Assessment of Nonmetric Skull Characters of the Franciscana (*Pontoporia blainvillei*) in Determining Population Differences

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Abstract

The franciscana (Pontoporia blainvillei) is a small endemic dolphin of the Atlantic coast of Brazil, Uruguay, and Argentina that presents conservation problems because of its incidental mortality in nets of artisanal fisheries throughout its entire distribution. An important step in managing small cetaceans is to define the populations involved because each identified population requires evaluation and treatment as a separate unit. Since 1991, morphological and genetic differences among franciscanas of different regions have been detected. Nonmetric characters (i.e., coded by discrete states and also known as qualitative traits) have been employed for the analysis of population differentiation of more than 50 mammal species because it has been assumed that they are exposed to minimum selection pressure. The aim of this study was to identify potentially useful nonmetric skull characters of the franciscana for comparison among individuals from different locations in order to investigate geographic variation in these traits and to determine their frequencies in individuals of the Uruguayan coast. Twenty-six characters were examined for 115 skulls belonging to the cetacean collection of the National Museum of Natural History and Anthropology (Montevideo, Uruguay). The potential existence of character dependence on body length, sex, and time period was examined. A total of 12 characters were excluded from subsequent analyses: seven were not sufficiently variable, four were dependent on body length, and one showed sexual dimorphism. Only 14 characters were remaining, and their frequencies were calculated. None of them was dependent on time period. Due to the low number of potentially useful nonmetric skull characters found in this study, the utility of this technique as an additional tool for franciscana population assessment is uncertain. The authors give some general methodological recommendations for use of nonmetric characters in population differentiation studies.

Key Words: Nonmetric characters, discrete characters, skull, geographic variation, populations, franciscana, *Pontoporia blainvillei*

Introduction

The franciscana (Pontoporia blainvillei) (Gervais & d'Orbigny, 1844) is a small cetacean that inhabits the waters off the Atlantic coast of Brazil, Uruguay, and Argentina. The northern and southern limits of this species' distribution are Itaúnas (18° 25' S) (Espírito Santo, Brazil) and Golfo San Matías (41° 10' S) (Patagonia, Argentina) (Moreira & Siciliano, 1991; Crespo, 2002), respectively. This endemic distribution, together with its low reproductive potential (Pinedo et al., 1989) and its incidental mortality in nets of artisanal fisheries for more than half a century along its whole range (Praderi et al., 1989; UNEP/CMS, 2000; Ott et al., 2002), make the species the most threatened cetacean of the southwest Atlantic Ocean (e.g., Secchi et al., 2003a, 2003b; Bastida et al., 2007).

Research based on morphological (Pinedo, 1991; Higa et al., 2002; Ramos et al., 2002) and genetic data (Secchi et al., 1998; Lázaro et al., 2004) suggested the existence of at least two clearly defined populations of the franciscanaone to the north of Santa Catarina (~29° S), Brazil, and the other to the south. A later phylogeographic analysis by Secchi et al. (2003a), combining mtDNA data, morphometrics, and life-history parameters, provided evidence for separating the species into four management stocks: two inhabiting coastal waters of Brazil, a third occurring in Rio Grande do Sul State (southern Brazil) and Uruguay, and the fourth in coastal Argentinean waters. Furthermore, a recent study based on mtDNA data showed evidence for the presence of genetically distinct units in Argentina (Mendez et al., 2008). Identifying discrete units is critical for the creation and implementation of conservation and management plans, which should be applied throughout the whole distribution of a species. Even though the franciscana was previously

categorized as Data Deficient by the International Union for the Conservation of Nature (IUCN), with the stock of Rio Grande do Sul/Uruguay catalogued as Vulnerable, the species was recently categorized as Vulnerable (IUCN, 2008).

