Distribution and morphometrics of South American dolphins of the genus Sotalia

by

Ⓒ Mônica Borobia

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Department of Renewable Resources
Macdonald College of McGill University
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ABSTRACT

A marine form of the South American dolphin, *Sotalia fluviatilis*, has a broad and possibly continuous distribution, having been recorded from Florianópolis, Brazil (27°35'S 48°34'W), north to Panama at 9°22' N. In the Amazon, a freshwater form is commonly observed, having been found as far inland as southern Peru. The southern limit of coastal *Sotalia*'s range corresponds to the confluence of the Brazil and Falkland currents, suggesting low sea surface temperature as a limiting factor, while in freshwater the distribution of Amazonian *Sotalia* seems related to prey species' movements. Univariate and multivariate analyses were performed on 40 morphometric characters and four meristic counts on the skull of 59 museum specimens (38 marine; 21 freshwater) to assess geographical variation in the two forms. Sexual dimorphism was not detected. Marine specimens were significantly larger than those from freshwater, but growth curves of skulls from both forms were comparable. Principal component and cluster analyses confirmed that freshwater and saltwater specimens were separated on the basis of size. Canonical discriminant analysis also distinguished marine from riverine *Sotalia*; no overlap between forms occurred. The best discriminator character was preorbital width. Classification functions were developed that will allow future studies to allocate unknown specimens to one of the two forms. It was not possible to determine the extent of genetic divergence between the two forms, if any. At this point, assigning a subspecific level to the forms seems premature and the current recognition of a single species is supported. However, the marked differences in size and suggest that the two forms should be considered separately for management purposes.

RÉSUMÉ

La forme marine du dauphin d'Amerique du Sud, Sotalia fluviatilis, a une distribution très étendue et possiblement continue, puisqu'elle est connue de Florianópolis (27°35'S 48°34'W), au Brésil, jusqu'à 9° 22'N au Panama. En Amazonie, la forme dulcicole est abondante et a été observée aussi loin à l'intérieur des terres que le sud du Pérou . Au sud, la limite de la distribution côtière de Sotalia correspond à la rencontre des courants du Brésil et de Falkland, ce qui suggère que la température basse de l'eau de surface agit comme facteur limitante. La distribution en eau douce des Sotalia de l'Amazonie, parait dépendre du mouvement de ses proies. Des analyses univariées et multivariées ont été effectueés sur 40 caractères morphométriques et quatre paramètres méristiques provenant des crânes de 59 spécimens de musée (38 marins; 21 dulcicoles) afin d'évaluer la variation géographique des deux formes. Aucun dimorphisme sexuel n'a été noté. Les spécimens marins étaient significativement plus grands que ceux d'eaux douces, mais les courbes de croissance des crânes des deux formes étaient comparables. Les composantes principales ainsi que l'analyse de groupement ont montré que les spécimens marins et d'eau douce étaient separés d'aprés la taille. L'analyse discriminante canonique a aussi permis de séparer sans chevauchement la forme marine de la forme d'eau douce. Le meilleur caractère discriminatoire était la largeur préorbitale. Des fonctions de classification ont été élaborées afin de permettre la classification en fonction de l'habitat de spécimens d'origine inconnue. Il ne fut pas possible de déterminer l'étendue de la divergence génétique entre les deux formes, si toutefois elle existe. Dans l'état actual de nos connaissances, il parait prématuré d'attribuer le statut de sous-espèce aux deux formes; la reconnaissance actuelle d'une seule espèce est entérinée. Cependant, les différences marquées au niveau de la taille suggèrent que les deux formes doivent être considerées séparément à des fins de gestion.

TABLE OF CONTENTS

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LIST OF TABLES

PAGE

SECTION I

SECTION II

LIST OF FIGURES

PAGE

SECTION I

SECTION II

PREFACE

The small South American dolphins of the genus Sotalia that occur on the Atlantic coast and in the Amazon and Orinoco rivers systems have been poorly studied. In the past, Sotalia has been captured for live display in aquaria in the United States, Brazil and Europe (Allen and Neill 1957; Spotte 1967; Waterman 1967; van Foreest 1980). Since 14 October 1982 Sotalia spp. have been listed as endangered species, under appendix I of CITES.

Some aspects of the biology of Sotalia have been examined. Preliminary analyses of reproductive tracts came from animals that died in captivity (Harrison and Brownell 1971), and from accidental captures in the central Amazon (Best and da Silva 1984) and in Surinam (van Utrecht 1981). In captivity, observations of behaviour (Terry 1983, 1984, 1986) and sound production (Caldwell and Caldwell 1970; Norris et al. 1972) have been carried out.

Knowledge of the natural history and habits of Sotalia in the wild is limited. Short term studies on behaviour were conducted by Layne (1958), Magnusson et al. (1980) and Borobia (1984). Qualitative information on feeding habits of marine specimens is provided by Carvalho (1963) and Borobia and Barros (in prep.). The diet of central Amazonian specimens has received more detailed attention (da Silva 1983).

The coastal marine form of Sotalia is reportedly larger than the freshwater form (Mitchell 1975; Watson 1981). Casinos et al. (1981) suggested that differences in skull morphology may exist between specimens from the coasts of Venezuela and Surinam, however the comparison was based on few specimens. The problem of obtaining representative samples of *Sotalia*, due to its current endangered status, curtails studying many aspects of its biology. For this reason, this study was conducted using the available specimens from various collections in the United States, Brazil and Europe.

As *Sotalia* has not been comprehensively studied, much is still to be learned about its ecology in marine and freshwater environments. For example, its distribution patterns and limits have not been defined. Basic problems such as the taxonomic status and identification of different populations, which have long been confused (Hershkovitz 1966; van Bree 1974; Walker 1975; Rice 1977; Husson 1978), have not been previously resolved. The overall aim of this study was therefore, to address the relationship between marine and freshwater *Sotalia* by means of morphological characterization.

As permitted by the Faculty of Graduate Studies, this thesis contains the texts of two manuscripts, Section I to be submitted to Marine Mammal Science, with S. Siciliano, L. Lodi and W. Hoek as co-authors, and Section II to Canadian Journal of Zoology with Dr. D.E. Sergeant as co-author. I carried out the collection of data, analysis and writing of the manuscripts herein. The first paper describes the distribution of *Sotalia*, up-dating it and discussing the factors responsible for its distribution in freshwater and marine environments. The second examines patterns of variation in the skull of these dolphins. The majority of the information in the first manuscript, and all the information in the second, is new.

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THESIS OFFICE STATEMENT

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While the inclusion of manuscripts co-authored by the Candidate and others is not prohibited for a test period, the Candidate is warned to make an explicit statement on who contributed to such work and to what extent, and supervisors and others will have to bear witness to the accuracy of such claims before the Oral Committee. It should also be noted that the task of the External Examiner is much more difficult in such cases.

SECTION I

On the distribution of South American dolphins of the genus *Sotalia*

INTRODUCTION

Sotalia fluviatilis (Gervais 1853) is the most commonly accepted species name (Mitchell 1975; Rice 1977; Casinos et al. 1981; Honacki et al. 1982) for the South American dolphins of the genus Sotalia (Gray 1866). Two forms, i.e., a coastal marine form and a smaller freshwater form, have been distinguished based on skull morphology (this study, section II). Distribution records for this species are scattered in a diffuse literature, or concealed in museum collection records. The material currently available suggests that in marine waters Sotalia is reported from the Atlantic coast of South America from Cananéia, Brazil (Carvalho 1963) to Colombia and as far north as the Caribbean off the Panamanian coast (Bössenecker 1978). It has also been reported from Lake Maracaibo, Venezuela (Casinos et al. 1981) and Trinidad (van Bree 1975), although its presence has not been documented for other eastern Caribbean islands (Caldwell et al. 1971; Casinos 1986; Erdman et al. 1973). Recent observations by Simões-Lopes (1987, 1988) have extended the range southwards to Florianópolis, Santa Catarina, Brazil.

A major freshwater population of Sotalia is found in the tributaries of the Amazon and Orinoco rivers. In the Amazon drainage it has been seen as far up river as Ecuador (Best 1984) and Peru (B.A. Luscombe, in litt.). In the Orinoco, it is known as far up river as Ciudad Bolivar (Mitchell 1975). There is also an early account by Humboldt (1799) (cited in Hershkovitz 1963) which refers to the presence of dolphins, probably Sotalia, in the Manzanares and Apuré rivers and "higher up the Orinoco above the cataracts and in the Rio Atabapo", in Venezuela. Trebbau and van Bree (1974) suggest *Sotalia* can occur in the Caura River and upper part of the Orinoco river, although they have no definitive evidence for this.

This paper attempts to bring together existing often unpublished distribution records of *Sotalia*. These records are used to infer the biological and physical factors affecting the distribution of the species. Also reported are new records for the Brazilian coast, including 12 specimens collected since 1985 (MZUSP 23800-23802, 23809-23814, UFPB 544 and two specimens without register numbers; for museum acronyms see Tables 1 and 2).

MATERIAL AND METHODS

Data were compiled from the collections of various institutions in the United States, Brazil and Europe, and from the scientific literature and from personal observations. Four specimens (SMNH 1122, AMNH 237442, FMNH 99612 and MZUSP 18945) were originally misidentified as *Sotalia* and were not included here; their identities were confirmed as *Delphinus delphis*, *Stenella* cf. *frontalis*, *Tursiops* sp., and *Delphinus delphis*, respectively, based on morphological characteristics and geographic locality. Specimens of unknown or uncertain locality have not been considered. Specimens from Surinam, Guyana and French Guiana were placed with other marine records, since they came from coastal regions with limited influence of freshwater. The same reasoning was applied to the records for Marajó Island (MPEG 10945) and Salinópolis, a characteristic part of the Amazon Basin. These specimens were placed with the freshwater records. Three records were confirmed based only on good quality photographs, and a fifth photographic record was based on Castello and Pinedo (1986).

RESULTS

All confirmed occurrences found for the marine and freshwater forms are listed in Tables 1 and 2, respectively. Site locations are indicated in Figure 1.

There have been over 60 records to date of _Sotalia_ along the Brazilian coast. The new records presented here result from strandings, accidental net catches and sightings. The record from Salinópolis, Pará refers to an animal that was harpooned to serve as bait for the local shark fishery. Specimens accidentally caught in gill nets have been recorded from the coasts of Rio Grande do Norte, Sergipe, Bahia, Espirito Santo, Rio de Janeiro and São Paulo States. Accidental catches seem to be fairly common along the coast of Rio de Janeiro State according to interviews with fishermen and other inhabitants of coastal villages. From June 1987 to May 1988, 33 specimens were caught off Atafona, Rio de Janeiro State (Lodi and Capistrano, _in litt_.). Accidental catches have also been documented for river mouths in Surinam (Husson 1978).

Sotalia is regularly found in Cananéia, São Paulo to Regência, Espirito Santo, Brazil (Schmiegelow 1987; pers. obs.) and in the vicinity of Paramaribo, Surinam (Husson 1978). It is present year round in Guanabara Bay (Andrade _et al_. 1987; Borobia 1984) and Atafona, Rio de Janeiro (Lodi, _in litt_.).

Riverine _Sotalia_ are commonly observed throughout the Amazon system and are most frequently seen in areas with little floating vegetation, river mouths, and in deeper river channels (Layne 1958; Magnusson et al. 1980; da Silva 1983). Its occurrence has been reported for the Amazônia National Park, along the Tapajós river (George et al. 1988) and it has also been observed on the Corantijn river (Surinam) up to Apoera where the tidal influence is still felt (Duplaix 1980).

DISCUSSION

Sotalia can be considered as a tropical dolphin. The numerous coastal records between 20°S and 25°S reflect a higher number of observers in this region, while, conversely, the lack of records for the coast of Ceará, Piaui and Maranhão (between 1°S and 4°45'S.) probably reflects the absence of observers in that region rather than a disjunction in distribution. Sightings were made in different seasons and no apparent seasonality of occurrence was noted.

Cetacean distribution is often correlated with environmental variables such as bottom topography (Hui 1985; Kenney and Winn 1986; Payne et al. 1986) and sea surface temperature (Gaskin 1968; Au and Perryman 1985). This relationship between cetacean distribution and environmental parameters has been interpreted as a reflection of prey distribution (Leatherwood and Walker 1979; Whitehead and Carscadden 1985) since factors that concentrate prey species could directly and/or indirectly influence cetacean distribution. Foraging efficiency should be greater in areas of high prey concentrations and therefore, cetaceans are likely to abound in these areas (Hui 1985; Selzer and Payne 1988). The habitat utilization of Sotalia seems to support such a relationship. The annual rise and fall of Amazonian rivers induces a concentration effect on the fish fauna during the low water period (Goulding 1980). Estuaries are highly productive natural habitats (McLusky 1981; Schubel and Kennedy 1984) and are known to be the preferred feeding grounds of freshwater Sotalia (da Silva 1983; Best 1984). They are also a typical habitat of the marine form (Mitchell 1975; Leatherwood and Reeves 1983; pers. obs.).

Coastal Sotalia have not yet been reported south of Florianópolis (27°35'S 48°34'W). Confluence of the warm Brazil and cold Falkland currents off the coast of southern Brazil (Fig. 1) suggests that sea surface temperature might be acting as a factor limiting distribution of Sotalia. The southernmost 850 km of Brazilian coast are strongly influenced by the cold Falkland current, where sea water surface temperatures average 15°C during winter months. Although the fluctuations of the subtropical convergence have allowed the occurrence of the subantarctic fur seal (Arctocephalus tropicalis), the Antarctic crabeater seal (Lobodon carcinophagus) and the southern elephant seal (Mirounga leonina) on the coast of Rio de Janeiro and São Paulo states (Siciliano 1985), it is unlikely that Sotalia would venture beyond its present southern distribution limit, since over the past years several research groups have searched for stranded marine mammals south of the confluence of the two currents without collecting or sighting Sotalia. This information comes from the works of Pinedo (1982, 1986) along the coast of Rio Grande do Sul, Brazil, Ximenez et al. (1972) and Crespo et al. (1986) for Uruguay and Lichter and Hooper (1984) and Lichter (1986) for Argentinian waters. While the distribution of Amazonian Sotalia seems related to movements of prey species, the southern distribution limit of coastal Sotalia seem to be more closely related to sea surface temperatures. However, until more information on its feeding habits become available no definite conclusion should be drawn.

Marine Sotalia range northward to at least Panama (9°22'N 79°54'W) and, since similar environmental conditions prevail in the Caribbean and adjacent waters, the occurrence of more strandings in these waters might be expected. There exists no evidence for the presence of established populations in the Caribbean. Thus, the available data are not sufficient to allow a correlation of distribution with environment variables.

In summary, the records presented here suggest that Sotalia has a broad and possibly continuous distribution along the Atlantic coasts of Panama and South America, as far as Southern Brazil (27°S). The Amazon delta is an area where the freshwater and marine forms might intergrade.

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Table 1. Confirmed occurrences of the marine form of Sotalia.

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
off Panama	Jan. 1977 ?	________	sightings	Bössenecker 1978
San Antero, Colombia	26 Dec. 1977	ZMA 19784	compl. skel.	Bössenecker 1978
	29 Dec. 1977	ZMA 19775	compl. skel.	Bössenecker 1978
	Dec. 1977	ZMA 19780	compl. skel.	Bössenecker 1978
	Jan. 1978	ZMA 19776	compl. skel.	Bössenecker 1978
Magdalena estuary, near Barranquilla, Colombia	Jan. 1977 ?	________	sightings	Bössenecker 1978
Lake Maracaibo, Venezuela	June 1911	FMNH 18801	rostrum	Osgood 1912
	June 1911	FMNH 18802	rostrum	Osgood 1912
	May 1912	FMNH 34906	compl. skel.	D.L. Bitancourt-Suere
	May 1912	FMNH 34907	compl. skel.	D.L. Bitancourt-Suere
	18 Feb. 1981	EBRG 2748	a skull	Casinos 1981
	18 Feb. 1981	EBRG ?	a skull	Casinos 1981
	18 Feb. 1981	MBUCV 2819		Casinos 1981
Trinidad	?	?	stranding	van Bree 1975
	27 Feb. 1987	USNM ?	skull	Fisheries T.T.
Jct. Mazaruni and Cuyuni rivers, Guyana	11 Aug. 1925	USNM 253476	compl. skel.	S.H. Williams
Cuyuni river, near Kartabo, Guyana	11 Aug. 1925	CM 60941	in alcohol	Williams 1928
	1967	CM 60942	skull	McLaren et al. 1986
Mouth Coppename river, Surinam	13 Oct. 1972	ZMA 15515	compl. skel.	P.J.H. van Bree
	15/30 Nov. 1972	ZMA 15571	compl. skel.	J.J. van Dijk
Mouth Surinam river, Surinam	18 Apr. 1963	RNHL 18168	compl. skel.	Husson 1978
	8 June 1963	RNHL 18166	compl. skel.	Husson 1978
	15 June 1963	RNHL 18167	compl. skel.	Husson 1978
	19 June 1963	RNHL 18165	compl. skel.	Husson 1978
	15 Feb/13 Apr. 1971	RNHL 21755	compl. skel.	Husson 1978
		RNHL 21756	compl. skel.	Husson 1978
		RNHL 22256	compl. skel.	Husson 1978
		RNHL 22257	compl. skel.	Husson 1978
		RNHL 22258	compl. skel.	Husson 1978

Table 1. (Continued)

