *T. gillii* based on the three mandibular measurements but our results did not detect significant differences between the CA bottlenose dolphins and the common bottlenose dolphins collected outside the ETP when considering the overall skull. True (1889) had suggested that *gillii*-type skulls were similar to *truncatus*-type skulls based on shape and size, with the main difference between the two based on the size of the mandibular condyles and the position of the optic canal (True 1889; p. 160). Taken together, our morphological findings, therefore, agree with the description of *T. gillii* as a junior synonym of the common bottlenose dolphin, *T. truncatus*. In addition, as suggested by Walker (1981), previous skulls classified as *gillii*-type specimens might in fact represent the coastal common bottlenose dolphins of California and Baja California.

Based on these findings and considering that we are limited to a single line of evidence (i.e., cranial morphology), we recognize the offshore bottlenose dolphins in the ETP as a distinct subspecies of common bottlenose dolphins: *Tursiops truncatus nuuanu*, the Eastern Tropical Pacific bottlenose dolphin. Further studies examining its distribution and genetic differentiation are necessary to better establish the subspecies range and level of evolutionary divergence from the bottlenose dolphins found elsewhere, as well as its

conservation status. In particular, the full distribution of the ETP bottlenose dolphins remains unresolved. It is possible that the northern limit of the ETP offshore dolphins overlaps with the southern limit of the CA offshore ecotype. Although the southern limit of the CA offshore ecotype is not well defined outside the U.S. waters, it appears to be continuously distributed through the Pacific coast of Baja California (Carretta et al. 2021). For the suggested southern limit of the ETP offshore bottlenose dolphins (i.e., Galapagos), our single sample from the area was also classified as an ETP dolphin in our analyses. Sightings of bottlenose dolphins also continue south of the ETP, into the eastern South Pacific (ESP), where further coastal and offshore ecotypes have been recognized (Van Waerebeek et al. 1990, 2017). There are also suggestions that bottlenose dolphins in offshore waters off Colombia and Ecuador belong to the same population as the ETP offshore bottlenose dolphins rather than to bottlenose dolphins found closer to the coast or farther south (Van Waerebeek et al. 2017). However, although skulls (examined in the current study) from the eastern South Pacific (mainly from Peru and Chile) and those from upper Gulf of California were considered more similar to the CA and WNP samples, our ability to infer the identity of animals from these areas immediately to the north and south of the ETP range are based on a small sample size. Further, because our data set did not include samples from Hawaii, from east of approximately 90° W in the Costa Rica Dome, or from coastal waters in Central America, we cannot comprehensively define the distribution of this morphological form. Further work, which should include the use of genetic markers, is necessary to understand the distribution and hence to understand the ecological factors that may be driving the morphological divergence of this ETP offshore form.

Conclusion

In this study, we examined morphological differentiation among three previously recognized forms of bottlenose dolphins in the eastern North and tropical Pacific Oceans with the aim of clarifying their taxonomy and better defining their geographic distributions. We also compared the bottlenose dolphins of the eastern Pacific to bottlenose dolphins collected in western North Pacific waters offshore of Japan. Our results indicated significant morphological differentiation among bottlenose dolphins in the Pacific Ocean, with skulls separating into two distinct clusters. The ETP offshore bottlenose dolphin cluster comprised skulls that were smaller and more diagnosable than those from other groups. We did not detect diagnostic differences between the CA ecotypes; however, the observed differences suggest they are different populations, possibly in an early stage of divergence. We suggest that the distinct environmental conditions in the ETP (i.e., distinct oxygen, salinity and temperature conditions), associated with possible differences in feeding ecology, may be influencing the evolutionary differentiation of the bottlenose dolphins in the eastern Pacific. Given our morphological findings, we recognize the offshore bottlenose dolphins in the eastern tropical Pacific as a distinct subspecies: *Tursiops truncatus nuuanu*.

Systematics

Order Artiodactyla Owen, 1848

Cetacea Brisson, 1762

Odontoceti Flower, 1867

Family Delphinidae Gray, 1821

Subfamily Delphininae LeDuc 1997

Genus *Tursiops* Gervais, 1855

Tursiops truncatus (Montagu, 1821)

586 *Tursiops truncatus nuuanu* Andrews, 1911

587

588 **Type Specimen and Locality**

589 The name *Tursiops nuuanu* was originally used to describe the holotype of a
590 bottlenose dolphin collected by John T. Nichols from the eastern tropical Pacific on 6
591 December 1906 at approximately 12° N, 120º W (Nichols 1908). The total body length was 7
592 ¼ feet (approximately 221 cm) and sex unknown. The skull from this specimen is deposited
593 in the American Museum of Natural History as AMNH 35045, and was named and described
594 by Andrews (1911).