Nonmetric characters (i.e., discontinuous, qualitative, or epigenetic traits) have been used to discriminate populations of more than 50 mammalian species, including humans (Berry & Berry, 1967; Brasili et al., 1999; Bruner et al., 2003), rodents (Andersen & Wiig, 1982; Markov, 2001, 2003; Uhlíková, 2004), mustelids (Ansorge, 1992; Ansorge & Stubbe, 1995; Monakhov, 2001; Dubinin & Valentsev, 2003), pinnipeds (Berry, 1969), and small cetaceans (Perrin et al., 1982, 1994; Mikkelsen & Lund, 1994; Gao & Gaskin, 1996). These characters comprise skeletal variants that can be coded by discrete states such as presence/absence, number, or relative position (ahead, behind, same level) of different structures (e.g., sutures, foramina, fenestrations). The analysis of nonmetric characters as a morphological tool to discriminate populations relies on the comparison of the frequencies of several characters among populations. High variability in the frequency of trait expression among populations implies a large degree of epigenetic divergence (Ansorge, 2001).

Nonmetric characters have become highly attractive for population differentiation studies because of the following advantages (Perrin et al., 1994; Ansorge, 2001):

- Since they are usually not correlated with one another, a large number of relatively independent characters can be defined more easily.
- Since nonmetric characters are not directly related to survival nor reproduction, and they are probably of lower importance for an organism than selectively more relevant traits concerning feeding or the reproductive system, it has been assumed that they are exposed to minimum selection pressure. Therefore, these characters have been considered potentially valuable indicators of the degree of gene flow among populations.
- Nonmetric characters are to a large degree independent of sex, age, and ontogenetic developmental stage, so sample sizes do not have to be reduced because of these factors.
- The method is relatively simple: characters can be coded without large-scale equipment, and skulls, being frequent objects of study, are kept in museum collections, usually in large numbers. An additional attraction for cetologists is that nonmetric characters are little affected by preparation methods and specimen handling.

This technique also has some disadvantages:

- A high degree of heritability has never been confirmed in wild animals. Since it is impossible to prove that genetic factors are solely involved in character formation, the existence of potential environmental influence has to be considered (Ansorge, 2001). The results of a study that combined metric and nonmetric data of the short-beaked common dolphin (*Delphinus delphis*) were consistent with the hypothesis of non-neutrality of the nonmetric characters (Perrin et al., 1994).
- The resolving power of nonmetric skull characters has been shown to be less than that of metric skull characters in the population differentiation of the short-beaked common dolphin (Perrin et al., 1994) and the harbour porpoise (*Phocoena phocoena*) (Gao & Gaskin, 1996). Nevertheless, both types of characters were useful and efficient, and were suggested for use in combination (Sjøvold, 1973; Perrin et al., 1994; Gao & Gaskin, 1996).
- There are several methodological problems such as character definition; influence of intra- and interobserver variation on state coding; and how to consider sex, age, and asymmetry dependence during the data analysis (Brasili et al., 1999; Gualdi-Russo et al., 1999; Ansorge, 2001).

The aim of this study was to identify potentially useful nonmetric skull characters of the franciscana for comparison among individuals from different locations in order to investigate geographic variation in these traits and to determine their frequencies in individuals of the Uruguayan coast. Before making inter-regional comparisons, it is necessary to clarify and avoid additional sources of variation; therefore, the existence of character dependence on body length, sex, and time period was also examined.

Materials and Methods

Skulls Examined

The skulls included in this study belong to the Cetacean Collection of the National Museum of Natural History and Anthropology (MUNHINA, Montevideo-Uruguay). To avoid bias possibly related to ontogenetic changes, only skulls of mature individuals should be examined. However, as the information of sexual maturity was not available, the animals' total lengths were considered. Skulls were selected from specimens that had been sexed and were longer than the minimum total length found in a mature animal—137 cm in females and 121 cm in males (Pinedo et al., 1989). Nevertheless, because this criterion did not necessarily mean that the selected specimens were

mature, it was necessary to study for the existence of variation with total length.

