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SKULL MORPHOMETRY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) FROM THE GULF OF MEXICO

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Skull morphometry of 206 stranded juvenile and adult bottlenose dolphins (*Tursiops truncatus*) from Texas and Florida were examined. Juveniles differed significantly from adults in both Texas and Florida populations. Sexual dimorphism was present in skulls from Texas but not from Florida. Regional differences in females from Texas and Florida were apparent, especially in braincase height, whereas male bottlenose dolphins did not differ between regions. Females could be distinguished accurately to region (90% classification success) using skull morphometry. Cranial morphometrics of *T. truncatus* are concrete values that may aid in identification of a type specimen for each population. Furthermore, these results can be used as a standard for *Tursiops* in the Gulf of Mexico.

Key words: bottlenose dolphin, cranial morphometrics, Gulf of Mexico, skull morphology, *Tursiops truncatus*

The bottlenose dolphin (*Tursiops truncatus*) is cosmopolitan in its distribution except for the very high latitudes (Leatherwood and Reeves 1983). Researchers have disagreed on the parameters defining the systematic grouping of this genus. This confused state primarily is caused by results of past studies (Ross 1977; W. A. Walker, in litt.). More than 20 species of *Tursiops* have appeared in the literature since the genus was initially described by Montagu in 1821 (Hershkovitz 1966). Bottlenose dolphins found in different geographic areas appear to exhibit specific phenotypic traits, although the systematic implications of these characters have not yet been resolved in all oceans (Gao et al. 1995; Leatherwood and Reeves 1983; Mead and Potter 1995; Ross 1977, 1984; Ross and Cockcroft 1990; W. A. Walker, in litt.). Recently, the trend has been for consolidation into a single species, *Tursiops truncatus* (Leatherwood and Reeves 1983; Tomilin 1957), or splitting into 2 species, *T. truncatus* and *T. aduncus* (Hale et al. 2000; Rice 1998; Wang et al. 1999, 2000a, 2000b). Species-level distinction has been determined between *T. truncatus* and *T. aduncus* in Chinese and Indo-Pacific waters (Hale et al. 2000; Wang et al. 1999, 2000a, 2000b); however, the names *Tursiops gilli* and *Tursiops gephyreus* still remain in several taxonomic regimes (LeDuc 1997; Ross 1977; Ross and Cockcroft 1990; W. A. Walker, in litt.). A taxonomic review of the genus *Tursiops* ultimately will be necessary to resolve the conflicting views (Leatherwood and Reeves 1983; Ross 1977; Ross and Cockcroft 1990).

Morphology of bottlenose dolphins in the Gulf of Mexico has yet to be examined completely. Tolley et al. (1995) investigated the external morphology of dolphins from Sarasota Bay, Florida, to determine whether sexual dimorphism was present. Their study was conducted on live dolphins, however, and therefore excluded skeletal measure-

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ments. Hersh and Duffield (1990) compared skull and body morphometrics in a small sample of bottlenose dolphins from the Atlantic coast of Florida, including the Florida Keys. A true assessment of the bottlenose dolphins in the Gulf of Mexico has yet to be attempted. The aim of this study was to determine the effects of sex and ontogeny on variation in skull morphometry within populations of *T. truncatus* from the eastern and western Gulf of Mexico and to assess regional variation in skull morphometry between the 2 populations.

MATERIALS AND METHODS

Skull measurements.—Thirty-five cranial measurements (Appendix I) were obtained from stranded adult specimens of *T. truncatus* from Texas (males, $n = 46$; females, $n = 54$; unknown, $n = 24$) and Florida (males, $n = 12$; females, $n = 25$; unknown, $n = 8$). Measurements from juvenile specimens of *T. truncatus* from Texas (males, $n = 11$; females, $n = 11$; unknown, $n = 2$) and Florida (males, $n = 6$; females, $n = 7$) were included in some analyses. Bottlenose dolphins from Texas stranded all along the Texas coast, whereas those from Florida were localized around the Sarasota Bay. Voucher specimens from Texas are presently in the collection of the Texas Marine Mammal Stranding Network (TMMSN), Galveston, and in the Texas Cooperative Wildlife Collection (TCWC), College Station, and specimens from Florida are in the collection of the Mote Marine Mammal Laboratory, Sarasota, Florida. Thirty-four of the measurements we used were used by Perrin (1975) in his study of *Stenella*, and 1 (trait 35) was taken from W. A. Walker (in litt.) in his study of Pacific *Tursiops*. Measurements were taken using digital dial calipers (Fowler Ultra-Cal Mark III 150, Newton, Massachusetts) to the nearest 0.01 mm or aluminum slide calipers (Haglof Mantax 80 cm, Madison, Mississippi) to the nearest 0.5 mm, depending upon size. Number of teeth in each toothrow was counted by hand. Replicates of 10 measurements were obtained for each cranial character upon each skull and then averaged. Five skulls from the Texas group and 1 skull from the Florida group were missing all measurements of the lower jaw (traits 30–35). These skulls were removed from statistical analyses for which traits 30–35 were analyzed.