595

596 **Etymology**

597 The species name was derived from the name of the ship from which J. T. Nichols
598 collected the first specimen from the eastern tropical Pacific (Andrews 1911), which in turn is
599 from the Hawaiian word, "nu′uanu", meaning "cliff". The species was recognized and later
600 was considered as a junior synonym of the common bottlenose dolphin, *T. truncatus*. Walker
601 (1981) used the term Eastern Tropical Pacific offshore form to refer to the individuals of this
602 group. We recommend the common name, Eastern Tropical Pacific bottlenose dolphin for the
603 subspecies *Tursiops truncatus nuuanu* based on its restricted distribution to this region (see
604 *Distribution* below). The subspecies name was registered in ZooBank under the LSID:
605 urn:lsid:zoobank.org:pub:B9715F20-CEBF-419D-A456-3D9A9D8E22DE.

606

607 **Diagnosis**

608 The subspecies *Tursiops truncatus nuuanu* differs from the nominate subspecies *T. t.*
609 *truncatus* in California waters by skull morphometrics, where the former presents a smaller
610 skull, with relatively short and narrower rostrum. Further differentiation has been described

based on skull morphology (Andrews 1911; Walker 1981; this study), body length (this study), and distribution (Walker 1981; this study). There is also some indication of differentiation based on sexual maturity (Walker 1981). However, more studies are needed to investigate further differentiation based on other lines of evidence, such as genetic analyses.

This is a small subspecies of *Tursiops truncatus*, with total body length reaching at least 287 cm (mean ♀: 243.85 cm; mean ♂: 255.86 cm). The condylobasal length in physically mature skulls ranges from 423 mm to 512 mm (based on our data set). The physically mature skulls have a relatively short (based on our data set: 228 mm to 283 mm) and narrow (based on our data set: 68 mm to 83 mm) rostrum, and slightly narrow internal nares (based on our data set: 67 mm to 79 mm). No sexual dimorphism was detected based on the cranial morphology, but it is possible that males are larger than females based on total external body length.

The coloration of the holotype of *T. nuuanu* was described as "slaty black, grayer from throat to vent" (Nichols 1908) and its total body length was approximately 221 cm (originally described as 7 ¼ feet). A very brief description of its stomach contents was also provided: "mostly large shrimp-like animals; also a few fish, and perhaps other food matter, and many parasitic worms" (Nichols 1908).

Distribution

Tursiops truncatus nuuanu is restricted to the eastern tropical Pacific (ETP), with the northern limit around 25° N, southern limit around 2° S, and western limit at least at 120° W (based on the holotype location), and likely a more offshore habitat preference, i.e., preference for the deeper waters of the ETP (Walker 1981). Andrews (1911) suggested that two specimens stranded in Santa Catalina Island (25º40' N) in the lower Gulf of California (AMNH 31830 and AMNH 31831) were similar to the *nuuanu*-type based on the shape of the

636 vomer and size of the temporal fossa. However, in this study we were unable to confirm this
637 due to the extent of missing data from these skulls (i.e., several cranial structures were broken
638 and the mandibles were missing). Specimens from the upper Gulf of California and north of
639 25º N in the coastal and offshore waters of Baja California (Pacific side) and southern
640 California were considered more morphologically similar to the *truncatus*-type; however, our
641 inferences for the GoC were based on a small sample size. The suggested southern limit for
642 this subspecies encompasses the Galapagos area (Walker 1981) and might also include
643 offshore waters off Colombia and Ecuador (Van Waerebeek et al. 2017). This area is
644 influenced by both warmer (Panama Current) and colder (Humboldt/Peru Current) water
645 currents. The single skull from this region used in our study was considered more similar to
646 the *nuuanu*-type (USNM 258642), differing from other samples from the eastern South
647 Pacific (from farther south than the subspecies' southern limit) (Fig. 6). However, these
648 inferences were also based on a small sample size. Therefore, more samples from these
649 northern and southern locations, as well as samples from Hawaii and those east of
650 approximately 90° W in the Costa Rica Dome, and inhabiting coastal waters in the Pacific
651 Central America need to be included in future studies to better define the distribution of this
652 subspecies.
653
654 **Remarks**
655 Hershkovitz (1963) was the first to treat *Tursiops nuuanu* as a synonym of *T.*
656 *truncatus*, but the confusion of species recognition within *Tursiops* can be seen when
657 Hershkovitz (1966) reversed himself and made *T. nuuanu* a synonym of *Tursiops truncatus*
658 *aduncus.*
659
660 **Data Availability**

661 The dataset generated and analyzed during the current study is available in the Figshare
662 repository, https://doi.org/10.6084/m9.figshare.20769460
663
664 **References**

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846
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851 the Marine Mammal Protection Act of 1972. Additionally, he is considered the father of
852 modern marine mammal taxonomy due to his pioneering work on both small cetaceans and
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872 Department of Commerce.
873

874 **Supplementary Information**

875 **Online Resource 1:** Collection information for specimens measured.
876 **Online Resource 2:** Skull measurements taken (reprinted from Perrin 1975a).
877 **Online Resource 3:** Skull measurements for each *Tursiops* holotype used in this study.
878 **Online Resource 4:** Summaries of measurements for each group.
879 **Online Resource 5:** Ten most important variables explaining the differentiation between the
880 groups based on mean decrease in accuracy scores.