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
	1 Mar. 1971	ZMA 14641	compl. skel.	H. Lionarons & D. Dekker
	5 May 1971	RNHL 22259	compl. skel.	Husson 1978
		RNHL 22260	compl. skel.	Husson 1978
	23 Oct. 1972	ZMA 15527	compl. skel.	P.J.H. van Bree
nr. Paramaribo, Surinam	May 1964	ZMA 10745	compl. skel.	D.C. Geyskes
Mouth of Maroni river, French Guyana	9 Nov. 1861	IRSNB 1516	compl. skel.	P.J. van Bedenen
	1865	SMNH 26376	skull	A. Kappler
	1865	SMNH 26394	compl. skel.	A. Kappler
Between Oiapoque and Cabo Orange, AP, Brazil	Jul./Aug. 1978	________	sighting	R.C. Best (*in litt.*)
ca. 6km E. Baía Formosa, RN, Brazil	8 Dec. 1986	UFPB 547	skull	C. Bonvicino
Barra de Mamanguape, PB, Brazil	26 Jan. 1986	UFPB 544	compl. skel.	This study
João Pessoa, PB, Brazil	Nov. 1981	UFPB 548	Compl. skel.	A. Langguth
"port of Recife", PE, Brazil	15 Sep. 1986	________	sighting	K. Salwegter
"port of Maceio", AL, Brazil	1 Oct. 1986	________	sighting	K. Salwegter
Pirambú, SE, Brazil	12 Oct. 1986	MZUSP 23814	compl. skel.	This study
Praia do Forte, BA Brazil	27 Dec. 1986	MZUSP 23802	skull	This study

Table 1. (Continued)

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
Arembepe,BA, Brazil	Dec. 1987	UFBA-IB/no#	skull	E.P. de Lima
Baia de todos os Santos, BA, Brazil	30/31 Mar. 1986	——	sighting	This study
	6/7 Oct. 1986	——	sighting	K. Salwegter
Amaralina, BA, Brazil	2 June 1988	UFBA-IB/no#	compl. skel	E.L. de Queiroz
Itacaré, BA, Brazil	28 Apr. 1987	——	sighting	This study
Caravelas, BA, Brazil	12 Jan. 1987	MZUSP 23801	skull	This study
	13 Jan. 1987	MZUSP 23800	25 vert.	This study
Regência, ES,	Feb. 1984	MZUSP 19365	part. skel	Geise & Borobia 1987
	Feb. 1984	MZUSP 19366	part. skel.	Geise & Borobia 1987
	9 Jan. 1987	MZUSP 23809	skull	This study
Vila Velha, ES, Brazil	5 Jul. 1983	RG 926	skull	Barros 1984
Atafona, RJ, Brazil	Jul. 1981	UFRRJ-DGEOC V01	part. skel.	M.A.C. Vogel
	30 Jul. 1985	MZUSP 23813	skull	This study
	17 June 1987	——	sighting	This study
	20 Sep. 1987	——	sighting	This study
	2 Oct. 1987	——	sighting	This study
Ilha da Convivência, RJ, Brazil	1983	UFRJ-AC 01	skull	Geise & Borobia 1988
Barra de São João, RJ, Brazil	20 Oct. 1982	FBCN-GMA 26	photograph (skel. lost)	Borobia 1984
Búzios, RJ, Brazil	Apr. 1984	UFRJ-AC 03	skull	H. de G.Bergallo
	8 Jan. 1977	——	photograph	Castello & Pinedo 1986
Barra de Maricá, RJ, Brazil	21 Sep. 1985	MZUSP 23810	skull	This study
Niterói,RJ, Brazil	1968	?	stranding	Bandoli de Oliveira 1977
	May 1984	MZUSP 19541	skull	Borobia 1984
	8 Jul. 1985	MZUSP 23812	compl. skel.	This study

Table 1. (Continued)

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
	16 Mar. 1987	MZUSP no#	skull	This study
Rio de Janeiro, RJ, Brazil	1888	MNHN-1888-793	compl. skel.	E. van Beneden
		MNHN-1888-791	compl. skel.	E. van Beneden
		MCZ 7097	compl. skel.	Thayer Exp.
	Apr. 1933	MNRJ 123	skull	FIOCRUZ
	Jul. 1933	MNRJ 124	skull	FIOCRUZ
	5 Aug. 1983	FBCM-GMA 27	photograph (skel. lost)	Borobia 1984
	1 Jul. 1985	MZUSP 23811	compl. skel.	This study
	27 Feb. 1988	MZUSP	skull	This study
Ibicuí, RJ, Brazil	1 Feb. 1986	________	photograph	L.J. de Araújo Neto
Ilha Grande, RJ, Brazil	Nov. 1986	FEEMA 706	compl. skel.	N.C. Maciel
Santos, SP, Brazil	Feb. 1961	MZUSP 9417	compl. skel.	Carvalho 1963
	Oct. 1961	MZUSP 9611	compl. skel.	Carvalho 1963
	?	IPS	skull	IPS (publ. exhib.)
	?	IPS	compl. skel.	IPS (publ. exhib.)
S. Ilha Bela, SP, Brazil	1 Mar. 1981	________	sighting	Castello & Pinedo 1986
Cananéia, SP, Brazil	3 Aug. 1961	MZUSP 9605	compl. skel.	Carvalho 1963
	3 Aug. 1961	MZUSP 9606	part. skel.	Carvalho 1963
	Aug. 1962	MZUSP 9821	compl. skel.	Carvalho 1963
	30 Apr. 1964	MZUSP 10227	part. skel.	C.T. de Carvalho
	30 Apr. 1964	MZUSP 10228	part. skel.	C.T. de Carvalho
	23 May 1964	MZUSP 18923	compl. skel.	unknown
	17 Jul. 1964	MZUSP 10230	compl. skel.	C.T. de Carvalho
	17 Jul. 1964	MZUSP 10231	part. skel.	C.T. de Carvalho
	20 Aug. 1964	MZUSP 10232	compl. skel.	C.T. de Carvalho
	31 Aug. 1964	MZUSP 10402	compl. skel.	C.T. de Carvalho
	Aug. 1964	MZUSP 18943	skull	C.T. de Carvalho
	Aug. 1964	MZUSP 18944	skull	C.T. de Carvalho
	1964	MZUSP 19403	compl. skel.	C.T. de Carvalho
	21/23 June 1965	MZUSP 18874	skull	C.T. de Carvalho
	11/15 Apr. 1987	________	sighting	This study
Baía de Paranaguá, PR, Brazil	30 Jul. 1982	?	netted	Bittencourt 1984

Table 1. (Continued)

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
Florianópolis, SC, Brazil	12 Nov. 1985	UFSC 1010	part. skel.	Simões-Lopes 1987

Abbreviations: compl. skel. = complete skeleton; vert. = vertebrae; part. skel. = partial skeleton; skel. lost = skeleton lost; jct = junction; publ. exib. = public exhibit; AP = Amapá; PA = Pará; RN = Rio Grande do Norte; PB = Paraíba; PE = Pernambuco; AL = Alagoas; SE = Sergipe; BA = Bahia; ES = Espírito Santo; RJ = Rio de Janeiro; SP = São Paulo; PR = Paraná; SC = Santa Catarina; ZMA = Instituut voor Taxonomische Zoologie; FMNH = Field Museum of Natural History; EBRG = Estación Biologica de Rancho Grande; MBUCV = Museo de Biología de la Universidad Central de Venezuela; USNM = National Museum of Natural History; CM = Carnegie Museum of Natural History; RNHL = Rijksmuseum van Natuurlijke Historie; IRSNB = Institut Royal des Sciences Naturelles de Belgique; SMNH = Staatliches Museum fur Naturkunde; UFPB = Universidade Federal da Paraíba; MZUSP = Museu de Zoologia da Universidade de São Paulo; UFBA = Universidade Federal da Bahia; RG = Museu de História Natural de Curitiba; UFRRJ-DGEOC = Dept. de Geociências, Universidade Federal Rural do Rio de Janeiro; UFRJ-AC = Dept. de Anatomia, Universidade Federal do Rio de Janeiro; FBCN-GMA = Grupo de Mamíferos Aquáticos, Fundação Brasileira para a Conservação da Natureza; MNHN = Muséum National d'Historie Naturelle; MCZ = Museum of Comparative Zoology; MNRJ = Museu Nacional do Rio de Janeiro; FIOCRUZ = Fundação Instituto Oswaldo Cruz; FEEMA = Fundação Estadual de Engenharia do Meio Ambiente; IPS = Instituto de Pesca de Santos; UFSC = Universidade Federal de Santa Catarina;

Table 2. Confirmed occurrences of the freshwater form of *Sotalia*.

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
Urubamba river, Peru	1987	———	sighting	B.A. Luscombe (*in litt*.)
Pucallpa, Peru	26 Mar. 1965	UF 18785	skull	J. Schinke
Pastaza river, Peru	1987	———	sighting	B.A. Luscombe (*in litt*.)
Napo river, Peru	———	———	collected	Zam *et al*. 1971
Leticia, Colombia	4 Dec. 1956	UF 1215	skull	Layne 1958
	1957	———	sighting	Allen & Neill 1957
	25 Sep. 1963	MCZ 52235	compl. skel.	Tarpoon zoo
	Sep. 1964	LACM 19594	compl. skel.	Tarpoon zoo
	1966	UF 17546	compl. skel.	Tarpoon zoo
	1966	UF 18782	compl. skel.	Tarpoon zoo
Fonte Boa, AM, Brazil	1880	MNHN-1880-549	part. skel.	W.H. Bates ?
Juruá river, AM, Brazil	23 June 1980	MA 38	compl. skel.	Best & da Silva 1984
	23 June 1980	MA 39	compl. skel.	Best & da Silva 1984
Amanã Lake, AM,	29 Aug. 1979	MA 15	part. skel.	Best & da Silva 1984
	29 Aug. 1979	MA 16	part. skel.	Best & da Silva 1984
	5 Nov. 1979	MA 24	part. skel.	Best & da Silva 1984
	22 Nov. 1979	MA 25	compl. skel.	Best & da Silva 1984
	24 Nov. 1979	MA 26	part. skel.	Best & da Silva 1984
	12 Dec. 1979	MA 27	part. skel.	Best & da Silva 1984
	16 May 1980	MA 31	compl. skel.	Best & da Silva 1984
	17 May 1980	MA 32	part. skel.	Best & da Silva 1984
	9 Nov. 1980	MA ?	compl. skel.	Best & da Silva 1984
Tefé Lake, AM,	24 May 1979	MA 05	part. skel.	Best & da Silva 1984
	24 May 1979	MA 06	compl. skel.	Best & da Silva 1984
Purús river, AM, Brazil	4 Aug. 1980	MA 40	compl. skel.	Best & da Silva 1984
Solimões river, AM, Brazil	31 Aug. 1981	MA 51	part. skel.	Best & da Silva 1984
	31 Aug. 1981	MA 52	compl. skel.	Best & da Silva 1984

Table 2. (Continued)

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
Negro river, AM, Brazil	18 Mar. 1980	MA 28	part. skel.	Best & da Silva 1984
	23 Apr. 1980	MA 36	compl. skel.	Best & da Silva 1984
	Sep. 1980	MA 41	part. skel.	Best & da Silva 1984
Boiuçu Lake, RO, Brazil	11/12 Sep. 1968	MZUSP 18948	skull	EPA
	11/12 Sep. 1968	MZUSP 18949	skull	EPA
Cuieiras river, AM, Brazil	15/16 Oct. 1965	CAS 13947	part. skel.	E.S. Herald
	15/16 Oct. 1965	CAS 16658	part. skel.	R. Brownell & E.S. Herald
	15/16 Oct. 1965	LACM 49708	part. skel.	Harrison & Brownell 1971
	15/16 Oct. 1965	LACM 49709	part. skel.	Harrison & Brownell 1971
Manaus, AM, Brazil	25 Jul. 1930	AMNH 92203	compl. skel.	Ollala Bros.
Amazon river, AM, Brazil	30 Aug. 1980	MA 42	compl. skel.	Best & da Silva 1984
	30 Aug. 1980	MA 43	compl. skel.	Best & da Silva 1984
	31 Aug. 1980	MA 44	part. skel.	Best & da Silva 1984
	31 Aug. 1980	MA 45	compl. skel.	Best & da Silva 1984
	Aug. 1980	MA 46	compl. skel.	Best & da Silva 1984
	31 Aug. 1980	MA 47	compl. skel.	Best & da Silva 1984
	31 Aug. 1980	MA 48	part. skel.	Best & da Silva 1984
100 mi. from jct. of Negro and Amazon rivers, AM, Brazil	11 Aug. 1932	LACM 30790	part. skel.	A.E. Colburn
Madeira river, AM, Brazil	13 Jan. 1981	MA 48	compl. skel.	Best & da Silva 1984
Serpa Lake, AM, Brazil	9 Jul. 1937	MNRJ 6030	skull	Ollala Bros.
Faro Lake, AM, Brazil	11 Feb. 1931	AMNH 94169	skull	Ollala Bros.
Parintins, AM, Brazil	Oct. 1982	________	sightings	This study
	Jan. 1984	________	sightings	This study
Oriximiná, PA, Brazil	26 Aug. 1968	MZUSP 18924	part. skel.	EPA

Table 2. (Continued)

Locality	Date collected or observed	Museum number	Specimen or evidence	Reference or collector
Óbidos, PA, Brazil	1864	________	sighting	Bates 1864
Trombetas river, PA, Brazil	7/11 Oct. 1969	MZUSP 18946	skull	EPA
	7/11 Oct. 1969	MZUSP 19913	compl. skel.	EPA
Santarém, PA, Brazil	1856	BMNH 1856.8.2.2	skull	H.W. Bates
	1856	BMNH 1856.8.2.3	skull	H.W. Bates
Mouth of Tocantins river, PA, Brazil	1864	________	sighting	Bates 1864
Marajó Island, PA Brazil	9 Dec. 1982	MPEG 10945	compl. skel.	R. Barthem
Salinópolis, PA Brazil	25 Feb. 1984	________	photograph	This study

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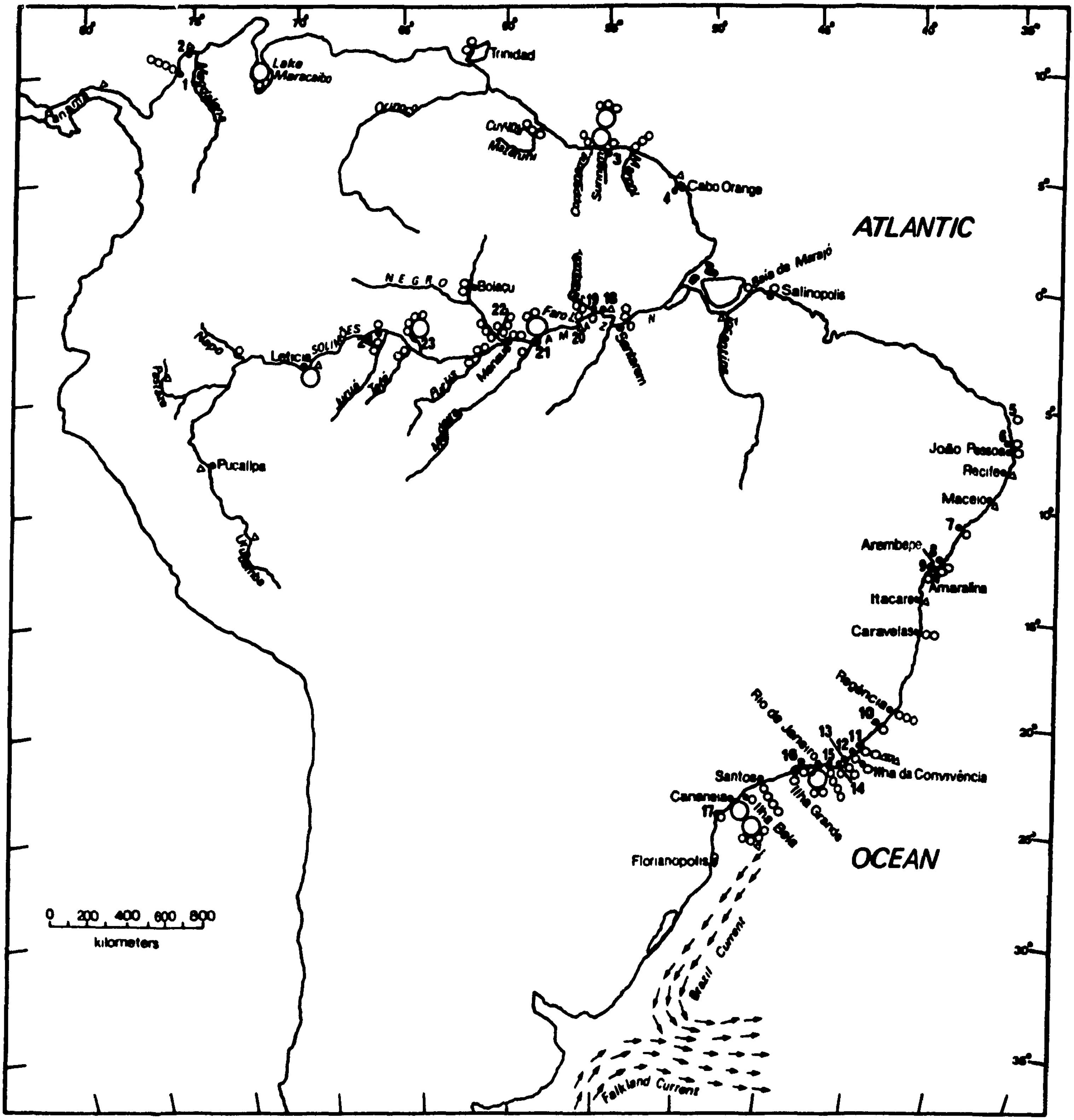
Abbreviations: comp. skel. - complete skeleton; part. skel. - partial skeleton; AM - Amazonas; RO - Roraima; PA - Pará; UF - The Florida State Museum; MCZ - Museum of Comparative Zoology; LACM - Los Angeles County Museum of Natural History; MNHN - Muséum National d'Histoire Naturelle; MA - Mamiferos aquáticos, Instituto Nacional de Pesquisas da Amazônia; MZUSP - Museu de Zoologia da Universidade de São Paulo; EPA - Expedição Permanente da Amazônia (MZUSP); CAS - California Academy of Science; LACM - Los Angeles County Museum of Natural History; AMNH - American Museum of Natural History; MNRJ - Museu Nacional do Rio de Janeiro; BMNH - British Museum (Natural History); MPEG - Museu Paraense Emílio Goeldi.