Juvenile specimens of *T. truncatus* were separated from adults to account for potential ontogenetic variation. Individuals were divided into these groupings based on degree of fusion of maxillary and premaxillary bones (Dailey and Perrin 1973; Mead and Potter 1990; Perrin 1984; Perrin and Heyning 1993; W. A. Walker, in litt.). Sex, standard length, and location of stranding were determined by observers from various stranding networks where specimens were collected.

Multivariate statistics.—A combination of statistical tests was used (SPSS 1997; SYSTAT 1997) including multivariate analysis of variance (MANOVA), Wilks' lambda tests, discriminant analysis, and principal components analysis (PCA). MANOVA was used to determine differences between age groups, sexes, and populations using all skull measurements, whereas discriminant analysis was used to determine the classification success that different skull measurements had upon each group. PCA was used as an exploratory tool to graphically illustrate key differences between groups using multiple variables.

RESULTS

Within-population variation in Texas.—Significant differences in skull morphometry were detected between juvenile and adult *T. truncatus* in Texas (MANOVA, $P \leq 0.0001$). All but 3 measurements were significantly different between age groups: width of external nares (trait 12), projection of premaxillaries beyond maxillaries (trait 21), and distance from nasals to supraoccipital crest (trait 22). Two of these measurements represent relationships between growth of 2 bones in the rostrum (trait 21) and position of nares relative to the braincase (trait 22). Only 1 measurement represented a true physical character of the skull (trait 12), although other measurements that correspond to similar features of the nares (internal nares width [trait 25] and pterygoid length [trait 26]) were significantly different between groups. There also were no significant differences within tooth counts, traits 28–31. Sex-specific differences in skull morphometry were observed for adults (MANOVA, $P \leq 0.0001$). Significant differences were found in all but 6 skull measurements: width of rostrum at base (trait 3), width of rostrum at midlength (trait 5), width of premaxillaries at midlength of rostrum (trait 6), projection of premaxillaries beyond maxillaries (trait 21), length of antorbital process of lacrimal bone (trait 24), and internal nares width (trait 25). Characters representing width of rostrum (traits 3, 5, and 6) as well as differences in growth of 2 bones in the rostrum (trait 21) were consistent in both sexes, as was width of internal nares (trait 25). In contrast, cranial measurements did not differ significantly between juvenile males and females (MANOVA, $P = 0.487$), although individual differences were identified in 3 skull measures: width of rostrum at three-fourth length (trait 7), vertical external height of braincase (trait 15), and length of posttemporal fossa (trait 17). Results from discriminant analysis indicated that group membership in Texas populations (adult male, adult female, and juveniles) could be predicted using skull morphometry (jackknifed classification success = 79.2%). Further analysis revealed 3 outliers (GA292-TMMSN, PA105-TCWC, PA177-TMMSN) that clustered outside the confidence ellipses of both juvenile and adult groups (Fig. 1). The 3 specimens were collected along the Texas coast in the Galveston (GA) and Port Aransas (PA) regions and are housed in the permanents collections of the TMMSN and TCWC, respectively. The outliers were identified by plotting studentized residual values (3.17, 1.80, and 1.91).