881 **Online Resource 6:** Loadings on first two principal components (PC1 and PC2) for 16 skull
882 measurements.

883 **Figure Legends**

884 **Fig. 1** Map of collection locations for bottlenose dolphin (*Tursiops* spp.) specimens measured.
885 Upper map: worldwide samples. Bottom map: eastern Pacific samples. aduncus: holotype *T.*
886 *aduncus*; CA: California; ESP: eastern South Pacific; ETP: eastern tropical Pacific; GoC:
887 Gulf of California; truncatus: holotype *T. truncatus*; WNP: western North Pacific. Scale bar
888 equals 3,000 km. Maps were created with R packages *ggplot2* (Wickham 2016) and
889 *rnaturalearth* (South 2017)

890 **Fig. 2** Frequency distribution of condylobasal length (CBLN) and zygomatic width (ZYGO)
891 in each of the three main groups. Points are randomly distributed about the centerline for each
892 group. CA: California; ETP: eastern tropical Pacific; WNP: western North Pacific. Figure was
893 created with R package *ggplot2*

894 **Fig. 3** Density clustering plots. Upper left plot shows the decision graph, a plot of δ
895 (minimum distances to observations of higher density) as a function of ρ (local density values
896 of each individual) where we can identify peaks of clusters. Upper right plot shows the
897 gamma (γ) graph depicting the decrease of γ (δ*ρ) across samples. Bottom plot shows the
898 multi-dimensional scaling (MDS) scatterplot based on the distance matrix of the
899 densityCluster object, with individual samples (represented by circles) colored according to
900 their clustering affiliation defined by the analysis. Figure was created with R package
901 *densityClust*

902 **Fig. 4** Distribution of skulls on first and second principal components. Point color indicates
903 cluster assignment from Density Clustering, while shape indicates group. CA: California;
904 ESP: eastern South Pacific; ETP: eastern tropical Pacific; GoC: Gulf of California; WNP:
905 western North Pacific. The holotype of *Tursiops nuuanu* is highlighted by the number 1.
906 Figure was created with R package *ggbiplot* (Vu 2011)

907 **Fig. 5** Frequency distribution of total body length (TL) in each of the main three groups.
908 Points are randomly distributed about the centerline for each group. White line shows the
909 standard deviation. White point shows the mean. CA: California; ETP: eastern tropical
910 Pacific; WNP: western North Pacific. Figure was created with R package *ggplot2*

911 **Fig. 6** Suggested distribution of *Tursiops truncatus nuuanu* in the eastern tropical Pacific. The
912 open triangle area represents the distribution area suggested by Walker (1981). The wavy area
913 indicates a potential expanded area of distribution based on the sampling records of the ETP
914 skulls examined in this study and suggestions of ETP offshore dolphins in offshore waters off
915 Colombia and Ecuador following Van Waerebeek et al. (2017). Nevertheless, further data are
916 needed to better clarify the limit ranges of the subspecies' distribution (see main text). Scale
917 bar equals 3,000 km. CA: California; ESP: eastern South Pacific; ETP: eastern tropical
918 Pacific; GoC: Gulf of California

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Tables

Table 1 Confusion matrices from Random Forest models to classify skulls to sex for California (CA), eastern tropical Pacific (ETP), and western North Pacific (WNP) groups. Classifications based on sex for each CA ecotype (coastal and offshore) are also provided. NA: Not Applicable.

Group	Sex	Female	Male	% Correct	Lower 95% CI	Upper 95% CI
All (n = 115)	Female	31	16	66.0%	50.7%	79.1%
	Male	28	40	58.8%	46.2%	70.6%
	Overall	NA	NA	61.7%	52.2%	70.6%
CA (n = 65)	Female	17	10	63.0%	42.4%	80.6%
	Male	14	24	63.2%	46.0%	78.2%
	Overall	NA	NA	63.1%	50.2%	74.7%
ETP (n = 29)	Female	9	4	69.2%	38.6%	90.9%
	Male	6	10	62.5%	35.4%	84.8%
	Overall	NA	NA	65.5%	45.7%	82.1%
WNP (n = 19)	Female	2	5	28.6%	3.7%	71.0%
	Male	8	4	33.3%	9.9%	65.1%
	Overall	NA	NA	31.6%	12.6%	56.6%
CA coastal (n = 28)	Female	10	3	76.9%	46.2%	95.0%
	Male	6	9	60.0%	32.3%	83.7%
	Overall	NA	NA	67.9%	47.6%	84.1%
CA offshore (n = 14)	Female	3	2	60.0%	14.7%	94.7%
	Male	5	4	44.4%	13.7%	78.8%
	Overall	NA	NA	50.0%	23.0%	77.0%

Table 2 Confusion matrix from Random Forest models classifying skulls to geographic groups. CA: California; ETP: eastern tropical Pacific; WNP: western North Pacific; NA: Not Applicable.