Figure 1. Distribution of marine and freshwater *Sotalia*. ○ - 1 specimen collected; ◯ - 5 specimens collected; △ - sighting; 1 - San Antero; 2 - Magdalena estuary; 3 - Paramaribo; 4 - Oiapoque; 5 - Baía Formosa; 6 - Barra de Mamanguape; 7 - Pirambú; 8 - Praia do Forte; 9 - Baía de todos os Santos; 10 - Vila Velha; 11 - Atafona; 12 - Barra de São João; 13 - Búzios; 14 - Barra de Maricá; 15 - Niterói; 16 - Ibicuí; 17 - Baía de Paranaguá; 18 - Óbidos; 19 - Oriximiná; 20 - Parintins; 21 - Serpa Lake; 22 - Cuieiras river; 23 - Amanã Lake; 24 - Fonte Boa.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Baía de Marajó
Salinopolis
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Boiaçu
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Tocantins
Napo
Leticia
SOLIMÕES
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Tefé
Purus
Manaus
Madeira
Pucallpa
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Recife
Maceio
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Amaralina
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Caravelas
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Rio de Janeiro
Ilha da Convivência
Santos
Cananeia
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Ilha Bela
Ilha Grande
Florianopolis
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kilometers
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Falkland Current

CONNECTING STATEMENT

Section I demonstrated that Sotalia has a continuous distribution from Florianópolis to Panama, and is frequently observed throughout its range. Their distribution may be affected by environmental factors such as sea surface temperature and food availability. In view of these findings, Section II examines the morphological variation of Sotalia in both marine and freshwater environments in an attempt to identify possibly differences in these morphs.

SECTION II

Patterns of variation in the skull of South American dolphins of the genus *Sotalia*

INTRODUCTION

The South American dolphins of the genus *Sotalia* (Gray 1866) have been little studied. Although Flower (1884) and True (1889) have raised the question of the existence of different species in this genus, it has remained a matter of taxonomic controversy (Hershkovitz 1966; van Bree 1974; Walker 1975; Rice 1977; Husson 1978). Historically, the following five nominal species have been described: *Sotalia* *fluviatilis* (= *Delphinus* *fluviatilis* Gervais 1853); *S*. *pallida* (= *Steno* *tucuxi* Gray 1856); *S*. *guianensis* (= *Delphinus* *guianensis* P.J. van Beneden 1864) and *S*. *brasiliensis* E. van Beneden 1875. Of these, *S*. *guianensis* is from French Guiana; *S*. *brasiliensis* from the Bay of Rio de Janeiro and *S*. *fluviatilis*, *S*. *pallida* and *S*. *tucuxi* from different portions of the Amazon. Currently, only *Sotalia* *fluviatilis* (Gervais 1853) is recognized (Mitchell 1975; Honacki *et* *al*. 1982; Leatherwood and Reeves 1983) with a freshwater form inhabiting the Amazon and Orinoco river systems (Hershkovitz 1963; da Silva 1983; Best 1984), and a marine coastal form occurring on the Atlantic coast of South America, from Florianópolis, Brazil (Simoes-Lopes 1987, 1988) to Panama (Bössenecker 1978) (Fig. 1).

Mitchell (1975) and Watson (1981) reported that marine *Sotalia* have a larger body size than the freshwater form. However, Casinos *et* *al*. (1981) compared condylobasal length of three specimens from Lake Maracaibo, Venezuela with those of five specimens from the Surinam coast and found that the former specimens were smaller. They suggested that marine *Sotalia* might not be as morphometrically uniform as previously thought.

This paper examines skull morphology of marine and freshwater forms of Sotalia, and estimates growth parameters of the marine form. Patterns of morphological variation of skulls are used to assess relationships between the two morphs.

Accidental killing of both forms of Sotalia occurs in the Amazon (Best and da Silva 1984), Surinam (Husson 1978) and different regions of Brazil (Geise and Borobia 1987; this study, section I). The ability to recognize morphs can be critical in identifying populations and implementing conservation and management measures by taking into account their habitat utilization.

MATERIAL AND METHODS

Data collection

A total of 108 specimens were examined from different collections in Brazil, the United States and Europe. Four of these specimens (AMNH 237442, FMNH 96612, MZUSP 18945 and SMNH 1122) were originally misidentified as Sotalia. Of the remaining 104 specimens (Appendix 1), 15 have been excluded, either because a large number of characters could not be measured due to skull damage, or due to unknown geographical origin. Specimens considered for analyses numbered 89.

Characters selected for the study were based on those used by Perrin (1975), Schnell et al. (1985), and characters suggested by E. D. Mitchell (pers. comm.).

A series of four meristic counts and 56 morphometric cranial characters were measured. Due to small sample sizes, 16 variables were deleted from the analysis, including those dealing with the hyoid complex and the tympanoperiotics. A total of 40 cranial characters remained from the original 56. These measurements together with the meristic counts are listed in Appendix 2 and illustrated in Figures 2 to 6. Most measurements were recorded to the nearest 0.10 mm with a dial vernier caliper, while others were taken to the nearest millimeter with larger outside calipers.

Following Perrin (1975), internal length of the braincase was measured with the interior extension of the dial caliper. The angle of asymmetry of the skull was measured in degrees with a two-armed plastic flexible protractor. In cases where the rostrum was warped during preparation the tip of the maxillaries were squeezed so that the premaxillaries could meet in the midline. When teeth were missing, their alveoli were included in the tooth counts. All measurements were taken by the first author.

Complementary qualitative observations on state of closure of cranial sutures and other features on the skull were made. In addition, black and white photographs were taken from all specimens. Data on locality, date of collection, sex, collector, and information on body length and reproductive status were recorded when available.

In order to age the specimens, 1 to 4 teeth were taken, when possible, from the middle portion of the lower left jaw. Teeth from this portion are less likely to be worn or cracked. If these teeth were not in place, 1 to 4 large straight teeth were selected from those available. Teeth from 19 specimens, including two type specimens (BMNH 1856.2.2.2. and MNHN 1880-550) and nine specimens from the Instituut voor Taxonomische Zoólogie, Amsterdam (ZMA) could not be obtained. Four of these and seven from the Rijksmuseum van Natuurlijke Historie, Leiden were previously aged by van Utrecht (1981). His age estimates were used only for the ZMA specimens.

The presence of layers in tooth dentine has been used for age determination in several odontocete species (Sergeant 1959; Kasuya 1972; Ross 1977; Hohn 1980; Miyazaki 1980; Akin 1988). Growth layer groups (GLGs) counts in dentine were used as the method to estimate age of the specimens here, and were counted through polarized transmitted light. Readings were done on the basis of the overall pattern of layering. One GLG was composed of one outer opaque and one inner transluced layer. A low speed diamond circular saw was used to cut thin longitudinal sections of about 75μm thick. Sections which passed through the most central portion of the tooth were used. Age estimates were the mean of three determinations, which were done "blind" with an interval ranging from two days to a week between successive readings of the same section.

Recognition of juveniles

Morphometric characters are affected by changes in proportional growth in juveniles (Perrin 1975; Douglas et al. 1986; Schnell et al. 1986; Walker et al. 1986). Thus, juveniles should be identified and excluded from this study. Specimens that met at least one of the following criteria were used in these analyses:

1. had attained sexual maturity,
2. had five or more growth layer groups (GLGs) in tooth sections (see data analysis, p. 28),
3. had a high degree of cranial ossification, characteristic of adulthood.

From the 89 specimens initially considered for analysis, 59 met the above criteria.

Data analysis

Skull measurements and body lengths were plotted against aged animals to describe patterns of growth. The von Bertalanffy growth equation was used to fit only the age-body length data of marine specimens. The equation is:

$$\text{Body length} = B_o\ [1-\exp\ (-B_1\ X + B_2)],$$

where B_o is the limiting (or asymptotic) length; B_1 is a rate constant; X is age in years and B_2 is the age at which body length is equal to zero, as determined by the growth model. The growth curve was produced using the NONLIN procedure of PC-SAS (SAS Institute Inc. 1987). In general, the growth curves of skull characters began approaching a plateau at about five GLGs. Thus, specimens with less than or with five GLGs were considered juveniles and were deleted from the analyses. The possibility of sexual dimorphism was assessed before proceeding with an analysis of geographical variation using Student's t-test (TTEST procedure, PC-SAS). Mean differences between sexes were compared, but only for marine specimens, as aged and sexed riverine specimens were few (3 males and 8 females). Homogeneity of variances were checked using an F-test. Given that t-tests showed no significant differences for marine Sotalia (see Results), it was assumed that there was no prominent sexual dimorphism present in the skull of either form. Sexes were combined for all further analyses.

Univariate comparisons of mean characters between freshwater and marine

Sotalia were carried out as an initial step in the assessment of morphological variation of the two groups. The interrelationship among individuals was further explored using a principal component analysis (PRINCOMP procedure PC-SAS) based on a correlation matrix computed from the values of the variables, rather than on a covariance matrix. This is recommended when dealing with variables measured in different units (Neff and Marcus 1980; Reyment et al. 1984). The use of ratios is common in morphometric studies, however, they have several drawbacks (Sokal and Rohlf 1981; Reyment et al. 1984) and were not used here.

Specimens could be classed a priori as marine or freshwater based on collection region. A canonical discriminant analysis (CANDISC procedure PC-SAS) was applied in order to identify the variables that, in a linear combination, provide the best morphological differentiation between the two forms by evaluating their relative contribution to the discrimination. This was done through the absolute value of the standardized coefficients, i.e, the larger the magnitude, the greater the contribution of the variable (Klecka 1986). Specimens from Surinam and one from French Guiana were placed with other marine specimens since they came from coastal regions with limited influence of freshwater. Specimens were plotted onto the resulting canonical axis; their position in the canonical space was located by multiplying the matrix of centered data with the raw coefficients obtained from the procedure. The canonical discrimination was also carried out on log-transformed data. Classification functions were developed by the DISCRIM procedure PC-SAS, based on the whole set of 44 characters as well as on the best discriminating variables given by the discriminant function. These functions can be used to assign a specimen of unknown form to one of the two groups, i.e., marine or freshwater form. The values of the characters are multiplied by the classification coefficients of the two functions, and each resulting product is then added to the constant of these functions. A specimen would belong to the form for which the resulting classification value is the largest. Eight freshwater and 20 marine specimens that were not used to compute the classification coefficients were selected to test the efficiency of the classification functions in correctly identifying new specimens. This test was only done for the classification functions generated by the best discriminating variables since all 28 specimens in the test data set had missing values, and therefore could not be used in the 44 variable classifications.

To further investigate the degree of similarity between individuals and the possible existence of morphologically distinct subgroups within each form, an average linkage cluster analysis (CLUSTER procedure PC-SAS) was performed. As indicated by the principal component analysis (see Results), the first component was interpreted as a general measure of size. In an attempt to minimize the influence of size, and maximize the contribution of components assumed to contain skull shape information , clustering was also performed on the generated scores of the components II to IX only.

RESULTS

A growth curve for Sotalia is shown in Figure 7. The model seemed acceptable when applied to growth of Sotalia, since visual inspection revealed no systematic discrepancies between data and the fitted curve. The parameters estimated for the fitted curve were as follows: B_0 = 187.21 cm

(SD= ± 9.91), B_1 = 0.2 (SD= ± 0.12) and B_2 = - 0.81 (SD= ± 0.08). Based on the model, the estimated length at birth is 105.0 cm. Approximately 85% of asymptotic length is reached at about five GLGs and 95% at about 10 GLGs. Data from riverine specimens, plotted for comparison, suggested an attainment of smaller body size.

Representative scatterplots of skull measurements versus number of dentinal layers illustrate some of the patterns of skull growth in both freshwater and marine forms (Figs. 8 to 12). Portions of the skull related to feeding, especially those involving length measurements of rostrum and mandible (length of rostrum, length of upper and lower tooth row, and length and height of ramus), exhibited a similar pattern of growth in both forms (Figs. 9 and 10). In these characters there was a rapid initial growth phase in young animals (≤ 4 GLGs), followed by attainment of a plateau which was about 1.8 X measurements in the 1 GLG age class. In comparison to the feeding apparatus, characters related to breathing and sound-production such as width of external nares and length of mandibular fossa (Fig. 11) and those in the braincase (Fig. 12) showed precocious development with a plateau achieved shortly after birth (≤ 2 GLGs) of about 1.4 X the size of 1 GLG animals. At corresponding GLGs, measurements from freshwater Sotalia tended to be smaller than those from marine forms, although some overlap occurred (Figs. 8 to 12). Examination of the growth curves indicated that at ≥ 5 GLGs both forms had reached adult size in all characters.

The dentinal patterns of Sotalia were basically similar to those observed in other delphinids. The prenatal dentine was poorly layered or unlayered. Neonatal lines were thin translucent layers. Growth layer groups (GLGs) in the postnatal dentine were composed of a first thick opaque layer followed by a thinner translucent layer. Subsequent GLGs were formed of opaque and translucent layers of similar thickness. The cementum usually contained very fine layers. When three repeated readings of each section were done, about 80% of the specimens were within a range (max-min) of ≤ 3 GLGs. No representative samples of known age classes were available to permit a detailed serial description of dentinal patterns. There exists no adequate calibration of deposition rate of GLGs for Sotalia, therefore no correspondence to age in years was attempted.

Results of the t-tests between sexes for marine Sotalia revealed that only two characters (distance from nasals to supraoccipital crest and length of orbit) showed significant differences between males and females (Table 1). However, differences between sexes were still smaller than those between forms. This might have also been a chance result, since a large series of t-tests are likely to produce chance significant values (about one in 20 at the 0.05 level of significance). Other than this, there was no evidence of significant sexual differences in the skull of marine Sotalia. It was assumed that similar, low levels of sexual dimorphism occurred in the freshwater form and, therefore, sexes were grouped for all subsequent analyses. Comparisons of character means between freshwater and marine forms demonstrated significant differences in 32 of 37 characters (Table 1); seven characters of the original 44 were not tested because of non-homogeneity of variances. Variation between marine and freshwater forms was highly significant ($p<0.01$) for upper tooth counts and nonsignificant for lower counts, width at pterygobasioccipital sutures and skull asymmetry. All other character differences were highly significant ($p<0.001$). Overall, marine Sotalia were significantly larger than freshwater animals in most characters.

The principal component analysis revealed that the first nine principal components accounted for 83% of total variation, with principal component I explaining 52% of character variance and components II to IX, the remaining 31% (Table 2). The first component had positive loadings on 43 of the 44 characters (Table 3), the exception being a small negative loading for skull asymmetry. This was interpreted as suggesting that component I was a measure of overall skull size. All other eight components (II to IX) had combinations of positive associations in some variables and negative associations on others (Table 3). This was interpreted as indicating that these components contained information on shape of the skull. Figure 13 shows that the first component separates marine specimens from those of freshwater; no separation of groups seems to occur along the principal component II. Similarly, plots of other shape components (III-IX) showed no evidence of the separation of the two groups. Marine specimens in general exhibited larger skulls than those from freshwater.

Coefficients from a canonical analysis can be used to indicate the discriminating potential of each character (Legendre and Legendre 1983). Evaluation of standardized coefficients resulting from the canonical discriminant analysis (Table 4) showed that the best character for separating the two forms was preorbital width. The other characters related to orbital region (supraorbital and postorbital widths) together with condylobasal length were among the top four that provided best discrimination (Table 4). Figure 14 shows the projection of all specimens into the discriminant function. No overlap occurred between marine and freshwater forms, which were completely separated along the canonical axis that represented 97% of the variance between groups. Comparable results were obtained from a discriminant analysis conducted on log-transformed data and therefore are not presented here.

The coefficients of the classification functions developed from the 10 best discriminating variables appear in Table 5. Of the 28 specimens of known provenance used to test the classification functions, 100% of the freshwater group and 75% of the marine group were properly identified. Although it was not possible to test the efficiency of the classification functions generated from the 44 characters due to missing data, their coefficients are shown in Table 6, since they can be used to allocate complete unknown specimens.

The dendrogram obtained from the cluster analysis on the correlation matrix of raw data is illustrated in Figure 15. At the five cluster level (average linkage= 0.9), two large clusters were formed; cluster D, mainly composed of freshwater animals, with few specimens from saltwater, and cluster E, solely composed of marine specimens. Cluster A included three specimens from the central Amazon region. One specimen from the upper Amazon and another from southeastern Brazil formed separate clusters (B and C) from all other specimens. Further examination of clusters D and E at the 0.6 level revealed no indication of defined subgroups on a geographic basis. The dendrogram resulting from the analysis carried out on the scores of the principal components was somewhat similar, in terms of general configuration and number of clusters formed, to that shown in Figure 15. However, they differed as to which specimens were clustered together, and marine and freshwater specimens were mixed in different clusters. None of the subgroups within major clusters of either dendrogram corresponded with sex.