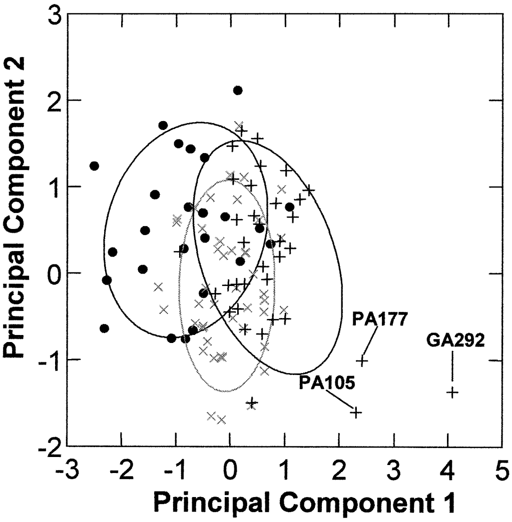

FIG. 1.—Scatterplot of principal components analysis for cranial measurements of bottlenose dolphins. Symbols represent *Tursiops truncatus* from Texas juvenile (●), adult female (×), and adult male (+) groups. PA177, PA105, and GA 292 represent 3 specimens located outside the confidence interval of all 3 Texas groups and were noted as "outliers" in the text.

Within-population variation in Florida.—Significant differences in skull morphometry were detected between juvenile and adult specimens of *T. truncatus* in Florida (MANOVA, $P = 0.009$). All measurements were significantly different between age groups except for width of external nares (trait 12), projection of premaxillaries beyond maxillaries (trait 21), and distance from nasals to supraoccipital crest (trait 22), which is consistent with results identified in the Texas population. Two of these represent relationships between growth of 2 bones in the rostrum (trait 21) and position of nares relative to braincase (trait 22). Again, as with the Texas population, these were the only 2 measurements to be reduced in size throughout development from the juvenile stage toward physical maturity. Only 1 measurement represented a true character of the skull (trait 12, greatest length of internal nares), although other measurements that correspond to similar features of the nares (internal nares width [trait 25] and pterygoid length (trait 26]) were significantly different between groups. Correspondingly, there were no significant differences within tooth counts, traits 28–31. No significant sex-specific differences in overall skull morphometry were observed for adults (MANOVA, $P = 0.150$). Significant differences were found, how-

TABLE 1.—Stepwise discriminant analysis results for separating bottlenose dolphin groups.

Groups	Skull variables[a]	Jackknifed classification score (%)
Florida female adults versus Texas female adults	9, 14, 15, 17, 23, 25	89.5
Texas male adults versus Atlantic and Pacific adults	1, 13, 15, 18, 22, 24, 25, 26	100
Texas male adults versus three outliers (PA105, PA177, GA292)	1, 2, 13, 25	100

[a] Variable names and descriptions are given in Appendix I.

ever, in 6 individual skull measurements: width of rostrum at 60 mm (trait 4), width of rostrum at midlength (trait 5), width of premaxillaries at midlength of rostrum (trait 6), width of rostrum at three-fourth length (trait 7), length of internal braincase (trait 16), and width of posttemporal fossa (trait 18). Characters representing width of rostrum (traits 4–7) were significantly different in the Florida population, contradicting results for *T. truncatus* from Texas. Interpretation of internal braincase length and width of posttemporal fossa is difficult without significant differences in other possibly related measures. In contrast, cranial measurements did not differ between juvenile males and females (MANOVA, $P = 0.873$), with no measurements exhibiting significant differences based on sex. Results from discriminant analysis indicated that group membership (adults and juveniles) could be predicted accurately using skull morphometry (jackknifed classification success = 92.3%). Due to similarity in skull morphology for males and female adults, group membership could not be predicted accurately when adults were separated by sex (jackknifed classification success = 43.6%).

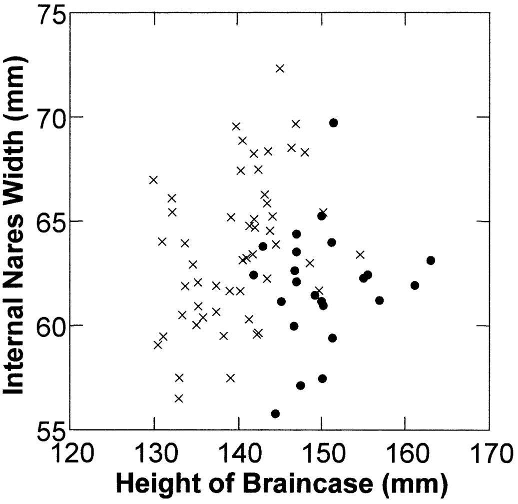

FIG. 2.—Scatterplot of internal nares width versus height of braincase for female bottlenose dolphins from Texas and Florida. Symbols represent females from Florida (●) or Texas (×) populations.