The above criteria for selection and inclusion in the study resulted in 115 skulls for examination (35 females and 80 males), which were collected along the Uruguayan coast between 1959 and 1998 (for details, see Appendix 1).

Selection of Nonmetric Skull Characters

Most of the characters examined in this study were selected based on Perrin et al. (1982, 1994), and others were defined after a thorough search for traits with interindividual variation. Characters involving the pterigoyd hamuli were not included because the hamuli were commonly damaged. Characters that consisted of counting foramina were not included because the assessment was not accurate. Other characters were not included because their gradual variation made defining discrete states difficult (e.g., the presence of a groove between the occipital condyles).

Twenty-six nonmetric skull characters were initially identified and scored; seven were dropped, however, because they were not sufficiently variable (i.e., the same state was found in every skull) (Table 1), and our aim was to determine the frequencies of the different states of each character. The remaining 19 characters (9 dorsal, 4 ventral, 5 occipital, and 1 of the mandible) were coded for two (e.g., 1 = present, 2 = absent) or three possible states (e.g., 1 = ahead, 2 = behind, 3 = atlevel) (Table 2). Additionally, the "0" state was used in cases in which the character could not be coded-for example, when the skull area of interest was damaged or covered by tissue or when the observer was not sure of which state to assign. Therefore, the number of skulls examined varied according to each character.

Skull Analysis

The skulls were scored by one observer (MT). The characters were first coded from digital images of each skull and then by direct observation. When there was disagreement between the two scores, skulls were re-examined and the correct score was determined based on direct observation.

Data Analysis

To examine the possible existence of dependence of score on total body length, the sample was divided into two groups at body lengths of 146 cm in females and 137 cm in males (the maximum length of sexually immature animals) (Pinedo et al., 1989).

Characters that were dependent on total length were dropped, and sex-related differences were studied in the rest. Similarly, characters with sex dependence were deleted from further analysis. Samples from two time periods roughly 10 years apart (1971 to 1974 vs 1980 to 1983) were compared, and no significant relationship with period was found, allowing the samples to be pooled over time. Finally, in bilateral characters, the existence of dependence between the left and right sides was studied.

In every analysis, the authors used $r \times c$ contingency tables or the Fisher exact test (when expected frequencies were smaller than 5) (Sokal & Rohlf, 1979). The null hypothesis of no difference among the samples was rejected at $p \le 0.05$.

Results

Of the 19 characters examined, state frequencies depended on body length for four characters: one in females (No. 10: n = 35, p = 0.007) and three in males (No. 4: n = 79, p = 0.004; No. 11: n = 77, p = 0.003; No. 12: n = 77, p = 0.022). Of the remaining 15 characters, one was found to be significantly sex-dependent (No. 5: n = 113, p = 0.013). The frequencies of the other 14 characters are shown in Table 3.

Regarding asymmetry, five pairs of the 19 characters were bilateral (3-4, 6-7, 11-12, 15-16, and 17-18). Asymmetry was not studied for the 11-12 pair because both characters were total length dependent. In the remaining pairs, lateral frequencies were compared. In the 3-4 pair, the sexes were analyzed separately because males had shown total length dependence. The only pair that showed significant difference was 6-7 (n = 230, p = 0.004).

Table 1. Description of the nonmetric characters which were not variable

Character	State		
Antorbital notch (left and right sides)	Present (although in varying degrees, from slightly present to prominent)		
Position of the anterior edge of the premaxillary foramen, relative to the level of	Posterior		
the anterior edge of the antorbital process (left and right sides)			
Contact between the maxillary and the external nare (left and right sides)	Present		
Fenestrations in the basioccipital	Absent		