Lumping CA ecotypes						
Group	**CA**	**ETP**	**WNP**	**% Correct**	**Lower 95% CI**	**Upper 95% CI**
CA	57	5	10	79.2%	68.0%	87.8%
ETP	0	30	0	100.0%	88.4%	100.0%
WNP	3	0	16	84.2%	60.4%	96.6%
Overall	NA	NA	NA	85.1%	77.5%	90.9%

Separating CA ecotypes							
Group	**CA coastal**	**CA offshore**	**ETP**	**WNP**	**% Correct**	**Lower 95% CI**	**Upper 95% CI**
coastal	26	3	1	2	81.2%	63.6%	92.8%
offshore	2	6	2	4	42.9%	17.7%	71.1%
ETP	0	1	29	0	96.7%	82.8%	99.9%
WNP	1	3	0	15	78.9%	54.4%	93.9%
Overall	NA	NA	NA	NA	80.0%	70.5%	87.5%

Table 3 Assignment probabilities of specimens collected outside the three main groups (CA, ETP, WNP). CA: California; ESP: eastern South Pacific; ETP: eastern tropical Pacific; GoC: Gulf of California; U: Unassigned; WNP: western North Pacific.

Museum ID	Group	Location	CA	ETP	WNP
USNM 395381	ESP	30 mi of Caleta Padilo, South of Iquique, Tarapaca, Chile	0.09	0.05	0.86
USNM 550795	ESP	Pucusana, Lima, Peru	0.81	0.01	0.18
USNM 550798	ESP	Peru	0.68	0.04	0.28
USNM 550799	ESP	Peru	0.32	0.13	0.55
USNM 504236	GoC	Gulf of California - 34 mi south of San Felipe, Baja California, Mexico	0.66	0.03	0.31
USNM 396165	GoC	Gulf of California - offshore from San Felipe, Baja California, Mexico	0.38	0.03	0.59
AMNH 120920	U	Baja California, Mexico	0.39	0.25	0.36
AMNH 257133	U	Mexico	0.11	0.75	0.14
USNM 12054	U	Baja California, Mexico	0.81	0.02	0.17

Table 4 Number of skulls in each group and cluster as identified by Density Clustering. CA: California; ESP: eastern South Pacific; ETP: eastern tropical Pacific; GoC: Gulf of California; WNP: western North Pacific.

Group	Cluster 1	Cluster 2
CA	69	3
ESP	4	0
ETP	2	28
GoC	2	0
WNP	19	0
Unassigned	2	1

25 **Table 5** Assignment probabilities of type specimens to California (CA), eastern
26 tropical Pacific (ETP), and western North Pacific (WNP) groups.

Type	Museum ID	CA	ETP	WNP
T. gillii	USNM A13022	0.88	0.01	0.11
T. truncatus	NHMUK 353a	0.73	0.02	0.25
T. nuuanu	AMNH 35045	0.12	0.80	0.08
T. aduncus	ZMB 66400	0.28	0.69	0.03