Geographic variation.—Skull morphometry of adult females from Texas and Florida was significantly different (MANOVA, $P < 0.0001$). All but 8 measurements were significantly different between populations: width of premaxillaries at midlength of rostrum (trait 6), external nares width (trait 12), width of posttemporal fossa (trait 18), major diameter of temporal fossa (trait 19), projection of premaxillaries beyond maxillaries (trait 21), distance from nasals to supraoccipital crest (trait 22), length of antorbital process of the lacrimal bone (trait 24), and mandibular condyle width (trait 35). Females were classified correctly to region 87.5% of the time by using jackknifed classification scores. Stepwise discriminant analysis (F to enter: 3.84, F to remove: 2.71) determined that 6 traits best separated the Florida female skulls from Texas female skulls (Table 1), including distance from tip of rostrum to internal nares (trait 9), greatest width of premaxillaries (trait 14), height of braincase (trait 15), greatest length of posttemporal fossa (trait 17), length of orbit (trait 23), and internal nares width (trait 25; Fig. 2). These groups were classified correctly 89.5% of the time by using jackknifed classification scores (Table 1). In contrast, skull morphometry of adult males was similar in Texas and Florida (MANOVA, $P = 0.451$), with significant differences in only 3 skull measurements: width of rostrum at three-fourth length (trait 7), vertical external height of braincase (trait 15), and length of posttemporal fossa (trait 17). Similarly, skull morphometry of Texas and Florida juveniles did not differ significantly between regions (MANOVA, $P = 0.161$). Significant differences were identified in 3 measurements, including width of rostrum at three-fourth length (trait 7), vertical external height of braincase (trait 15), and internal nares width (trait 25).

DISCUSSION

Variation within skulls of bottlenose dolphin from the Gulf of Mexico is present based on ontogeny, sex of the individual, and geographic location of the population. Sexual dimorphism was identified in skull measurements of *T. truncatus* from Texas populations but not in dolphins from Florida populations. These results are consistent with a previous study of *T. truncatus* along the Atlantic Coast of Florida (Hersh et al. 1990). Significant variation was identified between adult female *T. truncatus* from Texas and Florida based on several traits, including height of the braincase and width of the internal nares (Table 1). Interestingly, male bottlenose dolphins from Texas and Florida populations were significantly different based on skull measurements when 3 extreme outliers from the Texas population were included in the analyses, although they were not significantly different when outliers were removed. The difference in the outcome of these tests when the outliers were removed raises several questions as to their identity.

Investigations of relatedness of populations of *Tursiops* from different geographic regions using mitochondrial DNA (mtDNA) indicate that offshore Atlantic, offshore Gulf of Mexico, and deep-water Pacific dolphins are more closely related to each other than to inshore–shallow-water *Tursiops* from the respective systems (Curry 1997; Curry and Smith 1997). To apply this hypothesis in the present study, measurements were taken for Pacific bottlenose dolphins ($n = 12$), as well as Atlantic offshore bottlenose dolphins ($n = 13$), in an attempt to determine the population identity of the 3 outliers. Pacific skull measurements were taken by one of us (JPT), and Atlantic skull data were from previously published material (Mead and Potter 1995). PCA placed these 3 dolphins outside the Texas population but within the Atlantic and Pacific confidence ellipse (Fig. 3). Turner (2001) conducted mtDNA analysis on one of the 3 outlier specimens and determined that it was genetically separate from Texas population of bottlenose dolphins. Clearly, additional samples must be collected so that further analyses may be conducted to determine the population structure of these extreme outliers.