DISCUSSION

The von Bertalanffy growth model is frequently used to describe growth of marine mammals (Kingsley 1979; McLaren and Smith 1985; Hammill 1987). This model provided a good fit when applied to data from marine Sotalia, and the estimated asymptotic size of 187.2 cm seems reasonable since the largest known specimen of marine Sotalia is a 206 cm female (Barros 1984) that was not included in the fitting of the growth curve. By contrast, largest known specimens of freshwater Sotalia are considerably smaller than the asymptotic length for marine forms. Best (1984) gives an average of 150 cm for freshwater Sotalia, while Layne (1958) refers to the type specimen of Delphinus pallidus (MNHN 1380-549 ?) (= S. fluviatilis) as being 165 cm. This suggests that either representative samples of freshwater animals over the entire range of body length have not been collected, or that freshwater Sotalia achieves a smaller asymptotic length than marine forms. The generally smaller size of all skull measurements in freshwater forms than in marine at corresponding GLGs supports the latter interpretation. This is in accordance with the hypothesis of Mitchell (1975) and Watson (1981) that freshwater Sotalia are smaller than marine Sotalia. The estimate of size at birth (105 cm) was about 20% larger than an independent report by Best and da Silva (1984). They suggested 75 cm as length of birth for Amazonian Sotalia, based only on body length data; their largest neonate was 83 cm. Harrison and Brownell (1971) reported a neonate of 85 cm. These body lengths for freshwater neonates are smaller than that of a 88 cm fetus (from specimen MZUSP 10230) from marine Sotalia. This indicates that the estimate of body length at birth by the model is probably close to an actual value. As there are no previous estimates of growth parameters for either form of Sotalia, and only limited data on age and body length are available, a more detailed comparison of body size between groups and areas awaits larger samples of aged animals.

In this study the dentinal layer counts were reasonably consistent as about 80% of the specimens were within a range of ≤ 3 GLGs. This contrasts with the study of van Utrecht (1981), who after examining teeth from 10 specimens found that in the case of older animals (more than 7 to 8 dentinal layers) the dentine tubules are no longer parallel to each other, coming together in one point to form a brush-like structure. Van Utrecht (1981) concluded that this feature disrupts the pattern of dentine layering and makes age determination in Sotalia unreliable. It is generally recognized that, for most odontocetes, growth layer groups in teeth become more difficult to be counted as the age of the specimens increases. Therefore, it is expected that unsuitable tooth sections may be encountered. Although some sections of lower quality made it hard to identify whether the brush-like structure reported by van Utrecht (1981) was present, in many good sections of older animals this structure was not detected. Our technique was similar to that used by van Utrecht, except that we examined much thinner sections (75 μm, as opposed to 120 μm). This might have contributed to his difficulty in assessing the dentinal layers. We suggest that by employing thinner sections, as used here, age determination in Sotalia may not be as unreliable as suggested by van Utrecht (1981).

Nevertheless, this question is not completely resolved, encouraging the development of other methods such as histological procedures, to determine if improved readings could be achieved.

The facial region of odontocetes is characterized by a cranial asymmetry, a feature unique among mammals. This is a result of a telescoping of the skull e.g. the posterior movement of the nares to a dorsal position (Miller 1923). This asymmetry was interpreted by Mead (1975) as being related to the function and form of the nasal apparatus in sound production and reception. Perrin (1975) hypothesized that, given the importance of the acoustic sense to odontocetes, development of breathing and sound-producing apparatuses should be precocious. Although the tympanoperiotics were not analysed, the development patterns found in Sotalia seem in accordance with his hypothesis. Perhaps an early development of the sound-producing apparatus has a survival value for Sotalia, since the turbid waters of coastal regions, and particularly those of the Amazon, may reduce visibility to a minimum. The dolphins may benefit from rapid development of an echolocating system, rather than relying on visual contacts to interprete the cues of its environment. Morgane and Jacobs (1972) reported that Sotalia has 19,500 fibers in the optic nerve, a very low count when compared with some 150,000 to 170,000 found in oceanic species. Furthermore, the Indian river dolphin, Platanista gangetica, also living in the turbid waters of the Ganges river, has no functioning eyes (Herald et al. 1969). The findings from this study that measurements involving the orbital region were among the best separating the two forms may be an indication of the differences in overall importance of vision between the marine and freshwater environments. Yurick and Gaskin (1988) found that in harbour porpoises (Phocoena phocoena) from the Bay of Fundy, the sound-producing apparatus is fully developed at a very young age. In general, the patterns of development observed for other functional portions of the skull of Sotalia agreed with those recorded for spotted and spinner dolphins, genus Stenella (Perrin 1975) and those for pilot whales, genus Globicephala (Polisini 1980).

Sexual dimorphism is a characteristic of several odontocete species (Sergeant 1962; Omura 1972; Machin 1974; McCann 1975). This study did not focus on sexual dimorphism, but only assessed whether or not the sexes would have to be treated separately in the analyses. Nevertheless, it is interesting to note that few significant sexual differences were found in the skull of Sotalia. The absence of prominent sexual differences was further supported by the results of the cluster analysis, which did not indicate subclusters formed on the basis of sex. Best and da Silva (1984) reported an apparent tendency for riverine females to be slightly larger than males, but acknowledged a small sample size. Other tropical dolphins, such as the bottlenose dolphin (genus Tursiops), only exhibit a mild dimorphism in skull morphology (Hersh 1987). If further samples become available, the issue of sexual dimorphism in external measurements and in the skeleton of freshwater Sotalia should receive a more detailed consideration.

The study of morphological variation has been used as a basis for characterization of different populations in various delphinids. Douglas et al. (1984) differentiated between offshore and inshore spotted dolphins (Stenella attenuata) in the eastern tropical Pacific Ocean and Schnell et al. (1985) evaluated sexual dimorphism in the skull of this species.

Recently, a revision of the species of spotted dolphins in the genus *Stenella* was completed (Perrin *et al*. 1987). Robineau and Buffrenil (1985) used a combination of metric and non-metric methods to study the relationship among Commerson's dolphins (*Cephalorhyncus commersonii*). Yurick and Gaskin (1987) identified four major populations of harbour porpoise using morphometric methods.

Results from univariate and multivariate tests suggest that freshwater and marine forms are distinct from each other. The skulls of marine specimens were considerably larger than those of dolphins from freshwater regions. However, differentiation in morphological characters seems to be largely based on differences in size alone. The principal component analysis failed to provide distinction between the two forms along any component other than the first, which contained primarily size information. Studies of morphological variation involving seals, whales and fish parasites (Machin and Kitchenham 1971; Shostak *et al*. 1986; Wiig 1986) have also interpreted the first principal component as a measure of overall size. Likewise, the clusters emerging from the analysis carried out on the remaining principal components scores, *e.g*. emphasizing shape information, were formed independently of geographic location and contained members from salt and freshwater.

The classification functions generated in this study will enable future workers to identify with a high degree of reliability the origin of *Sotalia* specimens based solely on skull measurements. This will be particularly useful for specimens obtained in the vicinity of the mouth of the Amazon, where both forms are expected to occur. The classification functions containing 44 variables are preferable, as they clearly separated the two forms. However, it is recognized that specimens may be damaged, particularly if found washed up on a beach and therefore unable to provide measurements for all 44 variables. In these circumstances, the classification functions based on the 10 best discriminating variables may be useful. Although the 10-variable classification functions did produce some misclassifications of test specimens, they involved misclassifying marine form juveniles (< 3 GLGs) as freshwater animals. Therefore, if an unknown specimen can be aged as adult through tooth sectioning, even the 10-variable classification functions may be considered highly reliable.

The lack of differentiation other than in size suggests that skull morphology tends to be uniform within each group. This does not agree with the suggestion of heterogeneity of marine populations (Casinos et al. 1981). The existence of a cline in geographic variation may be expected in mobile organisms with broad distributions such as Sotalia (this study, section I). In addition, in certain portions of its range Sotalia is seen all year round (this study, section I), suggesting possibly resident populations. The identification of clines is important since it may provide evidence of interbreeding and genetic exchange among populations. The presence of clines could not be detected here because sample distribution and size were not ideal. Although samples from extreme north and south ends of distribution were morphologically similar, as revealed by the dendrogram obtained from the cluster analysis, they should have exhibited greater differences if clines were present.

The larger skull of marine Sotalia appears to be merely a function of its overall larger body size, as the analyses here demonstrated no significant changes in proportion or shape of the skull. With the available data it was not possible to separate genetic or environmental bases as responsible for this difference. There are, however, many reasons to suspect that the nature of the morphological variability in the skulls of Sotalia is related to differences in environmental conditions. It is known that competition for the same resources may lead to ecological separation by character displacement in body size (Calder 1984). A potential cetacean competitor in freshwater, the primitive sympatric boutu (Inia geoffrensis), invaded what is now part of the Amazon basin from the Pacific Ocean during the Miocene epoch (Grabert 1984). Although there is no evidence as to when Sotalia invaded freshwater, it seems unlikely that this would have occurred earlier than Inia, as Sotalia is a member of the modern, recently evolved family Delphinidae (Barnes et al. 1985). Competition may have caused character displacement in the new 'modern' freshwater form Sotalia coming from marine descendants, and a number of changes in physiology, reproduction and skeleton might have followed, probably also including skull morphology. It is known that Inia and Sotalia, in order to coexist, have developed several specialized ecological aspects in their feeding habits, social structure and habitat utilization (da Silva 1986).

The size difference between saltwater and freshwater forms may also reflect energetic considerations. Since rates of heat loss scale with body weight, Downhower and Blumer (1988) were able to calculate the minimum size at which endothermy can be expected for an aquatic endotherm. The predicted value of 6.8 kg was found to be equal to or less than the size of neonate river dolphins. In view of this, it could be speculated that freshwater Sotalia can survive at a smaller size, since Amazonian waters suffer negligible temperature changes, as opposed to marine animals that inhabit cooler waters and would have increased rates of heat losses with smaller dimensions. Schnell *et al*. (1986) studying spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean found strong associations between cranial and environmental variables, such as solar insolation and sea surface temperature, although the physiological basis of the association was not addressed.

The food supply of the freshwater environment may also be a possible factor contributing to such differences. Most water bodies in the Amazon are poor in nutrients, particularly tributary rivers with clear waters, and the availability of food depends upon the annual flooding cycles. An animal with smaller body size might be better adapted to cope with the constraints of such unstable conditions. Although *Inia* has a larger body size, it has a lower basal metabolism than Amazonian *Sotalia* (da Silva 1983). Suboptimal productive environments have been invoked as a factor influencing variation in body size in white whales (*Delphinapterus leucas*) (Sergeant and Brodie 1969).

A larger body size would be also advantageous for animals living in an environment subjected to competition or predation, as appears to be the case for marine *Sotalia*. The killer whale (*Orcinus orca*) is a well known predator of marine mammals found in Brazilian waters (Geise and Borobia 1988). Sharks are also known to prey upon marine mammals (Brodie and Beck 1983). Other delphinids such as the bottlenose dolphin (*Tursiops truncatus*), common dolphin (*Delphinus delphis*), spinner and spotted dolphins occur through much of the range of marine *Sotalia* and could be competing for same food resources.

Although some environmental basis for differences between marine and freshwater forms seem to exist, the possibility of restricted gene flow between them should not be ruled out. The only area for potential range overlap of the two forms is the mouth of the Amazon river and adjacent coastal waters. The inclusion of some coastal specimens from French Guiana and Surinam in the larger cluster of freshwater animals (see Fig. 15) in this context, is interesting, as it suggests that some morphological similarity exists with other freshwater members of that cluster. The placement of these specimens could indicate that they might have been members of a freshwater population, which then could have affected the discriminant analysis towards a complete separation of groups, or it could pose questions with regard to the chance of interbreeding. It is not known whether riverine Sotalia enter saltwater or, conversely, how far up rivers marine animals can be found. The coastal shore from Amapá to Pará is hydrographically and phytogeographically part of the Amazon Basin with almost no influence of saltwater for several kilometers offshore (Domning 1981). Thus, the Amazon delta and surrounding waters are of crucial importance. Although the presence of Sotalia has been recorded for this area of possible sympatry (this study, section I), no specimens were available for inclusion in the analyses. Hence, it seems premature to assign a subspecific level to the forms until more specimens from this region become available, as the lack of intermediate phenotypes may simply denote the lack of such specimens in the visited collections.

Connection of the Amazon and Orinoco River systems does exist and Sotalia occurs in both systems. This again raises questions of possible mixing, although the presence of Sotalia has not to date been confirmed in the vicinity of the Casiquiare river, where connection of the two systems takes place. Furthermore, *Sotalia* would be unlikely to overcome the various rapids in this region, as its morphological characteristics provide it with a more rigid body structure than that of the boutu. In addition, *Inia*, unlike *Sotalia* has larger and broader flippers which increase maneuverability (Casinos and Ocaña 1979; Klima *et al*. 1980). Thus, further opportunity for isolation may exist concerning riverine *Sotalia* as they specialize to life in a riverine habitat.

This study dealt only with differences in cranial morphology and body size among marine and freshwater *Sotalia*. It is recognized that geographic variation may be manifested as changes in other biological aspects, *i*.*e*., physiology, behaviour, etc. Future studies on *Sotalia* should be designed to address these aspects especially in areas of probable overlap because they might prove valuable in clarifying the causes and consequences of isolation of the two groups. We could be dealing with a relatively recent isolation event in which detectable proportional changes in skull morphology have not yet occurred.

The results obtained by this study support the current recognition of a single species, *Sotalia fluviatilis*, with distinct marine and freshwater forms that possibly have limited mixing. Therefore, it is recommended that they be regarded, for the present, as different stocks for management purposes.

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Table 1. Mean comparisons of 44 skull characters between freshwater and marine <u>Sotalia</u>. N is sample size, $\bar{X}$ is the mean and SD is standard deviation.

Character	Freshwater				Marine				
	N	Range (mm)	$\bar{X}$ (mm)	SD (mm)	N	Range (mm)	$\bar{X}$ (mm)	SD (mm)	Absolute value of 't'
1. Condylobasal L.	21	288 - 369	334.3	18.4	38	337 - 400	375.2	15.8	8.97***
2. L. Rostrum	21	157 - 200	200.4	13.9	38	196 - 242	219.1	11.1	5.67***
3. W. Rostrum (at base)	21	61 - 79.6	70.5	4.4	38	68.2 - 90.6	79.8	5.1	7.07***
4. W. Rostrum (at 60 mm from antorb. notches)	21	42.1 - 51.7	48.4	2.9	38	47.7 - 63.7	56.1	3.9	7.76***
5. W. Rostrum (at ¼ L.)	21	45.9 - 53.7	50.6	2.4	38	50.2 - 65.1	57.0	3.4	7.63***
6. W. Rostrum (at ½ L.)	21	33.3 - 44.4	40.0	2.8	38	37.9 - 54.3	44.4	4.2	4.32***
7. W. Premaxillaries (at ½ L. Rostrum)	21	19.4 - 26.0	23.5	1.9	38	21.4 - 34.6	25.4	2.5	2.95***
8. W. Rostrum (at 3/4 L.)	21	15.7 - 37.4	27.1	6.5	38	26.5 - 50.0	31.4	4.5	3.02***
9. W. of lf. Premaxillary	21	19.1 - 23.8	21.7	1.3	38	20.8 - 38.7	24.4	3.8	----[1]
10. W. of rt. Premaxillary	21	25.1 - 34.7	31.1	2.6	38	23.8 - 38.9	34.5	3.5	3.90***
11. Tip of Rostrum to ext. nares	21	190 - 256	235.4	15.1	38	227 - 280	255.4	12.2	5.55***
12. Gr. preorbital W.	21	112.3 - 135.1	126.9	5.9	38	130.1 - 152.2	142.6	5.1	10.68***
13. Gr. postorbital W.	21	126 - 148	139.4	5.9	38	135.7 - 173	159.1	8.2	9.66***
14. Least supraorbital W.	21	110.9 - 133.8	125.4	6.1	38	124.4 - 158	139.8	6.0	8.72***
15. Gr. W. of ext. nares	21	23.1 - 36.4	32.3	2.9	38	33.4 - 42.6	37.4	1.8	----[1]
16. Gr. W. at zygomatic P.	21	142.1 - 155	141.7	23.8	38	147 - 173	162.4	6.8	----[1]
17. Gr. W. of premaxillaries	21	34.4 - 56.8	52.4	5.0	38	42.5 - 63.6	58.8	3.9	5.44***
18. Gr. parietal W.	21	112 - 122	116.6	3.5	38	122 - 138	130.6	5.2	10.97***
19. Ext. height of braincase	21	95 - 150	106.9	10.9	38	102 - 120	111.7	0.7	----[1]
20. Int. L. of braincase	21	87.6 - 107.1	96.9	4.9	38	94.2 - 116.7	106.1	0.8	6.66***
21. Gr. L. of lf. posttemporal fossa	21	65.6 - 79.3	74.5	3.8	38	77.3 - 91.4	83.9	3.9	9.06***
22. Gr. W. of lf. posttemporal fossa	21	48.6 - 62.8	56.9	3.4	38	57.9 - 73.9	65.4	4.3	7.71***
23. Major diameter lf. fossa proper	21	36 - 48	42.4	2.7	38	40 - 50	46.3	2.7	5.30***
24. Minor diameter lf. fossa proper	21	26 - 37	31.9	2.9	38	28 - 48	35.6	2.7	4.92***
25. Nasals to supraoccipital crest[2]	21	12.4 - 28.5	20.3	4.5	13 ♀	17.6 - 40.6	30.0	5.8	5.24***
					12 ♂	16.6 - 29.5	24.5	4.2	
26. L. of lf. orbit[1]	21	35.5 - 49.6	39.5	3.0	13 ♀	40.6 - 49.7	44.4	2.5	8.84***
					12 ♂	43.3 - 51.3	46.6	2.3	

Table 1. (Continued)