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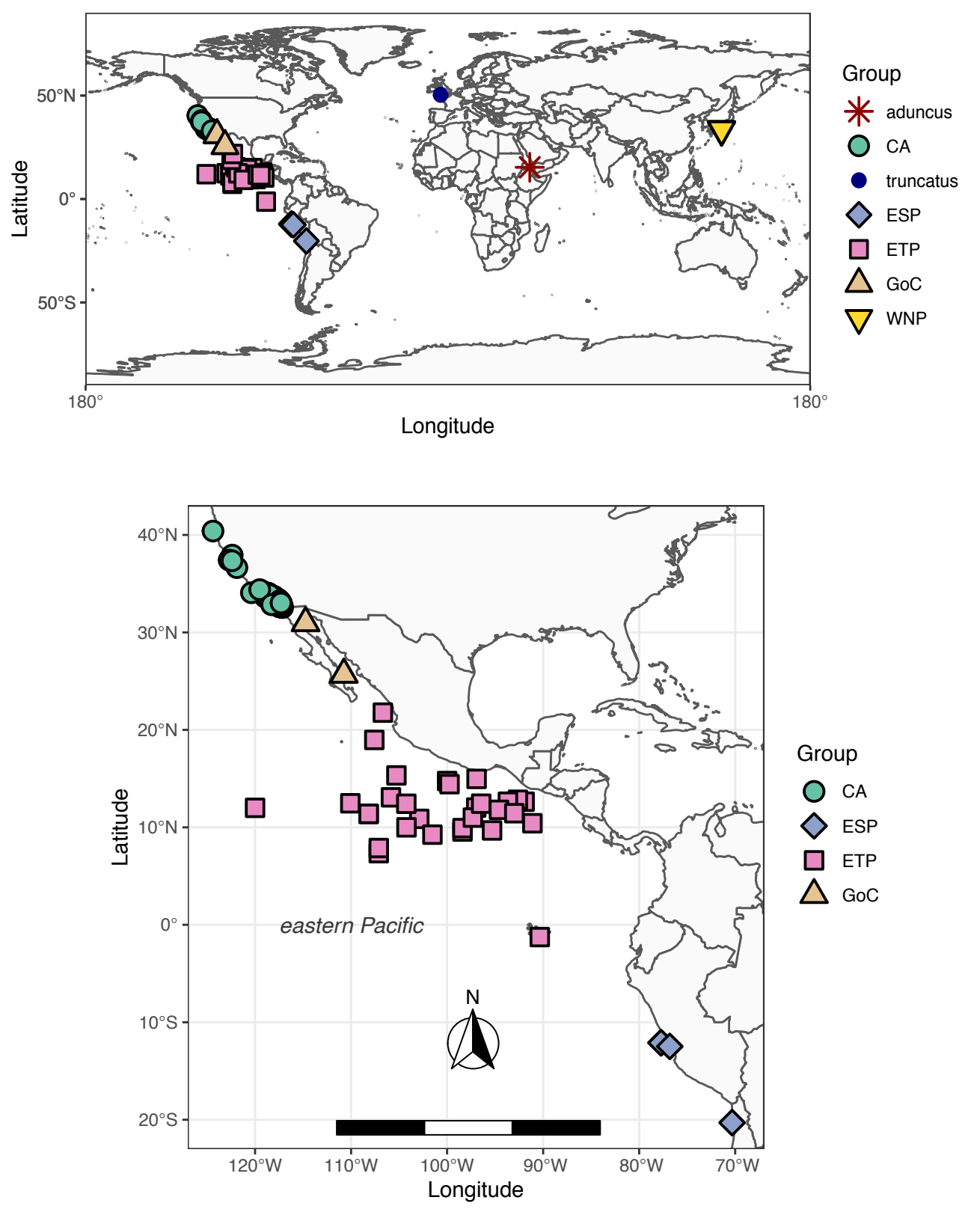
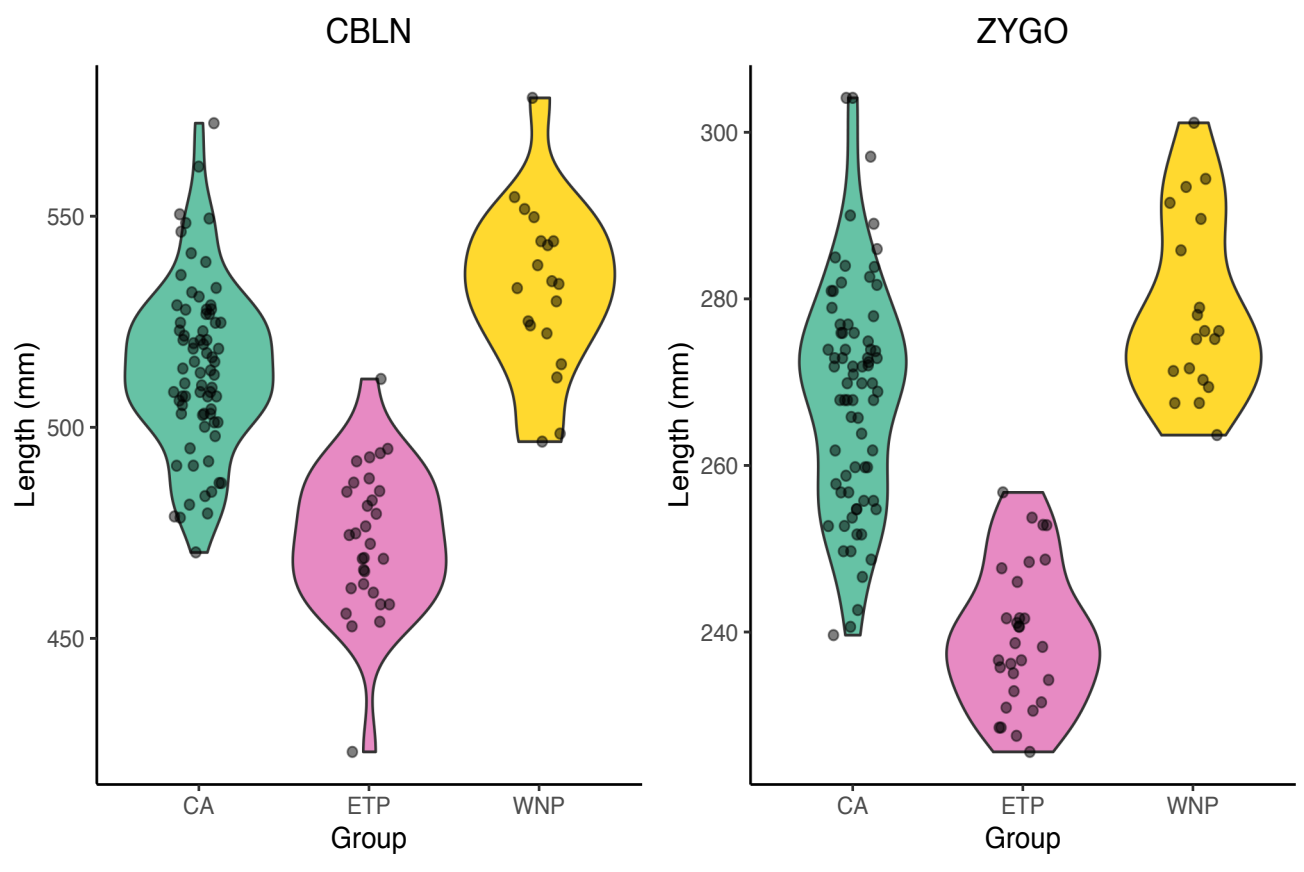
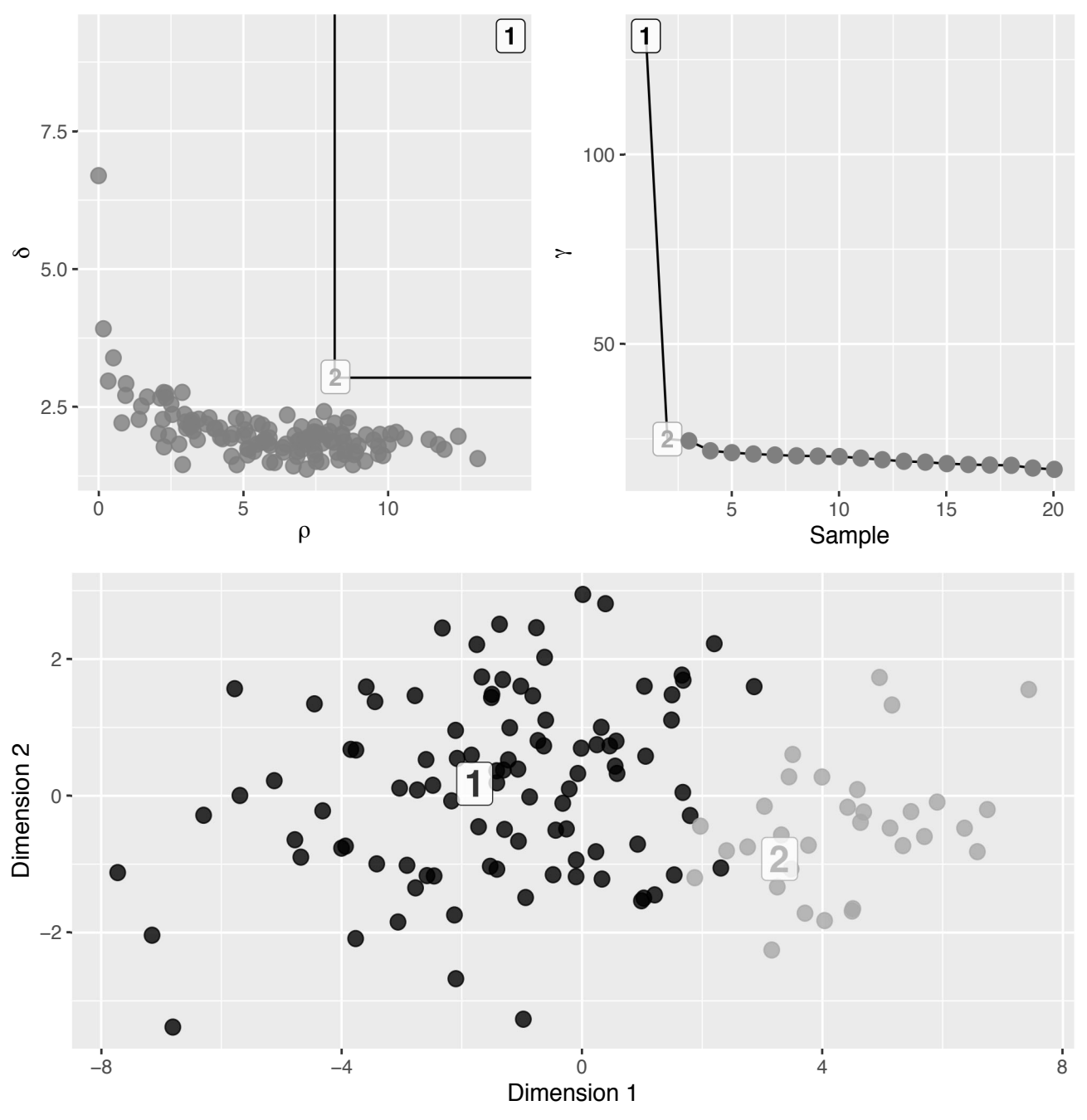
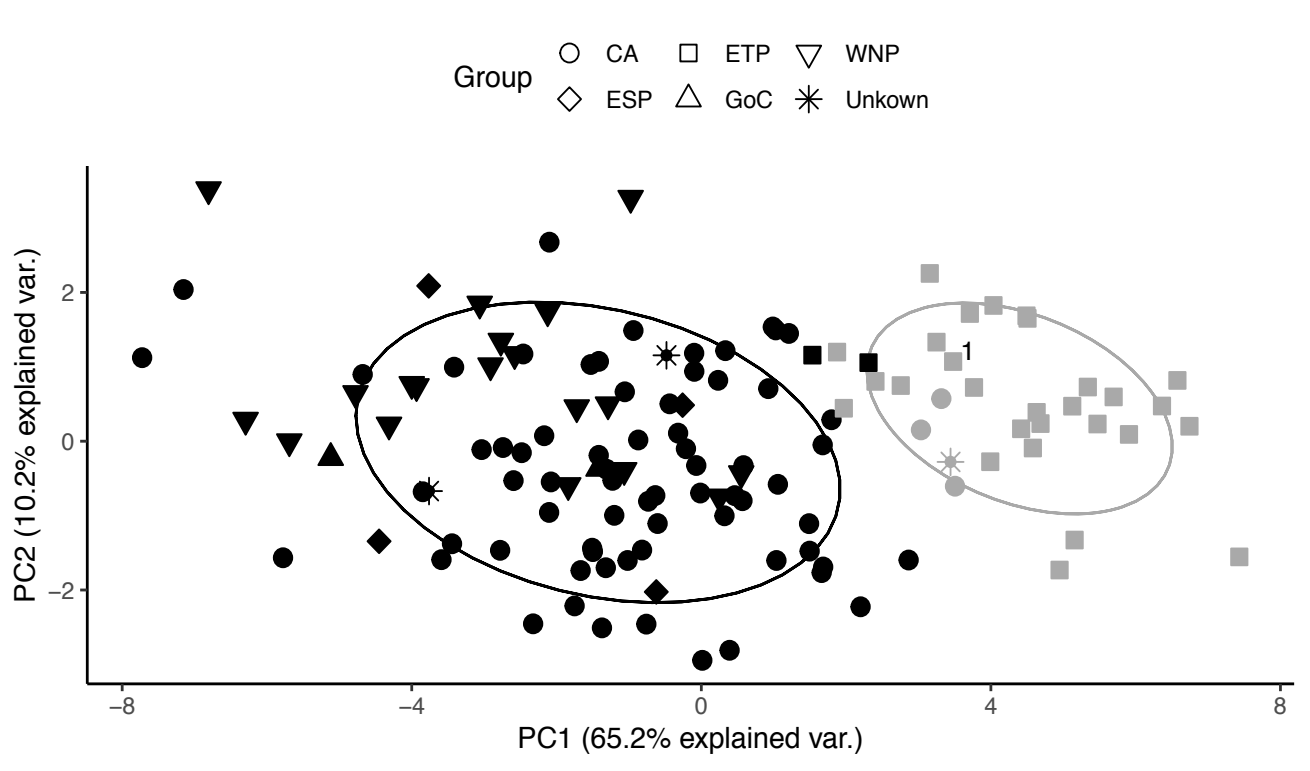
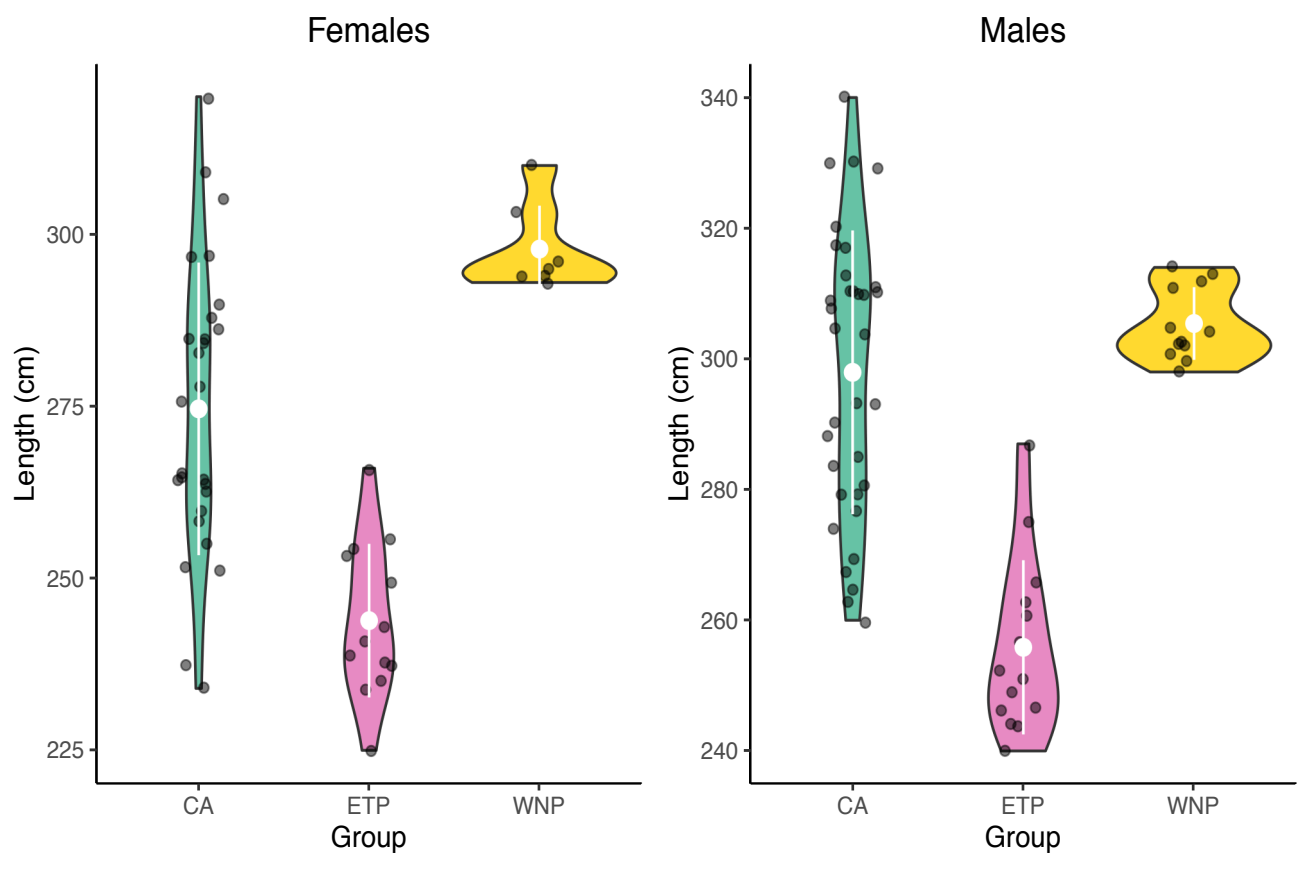