Table 2. Description of the nonmetric characters exa	mined
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Chara	cter	States					
In dor	In dorsal view (see Figure 1)						
1.	Position of the anteriormost projection of the antorbital process on left side, relative to the level of the same projection on right side	1 = ahead, 2 = behind, 3 = at level, 0 = uncertain					
2.	Position of the anterior edge of the left premaxillary foramen, relative to the level of the anterior edge of the same foramen on right side	1 = ahead, $2 =$ behind, $3 =$ at level, 0 = uncertain					
3.	Position of the anterior edge of the maxillary foramen, relative to the position of the anterior edge of the premaxillary foramen, on left side (Note: We called <i>maxillary foramen</i> the one situated in front of the premaxillary foramen.)	1 = ahead, 2 = behind, 3 = at level, 0 = uncertain					
4.	Same on right side						
5.	Position of the anterior edge of the maxillary foramen, relative to the position of the anterior edge of the same foramen on right side	1 = ahead, $2 =$ behind, $3 =$ at level, 0 = uncertain					
6.	Position of the anterior edge of the posteriormost maxillary foramen on left side, relative to the level of the anterior edge of the external nares	1 = ahead, $2 =$ behind, $3 =$ at level, 0 = uncertain					
7.	Same on right side						
8.	Position of the anterior edge of the posteriormost maxillary foramen on left side, relative to the position of the anterior edge of the same foramen on right side	1 = ahead, 2 = behind, 3 = at level, 0 = uncertain					
9.	Position of the posteriormost projection of the left premaxillary, relative to the level of the same projection on right side	1 = ahead, 2 = behind, 3 = at level, 0 = uncertain					
In ver	ntral view (see Figure 2)						
10.	Position of the posterior edge of the posteriormost alveolus on left side, relative to the level of the posterior edge of the same alveolus on right side	1 = ahead, 2 = behind, 3 = at level, 0 = uncertain					
11.	Fenestration in vomer	1 = present, $2 = $ absent, $0 = $ uncertain					
12.	Same on right side						
13.	Ridge in basioccipital (from slightly present to prominent)	1 = present, $2 = $ absent, $0 = $ uncertain					
In occ	cipital view (see Figure 3)						
14.	Shape of foramen magnum	1 = smooth oval or circular, 2 = irregular shape, $0 =$ uncertain					
15.	Fenestrations in supraoccipital, on left side	1 = one fenestration, $2 = $ two fenestrations, $0 =$ uncertain					
16.	Same on right side						
17. 18.	Fenestration in exoccipital (including the condyles), on left side. (Note: The edge between exoccipital and supraoccipital usually consists of a groove.) Same on right side	1 = present, 2 = absent, 0 = uncertain					
The m	andible						
19.	Position of the posterior edge of the posteriormost alveolus on left side, relative to the level of the posterior edge of the same alveolus on right side	1 = ahead, 2 = behind, 3 = at level, 0 = uncertain					

Discussion

Nonvariable Characters

Nonmetric characters that were not variable in franciscana skulls potentially could be considered species-specific features and possibly be used in taxonomic studies, but this cannot be confirmed until skulls from other regions are examined. It is worthwhile to compare the expression of these characters with their states in other odontocete species. Although the antorbital notch is a synapomorphic trait of odontocetes, in the pantropical spotted dolphin (*Stenella attenuata*), spinner dolphin (*S. longirostris*), and harbour porpoise, it can be absent (Perrin et al., 1982; Gao & Gaskin, 1996). In the pantropical spotted dolphin, white-beaked dolphin (*Lagenorhynchus albirostris*), and Atlantic white-sided dolphin (*L. acutus*), the premaxillary foramen can be anterior, posterior, or at the level of the antorbital process; while in a sample of 35 spinner dolphin skulls, only the last two states were found (Perrin et al., 1982; Mikkelsen & Lund, 1994). In the pantropical spotted dolphin, spinner dolphin, and short-beaked