Character	Freshwater N	Freshwater Range (mm)	Freshwater $\bar{X}$ (mm)	Freshwater SD (mm)	Marine N	Marine Range (mm)	Marine $\bar{X}$ (mm)	Marine SD (mm)	Absolute value of 't'
27. L. of antorb. P.	21	19.9 - 33.5	26.3	4.1	38	22.4 - 34.5	28.5	3.5	2.22*
28. Gr. W. int. nares	21	34.9 - 45.2	41.8	2.7	38	37.3 - 49.5	41.9	2.8	0.10 n.s.
29. Gr. L. cf lf. pterygoid	21	35.6 - 46.4	41.3	2.7	34	35.3 - 49.6	45.1	3.0	4.70***
30. L. of lf. tympanic cavity	21	40.8 - 50.3	45.8	2.9	38	44.9 - 60.3	53.6	3.4	8.79***
31. L. of rt. tympanic cavity	21	39.6 - 49.5	45.3	2.2	38	47.2 - 61.2	54.4	3.7	----[1]
32. W. at pterygo sutures	21	33.5 - 46.5	40.8	3.1	38	34.4 - 46.2	42.0	3.2	1.39 n.s.
33. L. of up. lf. tooth row	21	127 - 187	170.9	13.8	37	166 - 201	185.4	9.9	4.65***
34. No. teeth - up lf.	20	28 - 35	31.2	1.4	38	30 - 35	32.5	1.4	3.35**
35. No. teeth - up rt.	20	29 - 35	31.0	1.4	38	28 - 36	32.0	1.7	3.28**
36. No. teeth - lower lf.	21	26 - 32	30.7	1.5	37	29 - 34	31.4	1.5	1.83 n.s.
37. No. teeth - lower rt.	20	29 - 33	30.9	1.1	37	28 - 34	31.3	1.5	1.06 n.s.
38. L. of lower lf. tooth row	21	146.4 - 186	171.9	10.0	37	171 - 198	185.0	8.2	5.57***
39. Gr. L. of lf. Ramus	21	253 - 305	285.7	14.0	37	206 - 338	310.0	21.2	4.68***
40. Gr. height of lf. Ramus	21	55 - 70.1	62.1	3.9	37	61.8 - 74.9	69.0	3.1	7.33***
41. L. of lf. mandibular fossa	21	81.9 - 97.2	92.6	23.2	37	95.1 - 117.9	106.1	5.0	----[1]
42. Skull asymmetry[4]	21	2 - 8	5.4	1.3	38	3 - 8	5.3	1.3	0.21 n.s.
43. Height of foramen magnum	21	30.4 - 42.1	35.3	3.1	38	31.7 - 43.8	38.7	3.6	3.67***
44. W. of foramen magnum	20	33.6 - 39.6	36.7	1.8	38	32.9 - 49.4	38.8	3.5	----[1]

Abbreviations: L. = length; W. = width; antorb. = antorbital; lf = left; rt = right; ext. = external; Gr. = greatest; P. = process(es); Int. = internal; Pterygo. = Pterygobasioccipital; up. = upper.

1= no test performed because of variance non-homogeneous; 2,3 = characters for which the t-test among sex was significantly different at the 0.05 level; 4 = measured in degrees; * = $p< 0.05$; ** = $p< 0.01$; *** = $p< 0.001$; n.s. = not significant.

Table 2. Eigenvalues of the first nine principal component analysis for 19 freshwater and 33 marine *Sotalia* based on 44 characters.

Component	Eigenvalue	Proportion	Cumulative
I	22.8184	0.5186	0.5186
II	2.9343	0.0667	0.5853
III	2.5659	0.0583	0.6436
IV	1.8310	0.0416	0.6852
V	1.6826	0.0382	0.7235
VI	1.4668	0.0333	0.7568
VII	1.2228	0.0278	0.7846
VIII	1.0966	0.0249	0.8095
IX	1.0013	0.0227	0.8323

Table 3. Eigenvectors of the first nine principal components for 19 freshwater and 33 marine Sotalia based on 44 characters.

Character		I	II	III	IV	V	VI	VII	VIII	IX
1.	Condylobasal L.	0.19	- 0.02	- 0.18	0.03	- 0.02	- 0.02	- 0.02	- 0.82	0.02
2.	L. Rostrum	0.17	- 0.08	- 0.25	0.17	0.05	- 0.02	0.07	- 0.12	0.04
3.	W. Rostrum (at base)	0.19	0.01	0.13	- 0.04	0.04	0.07	- 0.06	0.06	0.12
4.	W. Rostrum (at 60 mm from antorb. notches)	0.19	- 0.04	0.09	- 0.08	0.09	- 0.03	0.09	0.03	0.002
5.	W. Rostrum (at ¼ L.)	0.19	- 0.03	0.12	- 0.10	0.08	0.00	0.05	0.04	0.05
6.	W. Rostrum (at ½ L.)	0.17	- 0.12	0.27	- 0.004	0.06	0.10	0.16	- 0.01	- 0.01
7.	W. Premaxillaries (at ½ L. Rostrum)	0.13	- 0.19	0.30	0.05	0.10	0.18	0.16	- 0.15	0.03
8.	W. Rostrum (at 3/4 L.)	0.11	- 0.14	0.29	- 0.11	0.24	0.13	0.17	- 0.34	0.01
9.	W. of lf. Premaxillary	0.08	- 0.10	- 0.11	- 0.32	- 0.33	0.31	0.37	0.09	- 0.05
10.	W. of rt. Premaxillary	0.13	0.09	0.01	0.16	0.33	- 0.15	- 0.40	- 0.06	- 0.05
11.	Tip of Rostrum to ext. nares	0.18	- 0.08	- 0.22	0.16	0.01	0.01	0.08	- 0.08	0.01
12.	Gr. preorbital W.	0.20	- 0.07	0.003	- 0.12	0.02	- 0.02	- 0.05	- 0.004	0.07
13.	Gr. postorbital W.	0.19	- 0.003	0.03	- 0.15	- 0.02	- 0.01	- 0.06	0.09	- 0.01
14.	Least supraorbital W.	0.19	- 0.07	- 0.02	- 0.09	0.01	- 0.02	- 0.03	- 0.02	0.06
15.	Gr. W. of ext. nares	0.16	0.04	- 0.17	0.13	- 0.04	0.06	- 0.18	0.07	- 0.02
16.	Gr. W. at zygomatic P.	0.14	0.02	0.02	0.01	- 0.17	- 0.35	0.04	0.13	0.21
17.	Gr. W. of premaxillaries	0.13	0.04	- 0.23	- 0.22	- 0.08	- 0.07	0.18	- 0.08	- 0.34
18.	Gr. parietal W.	0.18	0.14	0.05	- 0.12	- 0.08	- 0.10	0.02	0.01	0.06
19.	Ext. height of braincase	0.11	- 0.05	0.10	0.25	- 0.32	0.16	- 0.07	0.06	0.20
20.	Int. L. of braincase	0.17	0.07	0.06	0.04	- 0.06	- 0.17	0.03	- 0.09	- 0.06
21.	Gr. L. of lf. posttemporal fossa	0.19	0.06	0.09	- 0.15	0.05	- 0.03	- 0.05	0.05	- 0.10
22.	Gr. W. of lf. posttemporal fossa	0.18	0.08	0.06	0.01	- 0.03	- 0.17	- 0.08	0.04	- 0.15
23.	Major diameter lf. fossa proper	0.14	- 0.07	0.07	- 0.06	- 0.10	- 0.02	- 0.14	0.27	- 0.16
24.	Minor diameter lf. fossa proper	0.15	- 0.10	- 0.04	- 0.14	0.03	0.07	- 0.16	- 0.09	0.06
25.	Nasals to supraoccipital crest	0.11	0.15	0.24	- 0.12	0.02	- 0.19	- 0.14	- 0.26	0.16
26.	L. of lf. orbit	0.17	0.12	- 0.05	0.03	- 0.22	0.06	0.002	- 0.01	0.01
27.	L. of antorb. P.	0.10	- 0.01	0.19	0.21	- 0.32	- 0.05	- 0.09	0.23	0.32
28.	Gr. W. int. nares	0.10	- 0.04	0.23	0.33	0.23	0.15	0.10	0.26	- 0.17
29.	Gr. L. of lf. pterygoid	0.12	- 0.27	- 0.09	- 0.07	0.01	0.03	0.14	- 0.14	0.01
30.	L. of lf. tympanic carity	0.19	0.08	0.01	- 0.09	0.00	0.04	- 0.06	- 0.03	0.09
31.	L. of rt. tympanic cavity	0.19	0.09	0.03	- 0.15	- 0.04	- 0.02	- 0.02	- 0.06	0.09
32.	W. at Pterygo sutures	0.13	- 0.26	0.06	0.22	0.17	0.01	- 0.03	0.32	- 0.18

Table 3. (Continued)

Character	I	II	III	IV	V	VI	VII	VIII	IX
33. L. of up. lf. tooth row	0.15	- 0.13	- 0.30	0.18	0.10	- 0.07	0.10	- 0.03	0.04
34. No. teeth - up lf.	0.08	0.37	- 0.08	- 0.06	0.23	- 0.16	0.29	0.09	- 0.13
35. No. teeth - up rt.	0.09	0.40	0.01	0.07	0.12	- 0.14	0.30	0.06	- 0.09
36. No. teeth - lower lf.	0.06	0.32	- 0.07	0.03	0.13	0.43	- 0.23	0.06	0.28
37. No. teeth - lower rt.	0.04	0.37	- 0.04	- 0.02	0.14	0.48	0.02	0.04	0.07
38. L. of lower lf. tooth row	0.17	- 0.12	- 0.24	0.16	0.04	0.15	- 0.08	- 0.10	0.13
39. Gr. L. of lf. Ramus	0.13	- 0.05	- 0.31	0.20	0.10	- 0.01	0.16	- 0.16	0.07
40. Gr. height of lf. Ramus	0.20	- 0.08	0.03	- 0.06	0.02	0.06	- 0.09	0.02	- 0.03
41. L. of lf. mandibular fossa	0.18	0.01	- 0.03	- 0.03	- 0.04	- 0.11	- 0.01	- 0.16	0.01
42. Skull asymmetry	- 0.01	- 0.08	- 0.12	- 0.16	0.24	- 0.13	0.28	0.49	0.43
43. Height of foramen magnum	0.11	0.22	0.04	0.22	- 0.30	0.00	0.23	- 0.12	- 0.09
44. W. of foramen magnum	0.11	0.15	0.10	0.33	- 0.14	0.03	0.08	0.07	- 0.26

Abbreviations: L. = length; W. = width; antorb. = antorbital; lf = left; rt = right; ext. = external; Gr. = greatest; P. = process(es); Int. = internal; Pterygo. = Pterygobasioccipital; up. = upper.

Table 4. Standardized coefficients of the canonical discriminant function for freshwater and marine Sotalia. Bold type indicate most discriminant values.

	Character	Coefficient
1.	Condylobasal L.	**4.6899**
2.	L. Rostrum	**- 2.8169**
3.	W. Rostrum (at base)	1.2295
4.	W. Rostrum (at 60 mm from antorb. notches)	**- 2.9138**
5.	W. Rostrum (at ¼ L.)	2.3425
6.	W. Rostrum (at ½ L.)	- 1.1287
7.	W. Premaxillaries at ½ L. Rostrum)	0.8004
8.	W. Rostrum (at 3/4 L.)	0.1541
9.	W. of lf. Premaxillary	- 2.4926
10.	W. of rt. Premaxillary	**- 2.9879**
11.	Tip of Rostrum to ext. nares	**- 2.9009**
12.	Gr. preorbital W.	**5.2239**
13.	Gr. postorbital W.	**- 3.1618**
14.	Least supraorbital W.	**- 3.4653**
15.	Gr. W. of ext. nares	**2.7438**
16.	Gr. W. at zygomatic P.	- 0.3171
17.	Gr. W. of premaxillaries	0.6962
18.	Gr. parietal W.	1.6591
19.	Ext. height of braincase	- 0.7772
20.	Int. L. of braincase	- 0.2823
21.	Gr. L. of lf. posttemporal fossa	1.5899
22.	Gr. W. of lf. posttemporal fossa	- 1.8758
23.	Major diameter lf. fossa proper	0.5922
24.	Minor diameter lf. fossa proper	0.3307
25.	Nasals to supraoccipital crest	1.6898
26.	L. of lf. orbit	0.8505
27.	L. of antorb. P.	- 0.9840
28.	Gr. W. int. nares	0.4952
29.	Gr. L. of lf. pterygoid	0.1963
30.	L. of lf. tympanic cavity	1.7671
31.	L. of rt. tympanic cavity	- 0.3831
32.	W. at pterygo sutures	- 0.5924
33.	L. of up. lf. tooth row	2.2708
34.	No. teeth - up lf.	1.2821
35.	No. teeth - up rt.	- 1.0994
36.	No. teeth - lower lf.	- 0.7861
37.	No. teeth - lower rt.	- 1.2692
38.	L. of lower lf. tooth row	**2.8434**
39.	Gr. L. of lf. Ramus	- 0.9699
40.	Gr. height of lf. Ramus	- 1.5710
41.	L. of lf. mandibular fossa	0.5891
42.	Skull asymmetry	0.3784

Table 4. (Continued)

Character		Coefficient
43.	Height of foramen magnum	2.4213
44.	W. of foramen magnum	- 1.0361
	Eigenvalue	31.2982
	R. Squared	0.9690
	Wilk's Lambda	0.0310

Abbreviations: L. = length; W. = width; antorb. = antorbital; lf = left; rt = right; ext. = external; Gr. = greatest; P. = process(es);Int. = internal; Pterygo. = Pterygobasioccipital; up. = upper.

Table 5. Coefficients of the classification functions for freshwater and marine *Sotalia*, based on the best discriminating characters given by the canonical discriminant analysis.

	Classification functions	
Character	Freshwater	Marine
1. Gr. preorbital W.	4.3682	4.9831
2. Condylobasal L.	0.2950	0.6090
3. Least supraorbital W.	0.9225	0.7823
4. Gr. postorbital W.	0.7514	0.6754
5. W. rt. Premaxillary	-0.2890	-0.5511
6. W. Rostrum (at 60 mm from antorb. notches)	-6.3388	-6.5299
7. Tip of rostrum to ext. nares	1.0856	0.7526
8. L. of lower lf. tooth row	-0.6387	-0.7824
9. L. Rostrum	-0.0206	0.0708
10. Gr. W. of ext. nares	2.3022	3.2286
Constant	-387.014	-476.574

Abbreviations : Gr. - greatest; W. - width; L. - length; rt. - right; antorb. - antorbital; ext. - external; lf. - left.

Table 6. Coefficients of the classification functions for freshwater and marine *Sotalia*.

Character		Classification functions	
		Freshwater	Marine
1.	Condylobasal L.	- 4.7618	- 2.6050
2.	L. Rostrum	0.2631	- 2.0849
3.	W. Rostrum (at base)	17.7567	19.8779
4.	W. Rostrum (at 60 mm from antorb. notches)	- 41.5622	- 47.7859
5.	W. Rostrum (at ¼ L.)	33.6252	39.5273
6.	W. Rostrum (at ½ L.)	- 25.6586	- 28.5418
7.	W. Premaxillaries (at ½ L. Rostrum)	- 7.9805	- 4.2010
8.	W. Rostrum (at 3/4 L.)	3.6487	3.9474
9.	W. of lf. Premaxillary	- 20.1266	- 28.1252
10.	W. of rt. Premaxillary	- 33.9685	- 43.4937
11.	Tip of Rostrum to ext. nares	10.7063	8.5022
12.	Gr. preorbital W.	19.8388	26.1106
13.	Gr. postorbital W.	0.4423	- 2.5227
14.	Least supraorbital W.	- 0.9465	- 5.1293
15.	Gr. W. of ext. nares	20.4871	30.1263
16.	Gr. W. at zygomatic P.	- 1.7327	- 1.9242
17.	Gr. W. of premaxillaries	4.6382	6.1218
18.	Gr. parietal W.	19.4177	21.7607
19.	Ext. height of braincase	6.7451	5.6234
20.	Int. L. of braincase	17.2673	16.0826
21.	Gr. L. of lf. posttemporal fossa	- 0.1630	2.7959
22.	Gr. W. of lf. posttemporal fossa	10.4508	6.7871
23.	Major diameter lf. fossa proper	- 11.1593	- 9.1196
24.	Minor diameter lf. fossa proper	- 4.4270	- 3.3237
25.	Nasals to supraoccipital crest	9.8696	13.1884
26.	L. of lf. orbit	- 35.7265	- 33.3347
27.	L. of antorb. P.	- 3.5243	- 6.5042
28.	Gr. W. int. nares	- 15.1014	- 13.1316
29.	Gr. L. of lf. pterygoid	41.3761	42.0212
30.	L. of lf. tympanic cavity	- 33.7070	- 29.7333
31.	L. of rt. tympanic cavity	- 18.3361	- 19.1691
32.	W. at pterygo. sutures	- 4.4305	- 6.5045
33.	L. of up. lf. tooth row	13.0837	15.2866
34.	No. teeth - up lf.	9.5907	19.0460
35.	No. teeth - up rt.	- 28.6397	- 35.9617
36.	No. teeth - lower lf.	48.2571	42.1819
37.	No. teeth - lower rt.	63.7714	52.7442
38.	L. of lower lf. tooth row	- 20.4740	- 17.5415
39.	Gr. L. of lf. Ramus	- 1.4432	- 1.9302
40.	Gr. height of lf. Ramus	17.4696	13.8097
41.	L. of lf. mandibular fossa	5.1243	5.9399

Table 6. (Continued)

Character	Classification functions Freshwater	 Marine
42. Skull asymmetry	6.8271	10.1166
43. Height of foramen magnum	3.9892	11.1795
44. W. of foramen magnum	8.3843	4.8213
Constant	- 3752	- 4193

Abbreviations: L. = length; W. = width; antorb. = antorbital; lf = left; rt = right; ext. = external; Gr. = greatest; P. = process(es); Int. = internal; Pterygo. = Pterygobasioccipital; up. = upper.