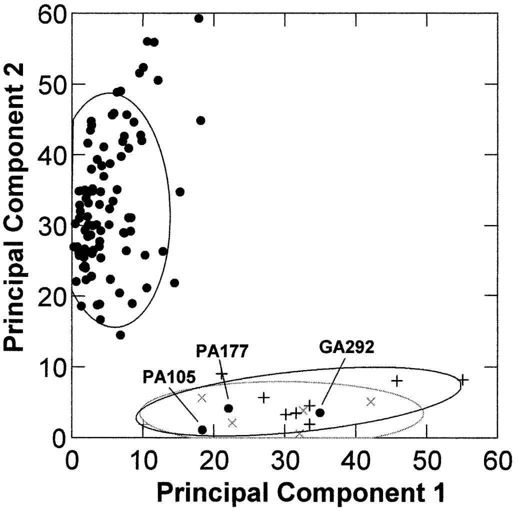

FIG. 3.—Scatterplot of principal components analysis for adult *Tursiops truncatus* specimens from Texas (●), Atlantic offshore (×), and Pacific Ocean (+). Outliers indicated as for Fig. 1.

The present study found that skull characters of stranded bottlenose dolphins in the Gulf of Mexico are dependent on ontogeny, sex, and geographic location of the population. Ontogenetic differences were identified between juvenile and adult groups from both Texas and Florida populations. Sexual dimorphism was found to be present in dolphins that stranded on Texas shores but was absent in those stranding on the Florida Gulf coast, which is consistent with the results of past studies (Fernandez and Hohn 1998; Hersh et al. 1990). Significant differences were identified in skull characters between females from Texas and Florida populations, whereas results from male specimens depend upon interpretation. Three extreme outliers were found to exist in the Texas collection of *T. truncatus* that may belong to a Gulf of Mexico morphotype, which is different from the dolphins found in inshore habitats. Further analysis verified that these dolphins had several traits in common with offshore *T. truncatus* from the Atlantic as well as large dolphins collected from the Pacific.

Bottlenose dolphins from the eastern and western Gulf of Mexico can be differentiated using skull characters. Application of values herein to stranded specimens will greatly aid in identification of source populations. Cranial morphometrics of *T. truncatus* are concrete values that can be applied in field collections and may aid in the identification of type specimen for each subsequent population. Furthermore, the results presented here can be used as a standard for the Gulf of Mexico, so that *Tursiops* may be examined on a global scale.

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APPENDIX I

Skull variables used in the present study.—(1) Condylobasal length—from tip of rostrum to hindmost margin of occipital condyles; (2) length of rostrum—from tip to line across hindmost limits of antorbital notches; (3) width of rostrum at base—along line across hindmost limits of antorbital notches; (4) width of rostrum at 60 mm anterior to line across hindmost limits of antorbital notches; (5) width of rostrum at midlength; (6) width of premaxillaries at midlength of rostrum; (7) width of rostrum at three-fourth length, measured from posterior end; (8) distance from tip of rostrum to external nares (to mesial end of anterior transverse margin of right naris); (9) distance from tip of rostrum to internal nares (to mesial end of posterior margin of right pterygoid); (10) greatest preorbital width; (11) least supraorbital width; (12) greatest width of external nares; (13) greatest width across zygomatic process of squamosal; (14) greatest width of premaxillaries; (15) vertical external height of braincase from midline of basospheniod to summit of supraoccipital, but not including supraoccipital crest; (16) internal length of braincase from hindmost limit of occipital condyles to foremost limit of cranial cavity along midline; (17) greatest length of left posttemporal fossa, measured to external margin of raised suture; (18) greatest width of left posttemporal fossa at right angles to greatest length; (19) major diameter of left temporal fossa proper; (20) minor diameter of left temporal fossa proper; (21) projection of premaxillaries beyond maxillaries; (22) distance from foremost end of nasals to hindmost point of margin of supraoccipital crest; (23) length of left orbit—from apex of preorbital process of frontal to apex of postorbital process; (24) length of antorbital process of left lacrimal; (25) greatest width of internal nares; (26) greatest length of left pterygoid; (27) length of upper left toothrow—from hindmost margin of hindmost alveolus to tip of rostrum; (28) number of teeth—upper left; (29) number of teeth—upper right; (30) number of teeth—lower left (31) number of teeth—lower right; (32) length of lower left toothrow—from hindmost margin of hindmost alveolus to tip of mandible; (33) greatest length of left ramus; (34) greatest height of left ramus at right angles to greatest length; (35) mandibular condyle width—greatest width of mandibular condyle.