1	n	104			13	n	111		
1	States	1	2	3	15	States	1	2	
	f	22	2 64	18		f	34	2 77	
	f/n	0.212	0.615	0.173		f/n	0.306	0.694	
2	n	115	0.015	0.175	14	n	110	0.074	
-	II States	1	2	3	14	States	1	2	
	f	1	50	16		f	3	107	
	f/n	0.426	0.435	0.130		f/n	0.027	0.073	
3	1/11 n	115	0.455	0.139	15	1/11 n	100	0.975	
5	II States	1	2	3	15	States	107	2	0
	f	20	01	3		f	1	1	63
	f/n	0.174	0 701	4		f/n	42	+	0.578
6	1/11 n	115	0.771	0.055	16	1/11 n	107	0.057	0.570
0	II States	115	2	2	10	II States	107	2	0
	f	1 02	6	16		f	50	2	9 54
	l f/n	95	0 052	0.120		l f/m	0.467	5	0 505
7	1/11	0.609	0.032	0.139	17	1/11	0.407	0.028	0.303
/	II States	115	2	2	17	II States	110	2	
	states	1	20	3		States	1	2	
	I e/	88	20	/		I C/	0	104	
0	1/n	0.705	0.174	0.061	10	1/11	100	0.945	
0	n Gi i	115	2	2	18	n Ct. t.	109	2	
	States	1	2	3		States	I	2	
	t ev	80	29	6		t ev	6	103	
0	f/n	0.696	0.252	0.052	10	f/n	0.055	0.945	
9	n	114			19	n	110		
	States	1	2	3		States	1	2	3
	f	10	82	22		f	37	58	15
	f/n	0.088	0.719	0.193		f/n	0.336	0.527	0.136

Table 3. State frequencies of the 14 characters which were independent on total length, sex, and time period (n = number of skulls examined without including the "0" state, f = absolute frequency, f/n = relative frequency)

common dolphin, the premaxillary sometimes connects to the nasal and, thus, the maxillary does not contact the external nares (Perrin et al., 1982, 1994). Lastly, fenestrations in the basioccipital exist in the pantropical spotted dolphin, spinner dolphin, short-beaked common dolphin, whitebeaked dolphin, Atlantic white-sided dolphin, and harbour porpoise (Perrin et al., 1982, 1994; Gao & Gaskin, 1994; Mikkelsen & Lund, 1994).

Dependence on Total Length

Four of 19 characters (21%) varied with total length. This finding does not agree with the advantage proposed by Ansorge (2001) that nonmetric characters were generally independent of age and developmental stage. Moreover, part of the ontogenetic variation had already been excluded by selecting skulls of individuals with total lengths greater than the minimum found in a mature animal. Therefore, it is undoubtedly true that the degree of dependence of these characters on body size varies among at least some species, making it essential to examine this possible dependence before using them in geographic variation studies. Since characters that depend on body length should be avoided when conducting regional comparisons, and character No. 3 presented values close to the significance level in males (n = 80, p = 0.057), we suggest it be avoided in future analyses. We recommend the same for character No. 13, whose state frequencies were close to significance level (females: n = 34, p = 0.067; males: n = 77, p = 0.079).

Dependence on Sex

One of 15 characters showed significant sex differences (No. 5). The proportion of characters with significant sex differences varies among odontocete species: 0/20 in the white-beaked dolphin and Atlantic white-sided dolphin (Mikkelsen & Lund, 1994), 2/38 in the harbour porpoise (Gao & Gaskin, 1996), and 5/34 in the shortbeaked common dolphin (Perrin et al., 1994). The character that was sex dependent in the franciscana (No. 5) was not studied in other odontocete species, so comparisons were not possible. Gao & Gaskin (1996) found that characters with sexual dimorphism in the harbour porpoise were the number of fenestrations in the supraoccipital and



Figure 1. Franciscana skull in dorsal view: (a) left antorbital process, (b) left premaxillary foramen, (c) left maxillary foramen, (d) posteriormost maxillary foramen on left side, (e) anterior edge of the external nares, and (f) posteriormost projection of the left premaxillary

the arrangement of mental foramina. The former was examined in franciscana skulls, but no sex difference was found.