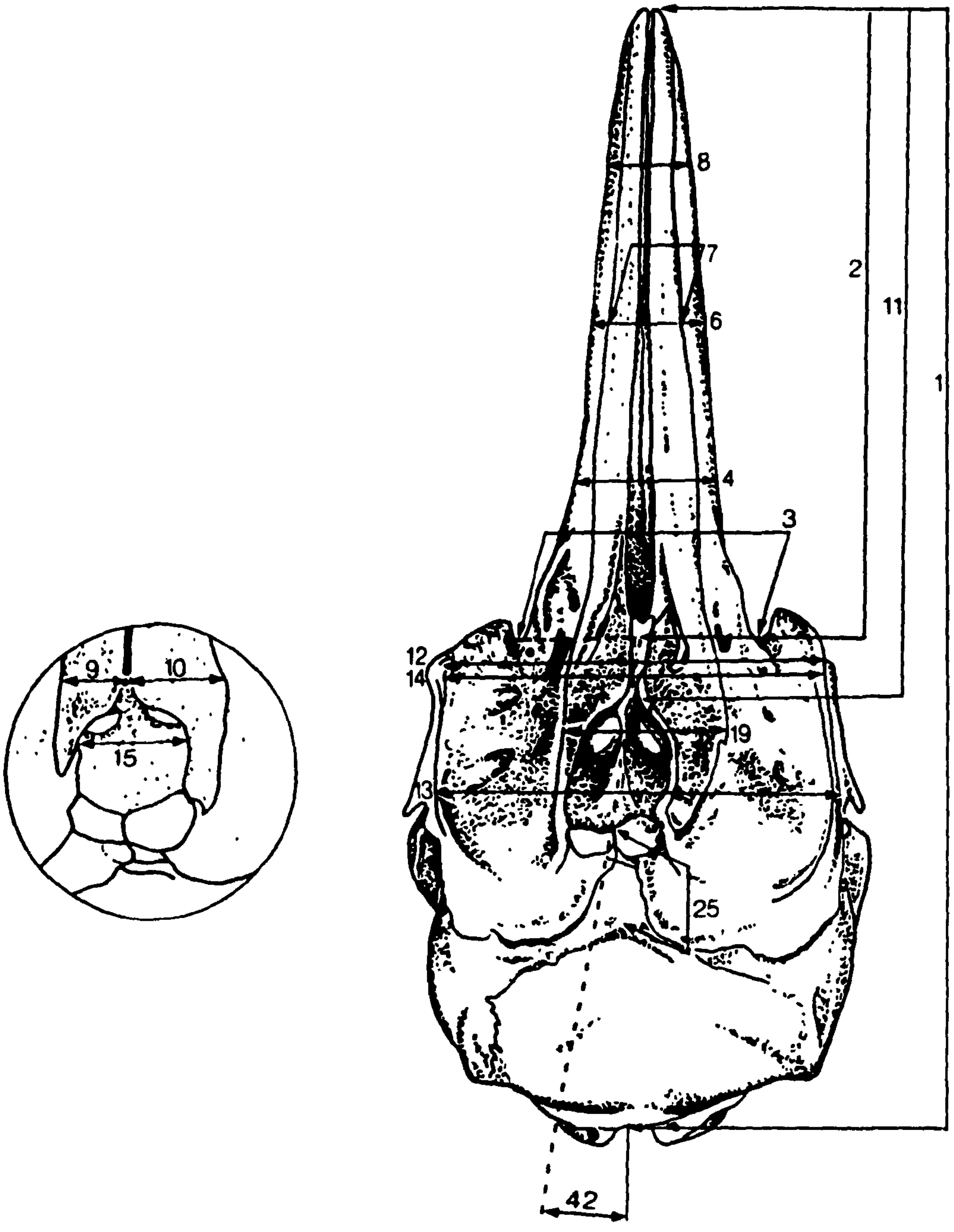

Figure 2. Dorsal view of a *Sotalia* skull showing the characters measured. Numbers refer to Appendix 2.

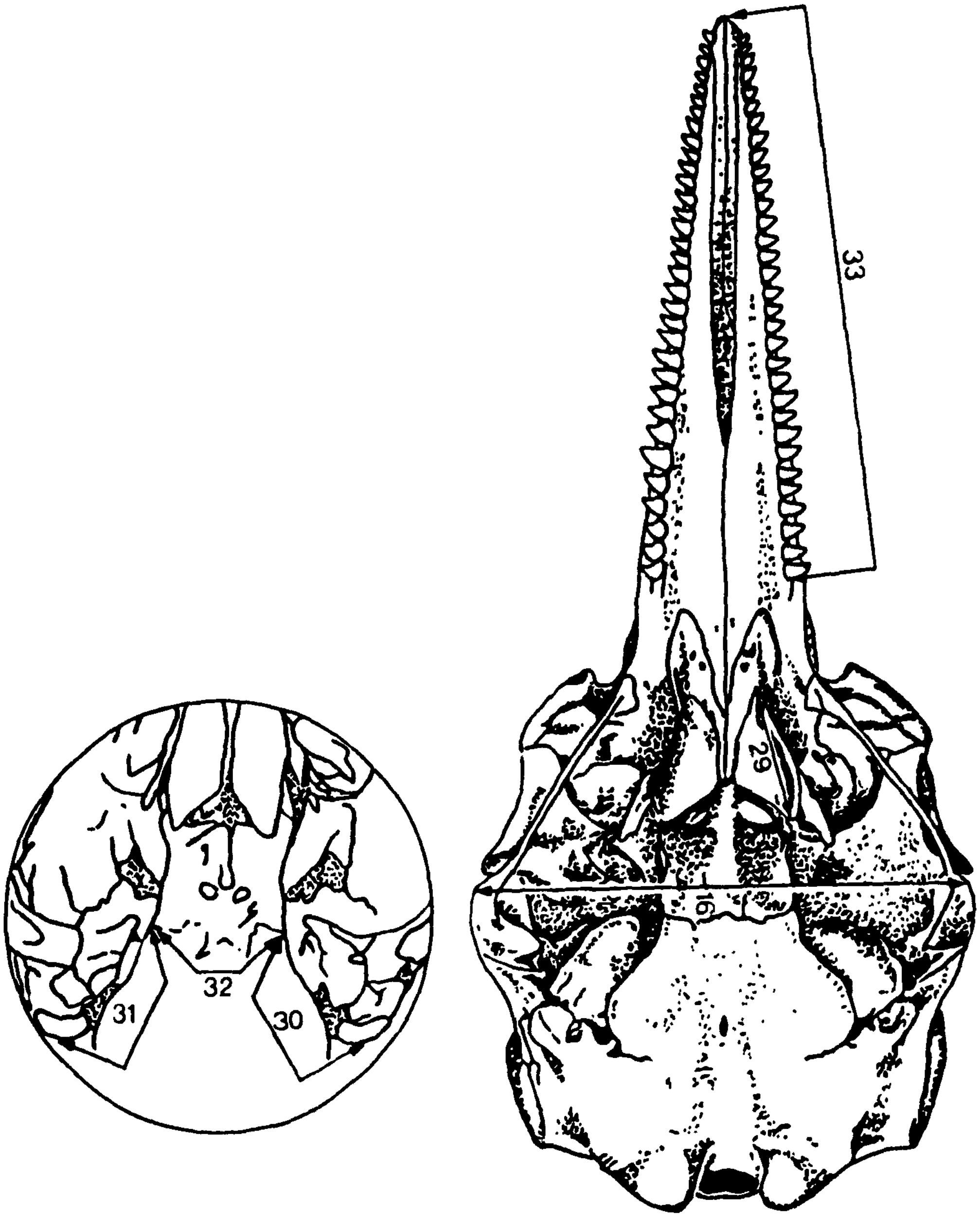

Figure 3. Ventral view of a *Sotalia* skull showing the characters measured. Numbers refer to Appendix 2.

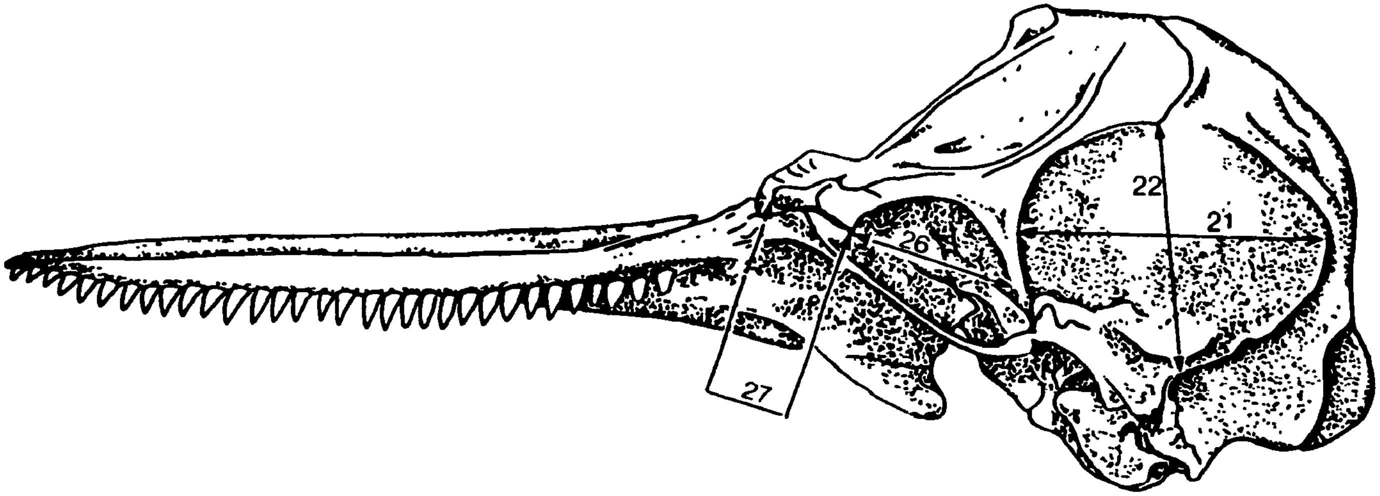

Figure 4. Lateral view of a *Sotalia* skull showing the characters measured. Numbers refer to Appendix 2.

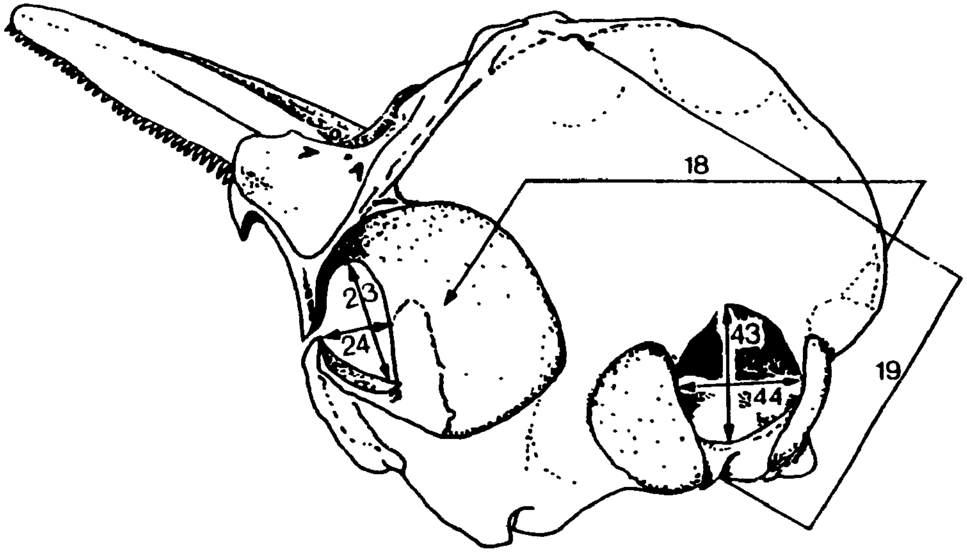

Figure 5. Three quarter view of a <u>Sotalia</u> skull showing the characters measured. Numbers refer to Appendix 2.

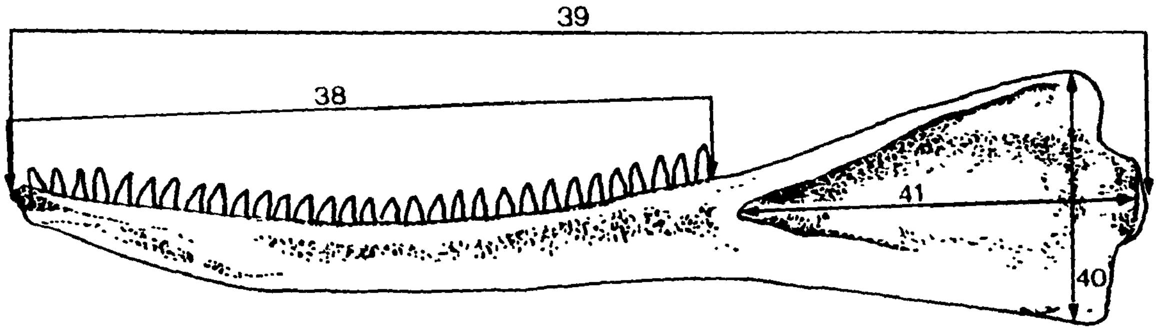

Figure 6. Lateral inside view of mandible showing the characters measured. Numbers refer to Appendix 2.

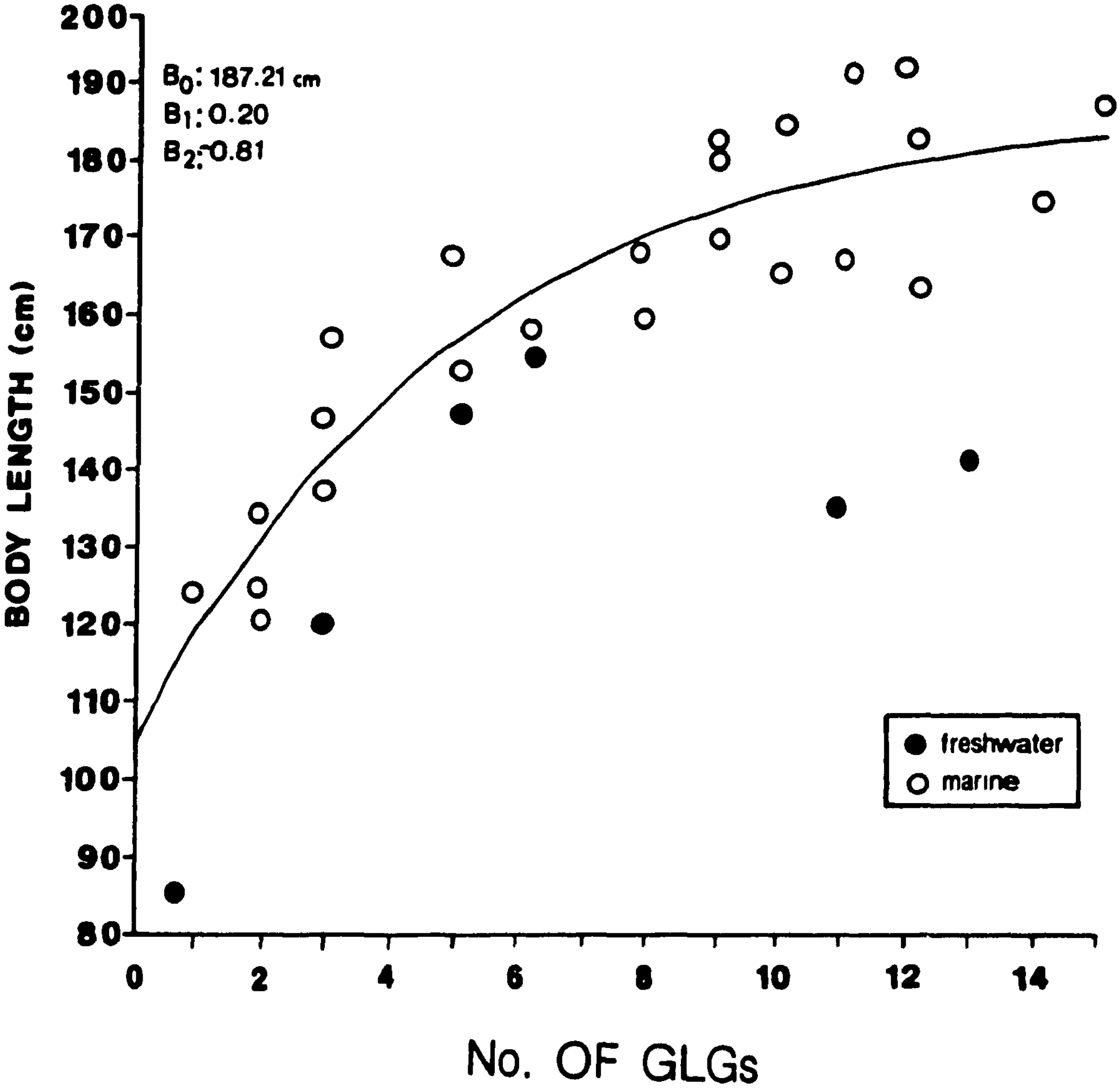

Figure 7. Growth curve fitted for marine specimens by the von Bertalanffy growth model. Data for freshwater specimens plotted for comparison.