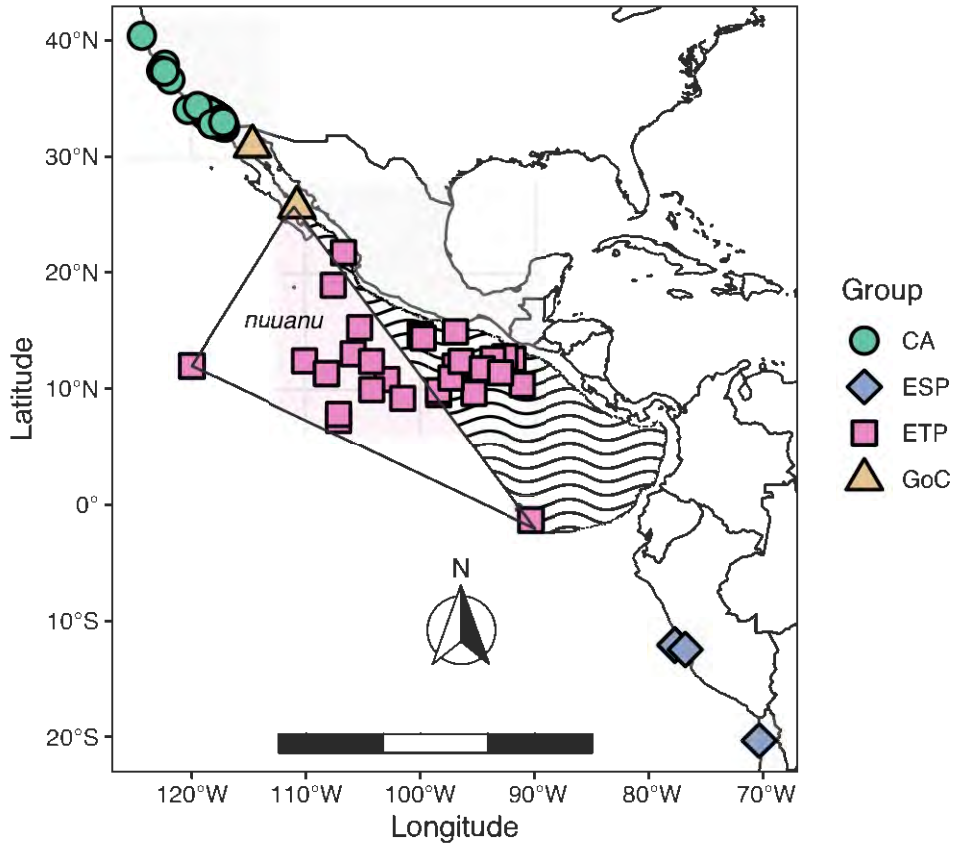

Group
aduncus
CA
truncatus
ESP
ETP
GoC
WNP
Latitude
50°N
0°
50°S
180°
180°
Longitude
eastern Pacific
N
40°N
30°N
20°N
10°N
0°
10°S
20°S
120°W
110°W
100°W
90°W
80°W
70°W


CBLN
ZYGO
Length (mm)
550
500
450
300
280
260
240
CA
ETP
WNP
Group


1
2
7.5
5.0
2.5
δ
0
5
10
ρ
1
2
100
50
γ
5
10
15
20
Sample
1
2
2
0
−2
Dimension 2
−8
−4
0
4
8
Dimension 1


Group
CA
ETP
WNP
ESP
GoC
Unkown
1
PC2 (10.2% explained var.)
PC1 (65.2% explained var.)
2
0
−2
−8
−4
0
4
8


Females
Males
Length (cm)
300
275
250
225
340
320
300
280
260
240
CA
ETP
WNP
Group


40°N
30°N
20°N
10°N
0°
10°S
20°S
120°W
110°W
100°W
90°W
80°W
70°W
Latitude
Longitude
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N
Group
CA
ESP
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