Interspecies differences in sex dependence are evident, so it is not clear to what degree the assumption of sex independence of nonmetric characters is true. This makes the study of sex dependence essential before conducting any other comparison. Brasili et al. (1999) found that the characters with sexual dimorphism varied according to the population examined, suggesting the importance of studying its incidence in every population included in an analysis. Several authors have shown that there exists significant variation in nonmetric characters both within and among populations (see Griffin, 1993).

State Frequencies

Twelve nonmetric characters were potentially useful for inter-regional comparisons. This number is much lower than observed in other odontocetes (Perrin et al., 1982, 1994; Mikkelsen & Lund, 1994; Gao & Gaskin, 1996). Some possible explanations for this difference are as follows:

- Some characters examined by these authors were not variable in the franciscana.
- Some characters were not selected for this study because of assessment difficulties.
- Some characters were dropped after having shown total length or sex dependence.

The low number of potentially useful nonmetric skull characters that could be defined during this study did not agree with the conclusion of Perrin et al. (1994) that a great number of relatively



Figure 2. Franciscana skull in ventral view: (a) posteriormost alveolus on left side, (b) fenestration in left vomer, and (c) basioccipital ridge

independent characters can be easily defined. Moreover, the putative advantage of being less affected by preparation methods is also doubtful since it was not possible to examine characters involving fragile bones (such as pterygoid hamuli) because they were frequently damaged.

Asymmetry

The characters that did not prove to be asymmetrical (pairs 15-16 and 17-18) will require special treatment when comparing samples from different regions. Each pair should be treated as one character (and state frequencies should be based on the total number of observable sides as suggested by Sjøvold, 1973) or just one of the two sides should be examined. The lack of significant differences between characters No. 3 and No. 4 reinforces the suggestion of avoiding the former in further analysis.

The frequent absence of asymmetry in nonmetric skull characters might be explained by the genetic basis that governs the expression of the characters in a similar manner on both sides (Brasili et al., 1999). Conversely, asymmetry, as found with characters 6-7 in this study, has been suggested as a consequence of random effects in small samples (not applicable here) or of physiological and/or environmental factors (Brasili et al., 1999). Furthermore, odontocete skull asymmetry has been suggested to be involved in sound production (Berta & Sumich, 1999).

Final Considerations

Due to the low number of potentially useful nonmetric skull characters found in this study, it is uncertain what utility this technique could have as an additional tool for determining franciscana populations. According to Ansorge (2001), the consideration of numerous characters is a prerequisite for the epigenetic value of nonmetric traits, which is the basis for a useful method for evaluating population variation with a mainly genetic expression.

When using nonmetric characters for population differentiation of any species, we recommend the following: (1) minimize subjectivity in skull examination, (2) avoid additional sources of variation before interpopulation comparisons, and (3) study interpopulation differences in each character. An important first step for minimizing



Figure 3. Franciscana skull in occipital view: (a) foramen magnum (irregular shape), (b) fenestration in left supraoccipital, and (c) fenestration in left exoccipital

subjectivity is to define the states of each character as accurately as possible. During this study, the observer found that there was a constant need to consult with other observers, which was not possible. Therefore, we recommend that two observers examine all skulls, first independently and then together. When scores do not agree, "0" state should be assigned. Also, ideally, all specimens to be included in a nonmetric study should be physically pooled and scored in random order in a short period of time in one location. This would lead to more reliable comparisons (see Perrin et al., 1994, for support of this procedure).

Nonmetric character dependence on body length and sex varies widely among different species. Therefore, we emphasize the importance of studying the relation between these variants so as not to attribute significant differences to inappropriate factors. If the skulls examined have been collected over a broad time period (i.e., several generations of the species being studied), we recommend investigation of the existence of character temporal variation. As an example, Zima (1986) provided evidence of genetic drift over time for the pine vole (*Pitymys subterraneus*) by examining 22 nonmetric traits over a period of four years. As there was definitely no population density cycle involved, the observed epigenetic variation between samples from different years appears to be due to genetic drift and microevolutionary changes.