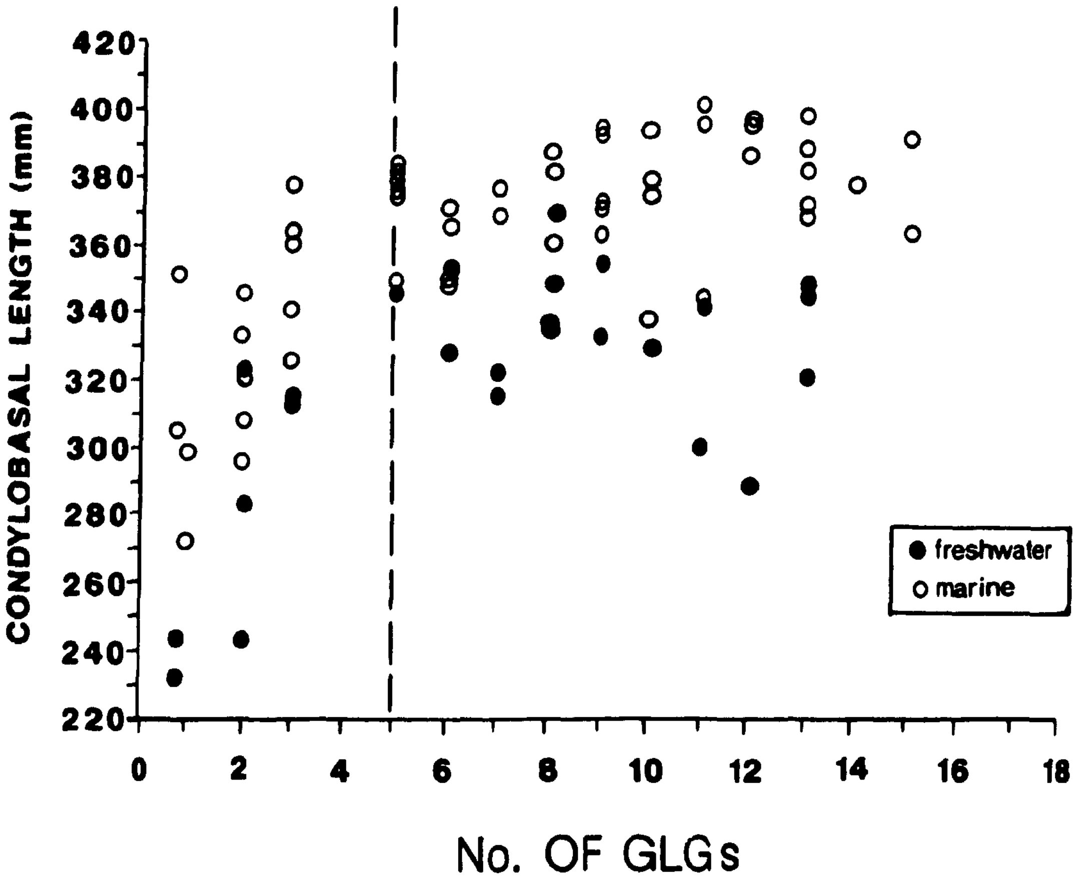

Figure 8. Scatterplot of Condylobasal length vs. age for marine and freshwater specimens. Points to the left of dotted line were deleted from further analyses.

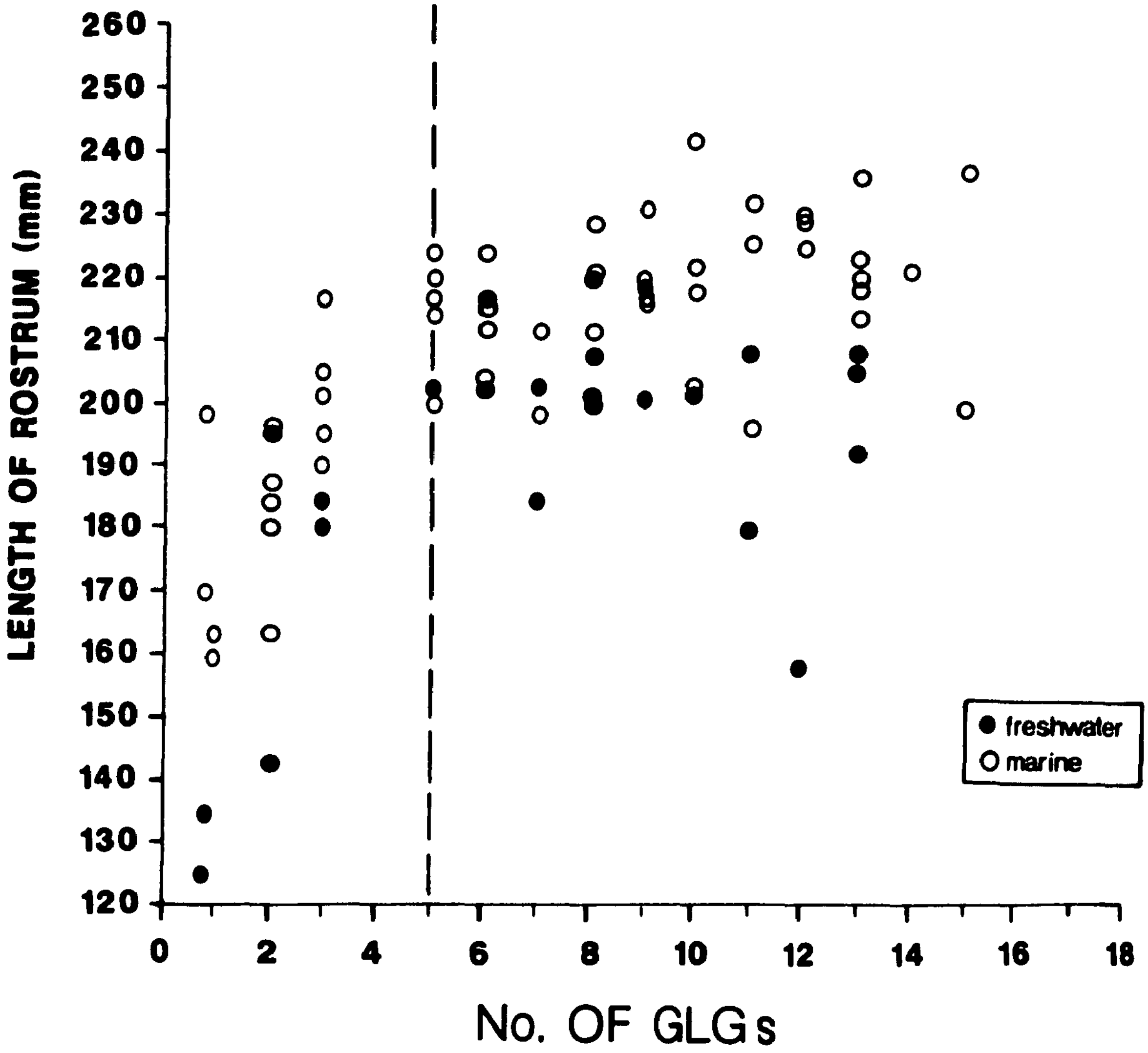

Figure 9. Scatterplot of length of rostrum vs. age for marine and freshwater specimens. Points to the left of dotted line were deleted from further analyses.

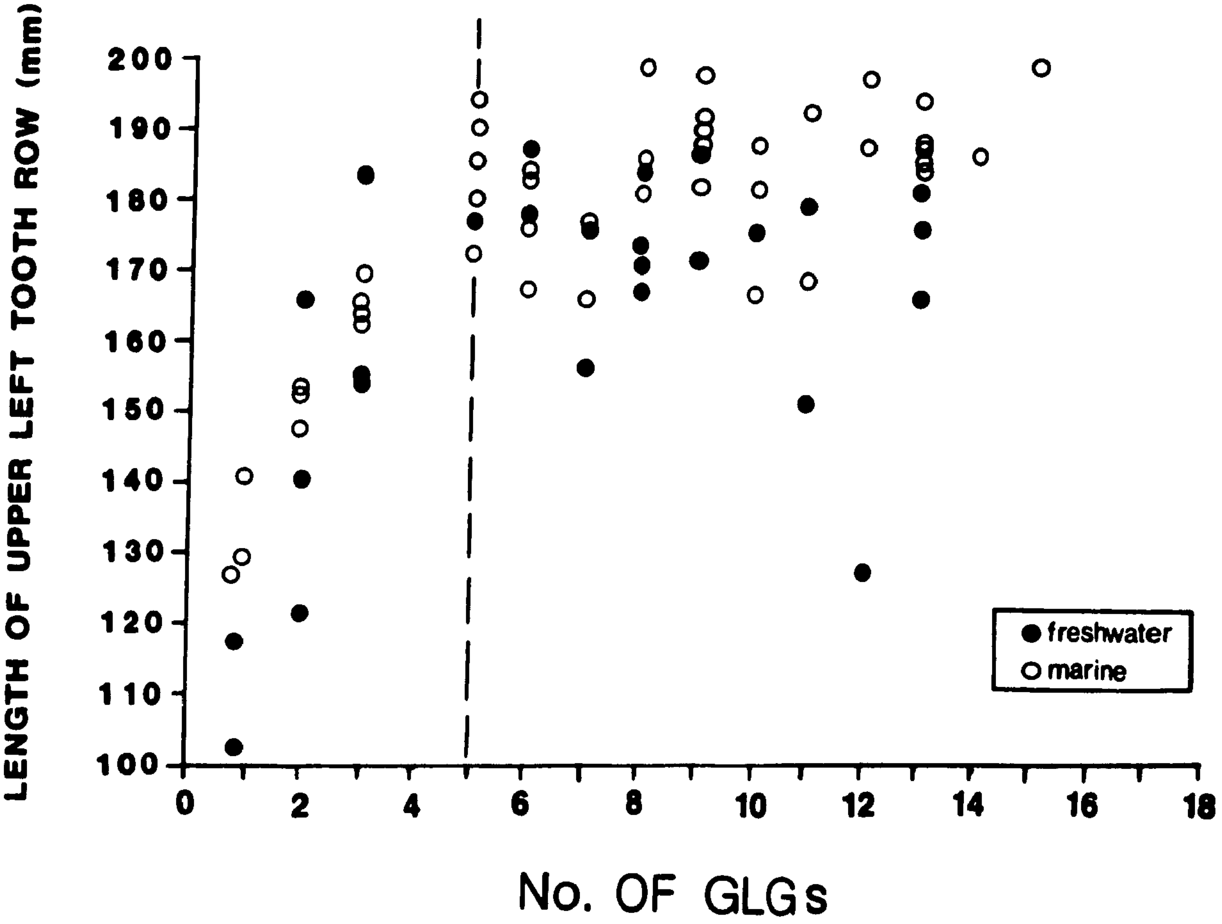

Figure 10. Scatterplot of length of upper left tooth row vs. age for marine and freshwater specimens. Points to the left of dotted line were deleted from further analyses.

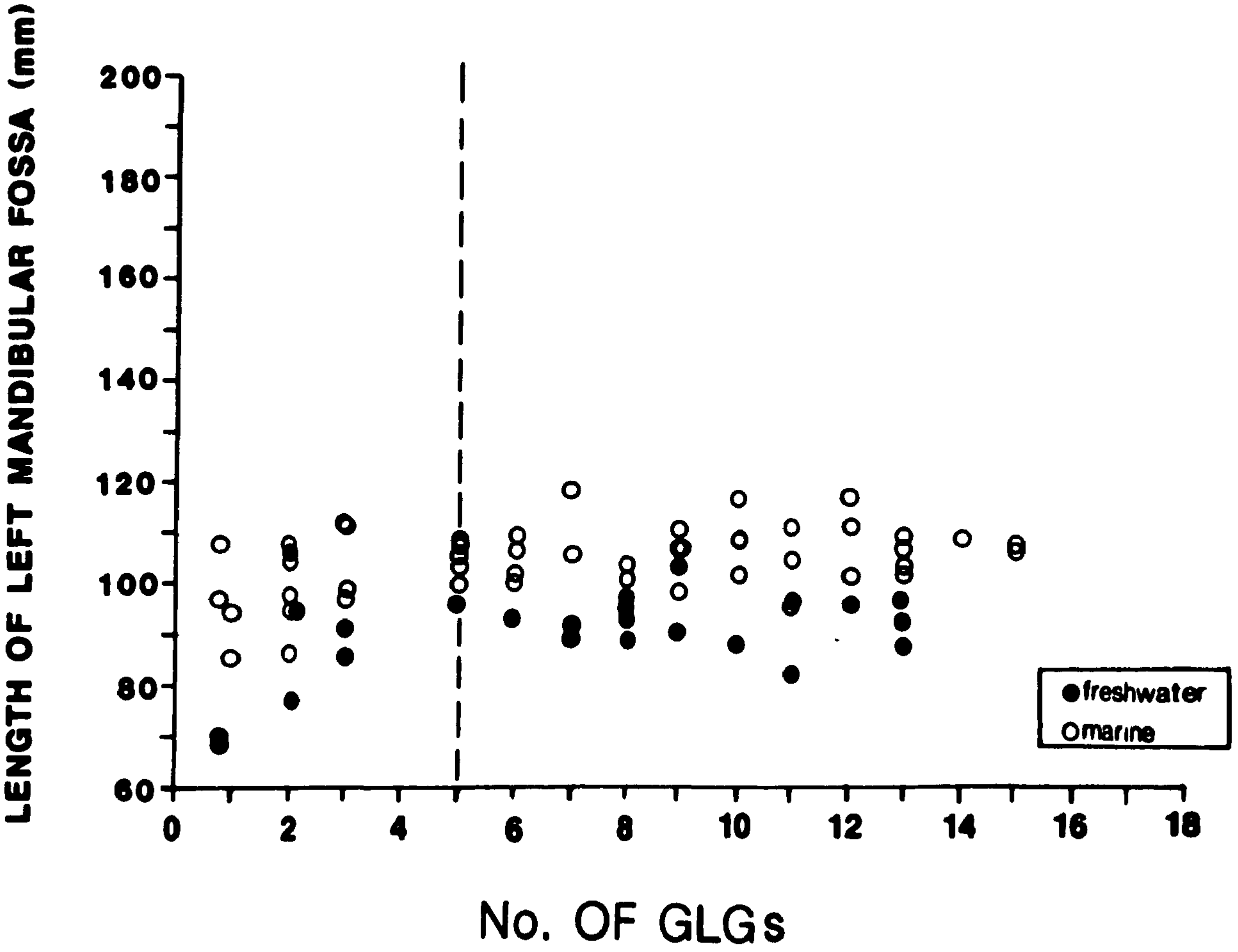

Figure 11. Scatterplot of length of left madibular fossa vs. age for marine and freshwater specimens. Points to the left of dotted line were deleted from further analyses.

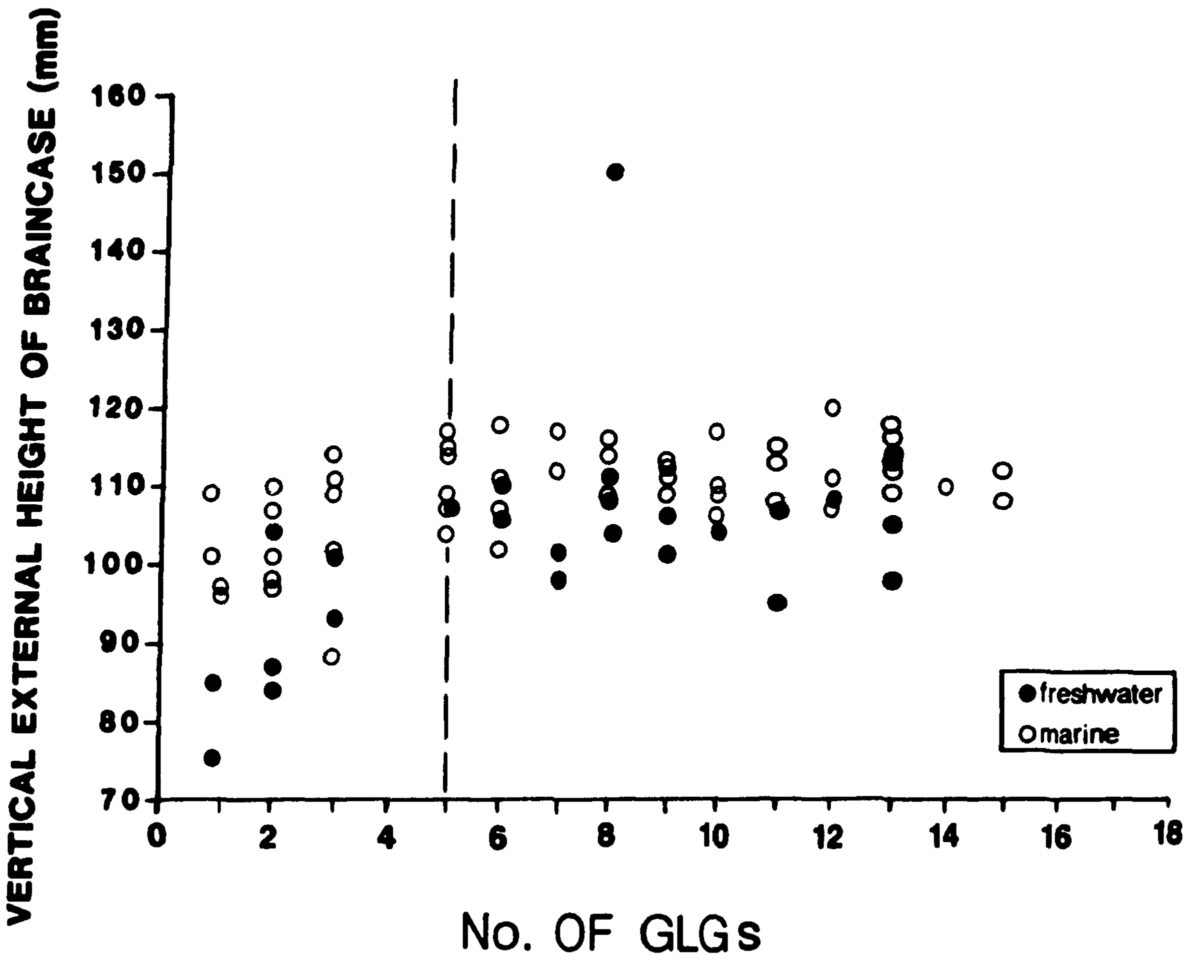

Figure 12. Scatterplot of vertical external heigth of the braincase vs. age for marine and freshwater specimens. Points to the left of dotted line were deleted from further analyses.

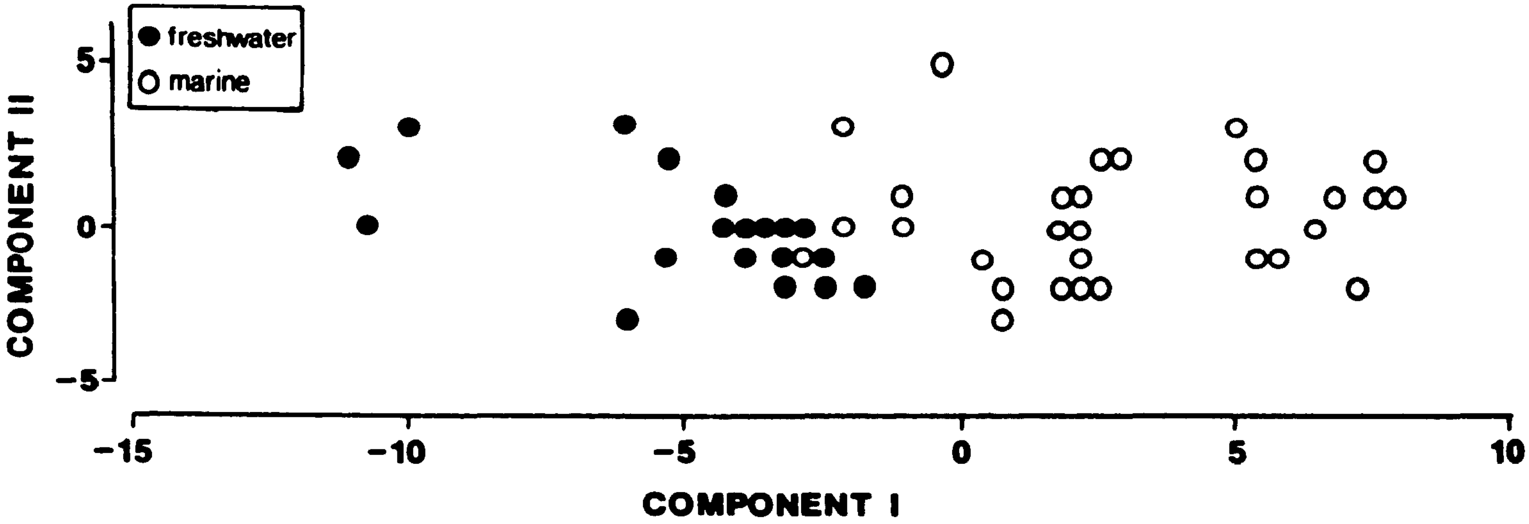

Figure 13. Projection of specimens onto the first and second principal components.

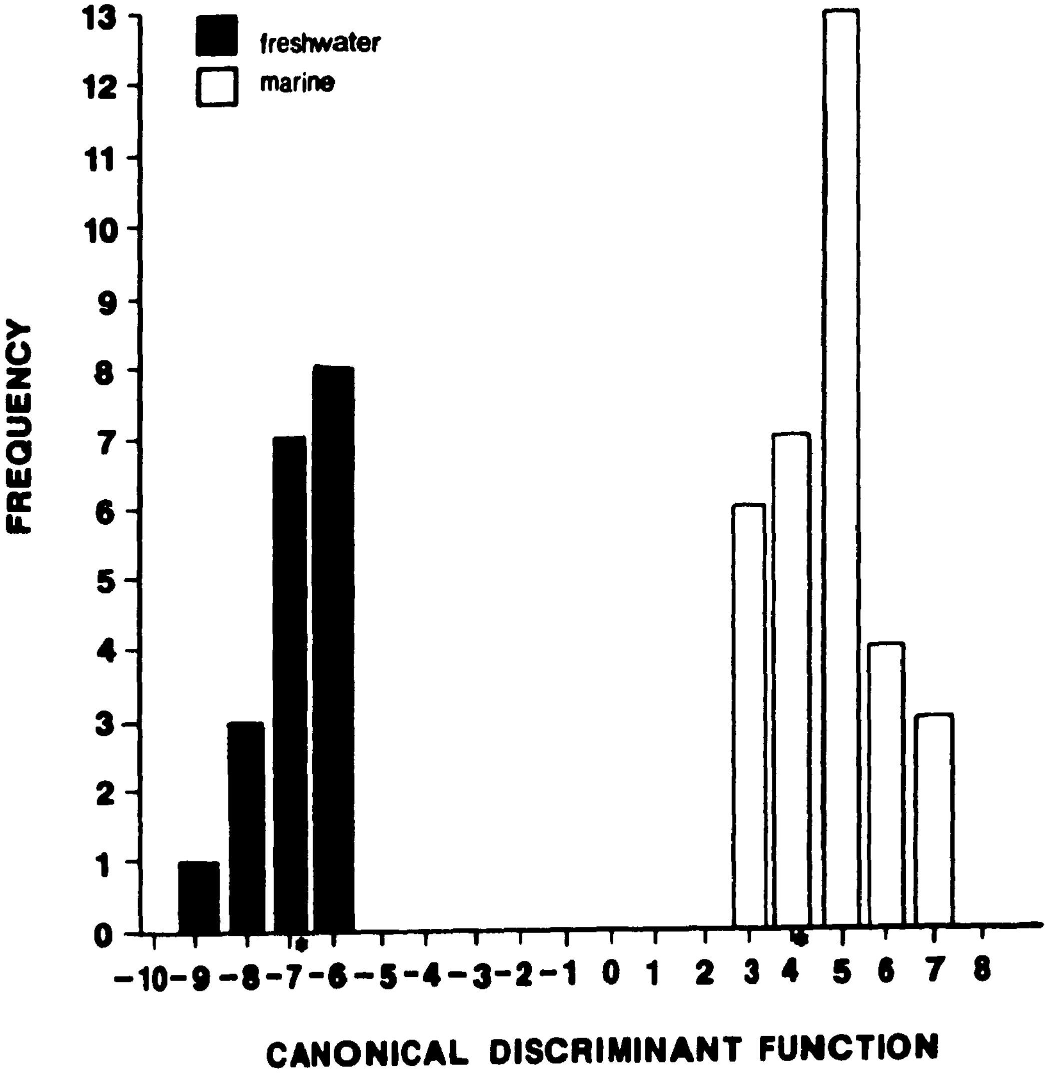

Figure 14. Representation of specimens in the canonical space. Asterisks (*) are the means of each form (centroids).

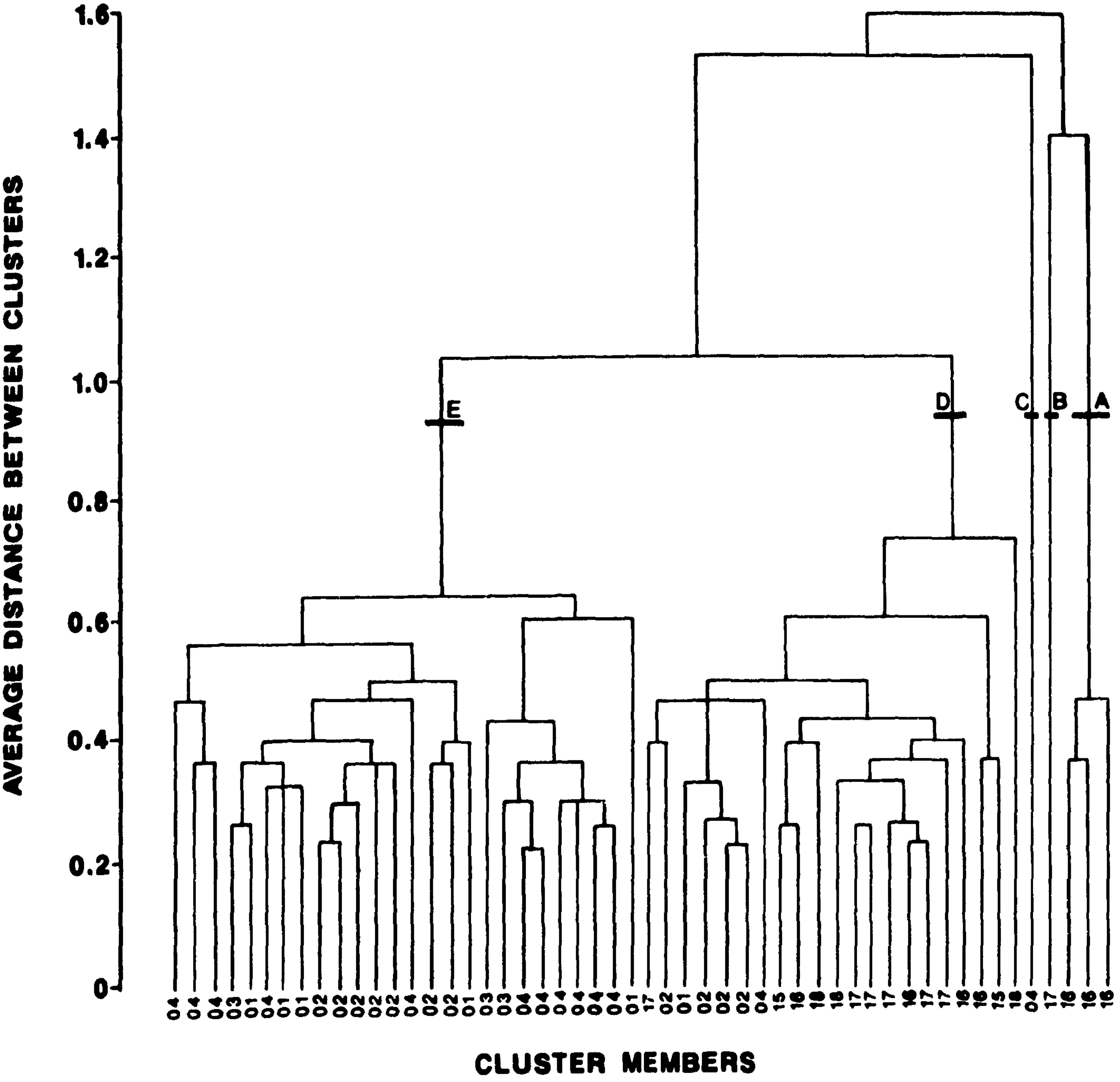

Figure 15. Dendrogram resulting from average linkage cluster analysis. Code for cluster members are as follows: Top row (area of provenance), 1-Coasts of Colombia and Venezuela, 2- Coasts of Surinam and French Guiana, 3- Northeastern Brazil, 4- Southeastern Brazil, 5- Lower Amazon, 6- Central Amazon, 7-Upper Amazon, 8-undetermined. Bottom row (form), 0-marine, 1- freshwater.

SUMMARY AND GENERAL CONCLUSIONS

Since little is known of the biology of Sotalia in marine and freshwater habitats, initial investigations should be on studies that provide basic knowledge. Section I contributes towards the acquisition of such knowledge by describing the distribution of the genus and discussing probable limiting factors. Results suggest that Sotalia is common along the Atlantic coast of Panama and South America as far as southern Brazil, as well as in Amazonian waters. Records suggest that the southern limit of distribution of marine Sotalia is correlated with sea surface temperature at its southern portion, while at present, no distinct pattern can be discerned for its northern limit. In freshwater, the habitat utilization of Sotalia seems related to food availability. Information on food habits from coastal Sotalia may contribute to a better understanding of its distributional patterns.

Section II also improved the basic knowledge of the genus Sotalia by addressing a topic that has long been controversial: the issue of differentiation of marine and freshwater forms. The von Bertalanffy growth model enabled the estimation of growth parameters for marine Sotalia. The estimates suggested an attainment of larger body size than that reported for riverine specimens. The skull of both forms grow in a similar manner with the sound-producing apparatus developing precociously.

Sexual dimorphism, although present in other odontocetes, was not detected here. Further studies should assess this question in detail. Comparisons between forms however, showed that marine specimens were significantly larger in most characters tested.

Sexes were grouped for all multivariate analyses. Principal component analysis was able to separate marine and freshwater forms along the first component which was interpreted as a skull size axis. Canonical discriminant function was also successful in discriminating the forms which can be best differentiated by the preorbital width. Classification functions were generated and tested for their efficiency. They can be used in future studies to assign unknown specimens to one of the two forms. However, they should not be applied for the identification of juveniles, since juvenile marine form individuals can be misclassified as freshwater form. Cluster analysis formed two major clusters, one of marine and the other of freshwater animals. This dichotomy however, was not generated when the analysis emphasized shape as opposed to size information. No distinct subgroups were apparent. These findings further confirmed separation of groups on the basis of size alone, and provide an argument for recognition of two distinct management stocks. The variability exhibited between marine and freshwater forms was consistent with predictions for environmentally based mechanisms. However, further studies should concentrate sampling efforts in the Amazon delta and adjacent waters. This region may be important in delineating interbreeding potential, identifying intermediate phenotypes, and addressing the important question of the extent of genetic isolation between these forms.

Appendix 1. Summary of origin of *Sotalia* specimens examined.

Origin of specimens	Number of specimens								
	Freshwater			Marine			Unknown		
	♀	♂	?	♀	♂	?	♀	♂	?
Mus. of Comparative Zoology (MCZ)		1				1			
American Mus. of Nat. Hist. (AMNH)	2								
National Mus. of Nat. Hist. (USNM)					1	1			1
Carnegie Mus. of Nat. Hist. (CM)	3		1			1			
Field Mus. of Nat. Hist. (FMNH)						4			
The Florida State Mus. (UF)	1	1	5						
California Academy of Science (CAS)	1	1							
Los Angeles County Mus. of Nat. Hist. (LACM)	3		1						
Museu Paraense Emílio Goeldi (MPEG)	1								
Univ. Federal da Paraíba (UFPB)					1	2			
Museu de Zoologia da Univ. de Sao Paulo (MZUSP)	3		2	9	4	8			4
Univ. Federal de Santa Catarina (UFSC)						1			
Univ. Federal Rural do Rio de Janeiro (UFRRJ)						1			
Museu Nacional do Rio de Janeiro (MNRJ)	1			1	1				4
Univ. Federal do Rio de Janeiro (UFRJ)						2			
British Mus. (Nat. Hist.) (BMNH)	1	1							
Inst. Royal des Sci. Natur. de Belgique (IRSNB)	1								
Mus. National d'Histoire Natur. (MNHN)			2			2			1
Staatliches Mus. fur Naturkunde (SMNH)						2			
Rijksmuseum van Natuurlijke Historie (RMNH)				3	8				
Instituut voor Tax. Zoölogie (ZMA)				4	5				

Abbreviations; Mus. = Museum; Nat. = National; Hist. = History; Univ. = Universidade; Inst. = Institut; Sci. = Sciences; Natur. = Naturelle(s); Tax. = Taxonomische.

Appendix 2. List of skull measurements and meristics.

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 ¼ length) - width of rostrum measured at one-fourth distance from line across hindmost limits of antorbital notches (not illustrated).

6. Width of rostrum at midlength.

7. Width of premaxillaries at midlength of rostrum.

8. Width of rostrum at 3/4 length, measured from posterior end.

9. Width of left premaxillary (midline nares) - greatest width of left premaxillary, measured from most anterior point on narial midline (inset).

10. Width of right premaxillary (midline nares) - greatest width of right premaxillary, measured from the most anterior point on narial midline (inset).

11. Distance from tip of rostrum to external nares (to mesial end of anterior tranverse margin of right naris).

12. Greatest preorbital width.

13. Greatest postorbital width.

14. Least supraorbital width.

15. Greatest width of external nares (inset).

16. Greatest width at zygomatic processes of squamosal.

17. Greatest width of premaxillaries.

18. Greatest parietal width, within posttemporal fossa.

Appendix 2. (continued)

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19. Vertical external height of braincase from midline of basisphenoid to summit of supraoccipital, but not including supraoccipital crest.

20. Internal length of braincase from hindmost limit of occipital condyles to foremost limit of cranial cavity along midline (not illustrated).

21. Greatest length of left posttemporal fossa, measured to external margin of raised suture.

22. Greatest width of left posttemporal fossa at right angles to gratest length.

23. Major diameter of left temporal fossa proper.

24. Minor diameter of left temporal fossa proper.

25. Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest.

26. Length of left orbit - from apex of preorbital process of frontal to apex of postorbital process.

27. Length of antorbital process of left lacrimal.

28. Greatest width of internal nares (inset).

29. Greatest length of left pterygoid.

30. Length of left tympanic cavity - length from the pterygobasioccipital suture to furthest point of left exoccipital (inset).

31. Length of right tympanic cavity - length from the pterygobasioccipital suture to furthest point of right exoccipital (inset).

32. Width of pterygobasioccipital sutures - greatest distance between left and right pterygobasioccipital sutures (inset).

33. Length of upper left tooth row - from hindmost margin of hindmost alveolus to tip of rostrum.

34. Number of teeth - upper left.

35. Number of teeth - upper right.

36. Number of teeth - lower left.

37. Number of teeth - lower right.

Appendix 2. (continued)

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38. Length of lower left tooth row - from hindmost margin of hindmost alveolus to tip of mandible.

39. Greatest length of left ramus.

40. Greatest height of left ramus at right angles to greatest length.

41. Length of left madibular fossa, measured to mesial rim of internal surface.

42. Deviation of skull from symmetry in dorsal view, in degrees.

43. Greatest height of foramen magnum.

44. Greatest width of foramen magnum.