Besides using multivariate techniques to compare several characters at a time among populations, we recommend the study of geographic variation in each character so as to find out which characters can act as good indicators of epigenetic divergence. As an example, characters whose state frequencies are not in agreement with the geographic distance between the regions studied might not really be neutral or somehow linked with metric characters directly subject to selection pressure (i.e., the results would reflect primarily differential selection pressures rather than genetic isolation) (Perrin et al., 1994).

A fourth consideration should focus on the time of publishing the results of interpopulation comparisons in nonmetric characters, for which we suggest the following:

- Defining the characters as exactly as possible
- Mentioning which characters were not variable and which showed body length, sex, or time period differences
- Showing state frequencies of every character examined, together with sample sizes
- Specifying which bilateral characters were asymmetrical and what criterion was considered for the analysis

Finally, both morphological and genetic techniques should be considered in population differentiation studies.

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Number	Sex	TL (cm)	Year	Number	Sex	TL (cm)	Date
4511	F	138	1981	4609	М	125	1974
4512	F	139	1974	4610	М	126	1973
4514	F	140	1974	4611	М	126	1973
4515	F	141	1973	4612	М	126	1973
4516	F	142	1983	4613	М	126	1975
4517	F	142	1973	4614	М	126	1981
4518	F	142	1980	RP821	Μ	127	1998
4520	F	143	1973	4615	Μ	127	1973
4521	F	143	1973	4616	М	127	1973
4522	F	143	1981	4617	М	127	1975
1394	F	145	1964	4618	М	127	1981
4523	F	145	1975	4619	М	127	1974
4524	F	145	1973	4620	М	127	1975
4525	F	145	1980	2462	М	128	1971
4526	F	145	1980	4621	М	128	1973
4527	F	146	1974	4622	M	128	1974
4528	F	146	1975	4623	M	128	1975
4529	F	146	1973	2441	M	129	1971
4530	F	149	1981	4624	M	129	1981
4531	F	150	1981	4625	M	129	1980
4532	F	150	1980	4626	M	130	1981
4533	F	150	1980	4627	M	131	1974
RP822	F	151	1998	4628	M	131	1981
4534	F	151	1980	4629	M	132	1975
4555	F	151	1981	4030	M	132	1981
4530	Г	151	1974	4051	M	132	1980
4537	F	153	1981	1595	M	133	1939
4542	F	157	1981	4633	M	133	1980
4543	F	157	1981	4634	M	134	1981
4544	F	161	1973	4635	M	134	1981
4545	F	163	1974	4636	M	134	1975
4546	F	168	1981	4637	M	134	1981
4547	F	169	1981	4638	М	135	1981
4548	F	174	1981	4639	М	135	1981
4587	М	121	1974	4640	М	136	1973
4588	М	121	1973	4641	М	136	1981
4589	М	121	1981	4642	М	136	1973
4590	М	121	1975	4643	М	138	1973
4591	М	121	1981	4644	М	139	1975
4592	М	122	1973	4645	М	140	1980
4593	М	122	1973	4646	М	140	1974
4594	М	122	1974	4647	М	141	1974
4595	М	122	1973	4648	М	143	1981
4596	М	122	1981	4649	М	143	1980
4597	М	122	1973	4650	М	144	1973
4598	М	123	1981	4651	М	145	1974
4599	М	123	1981	2465	М	146	1971
4600	M	123	1981	4652	М	146	1973
4601	M	123	1974	4653	M	147	1981
4602	M	124	1981	4654	M	147	1973
4003	M	124	1981	4655	M	148	1973
4604	M	124	1974	4656	M	150	1981
2467	M	124	1971	4657	M	151	1973
4005	M	125	1973	4659	M	152	19/4
4000	M	125	1973	4060	M	154	19/3
4608	IVI M	125	1975	4001	111	105	17/4
1000	141	120	1,200				

Appendix 1. Franciscana skulls examined, ordered by sex (F = female, M = male) and total length (TL)