

Porotic hyperostosis and cribra orbitalia in human remains from southern Patagonia

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Abstract Previous studies revealed a high frequency of porotic hyperostosis in hunter-gatherer populations from southern Patagonia. Nevertheless, the systematic recovery of new burials with detailed archaeological and paleodietary contextual information during the last two decades offers new opportunities to explore the prevalence of anemia and its possible variation among populations with different marine and terrestrial hunter-gatherer lifestyles. This paper reports the results of an analysis of porotic hyperostosis and cribra orbitalia in skeletal human remains from this region, discussing their most likely causes in the light of current evidence. The results showed a high prevalence of porotic hyperostosis and a low prevalence of cribra orbitalia, without significant differences between age and sexes. Moreover, marine hunter-gatherers presented a higher frequency of porotic hyperostosis than those individuals associated with terrestrial economies. Nutritional and zoonotic factors are proposed as the most probable causes of the high frequency of anemia observed in individuals with marine-based diets. Although no temporal differences were observed, different possible patterns of health in human native populations in the during-contact period are proposed.

Key words: anemia, human bone remains, southern Patagonia, paleodiet

Introduction

Porotic hyperostosis and cribra orbitalia are stress markers frequently recorded in human skeletons. It is currently accepted that porotic hyperostosis is produced by a thickening of the cranial diploë in response to marrow hypertrophy, resulting in the thinning and porosity of the outer table of the skull, while cribra orbitalia is a similar condition, affecting the orbital roofs (Stuart-Macadam, 1989; Roberts and Manchester, 2005; Walker et al., 2009). Both lesions are widely used as indicators of health and nutritional status of ancient human populations, and are generally recognized as evidence of anemia (Stuart-Macadam, 1985; Aufderheide and Rodríguez Martín, 1998; Ortner, 2003; Roberts and Manchester, 2005).

Besides the fact that porotic hyperostosis and cribra orbitalia have been documented in historic and prehistoric contexts worldwide (e.g. Walker, 1986; Grauer, 1993; Lovell, 1997; Wright and Chew, 1998; Piontek and Kozlowsky, 2002; Keita, 2003; Facchini et al., 2004; Blom et al., 2005; Keenleyside and Panayotova, 2006), the impact and causes of anemia in populations from southern Patagonia have been little documented. During the last decade of the 20th century,

several studies reported a high frequency of porotic hyperostosis and a low frequency of cribra orbitalia in populations from Tierra del Fuego (Pérez-Pérez and Lalueza Fox, 1992; Guichón, 1994; Schinder and Guichón, 2003; Suby and Guichón, 2010). However, the archaeologically decontextualized condition of most of the study samples, commonly lacking spatial and paleodietary information, limited the data interpretations, while no studies from the continental extreme of southern Patagonia are currently available.

The recovery of burials with detailed archaeological contextual information during the last two decades (e.g. Guichón et al., 2000; L'Heureux et al., 2003; Piana et al., 2006; Suby et al., 2009; Santiago et al., 2011) offers new opportunities to study the frequency of anemia and its possible association with different marine and terrestrial hunter-gatherer lifestyles proposed for native populations. This paper reports the results of an analysis of porotic hyperostosis and cribra orbitalia in skeletal human remains from southern Patagonia, discussing their most likely causes. As anemia is frequently related to environment, diet, and nutrition (Stoltzfus, 2001; Beutler and Waalen, 2006; Brotanek et al., 2007), it is proposed that marine and terrestrial lifestyles, ethnographically and archaeologically documented for human populations from the mid-late Holocene in southern Patagonia, could lead the basis for different patterns of this condition among human hunter-gatherers.

Ethnographic and archaeological context

Ethnographic accounts provide information about two main human groups in mainland southern Patagonia and

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Tierra del Fuego: (1) terrestrial hunter-gatherers (Tehuelches or Aonikenk in the continent and Selk'nam in the north of Tierra del Fuego), traditionally described as hunters of guanaco (*Lama guanicoe*), a southern camelid; and (2) marine hunter-gatherers (Kaweskar and Yamana in the littoral of southern Tierra del Fuego), based on the specialized exploitation of marine resources (e.g. Hyades and Deniker, 1891; Gusinde, 1982, 1986; see also Orquera and Piana, 1999, 2009). However, archaeological and paleodietary data suggest a more complex scenario, not completely coincident with the one described by ethnographical and historic accounts (e.g. Yesner et al., 2003).

Despite the fact that zooarchaeological data and isotopic values show that terrestrial foods constitute the main base of the diet for humans in continental and northern insular areas of southern Patagonia (Borrero and Barberena, 2006; Suby et al., 2009; Santiago et al., 2011), marine resources were exploited near the coasts at least seasonally, probably due to the low density of terrestrial mammals (Morello et al., 2012). In fact, although guanaco played a dominant dietary role (Borrero 1986), numerous zooarchaeological evidence of consumption of marine resources in near-coastal sites were reported, including sea mammals such as sea lions (*Arctocephalus australis* and *Otaria flavescens*), several species of mussels (e.g. *Mytilus* sp., *Aulacomya* sp.) and sea birds such as shags (*Phalacrocorax atriceps*) and Magellan penguins (*Spheniscus magellanicus*). All these species are represented in the archaeological record from the Atlantic coast and Magellan Strait (e.g. Borrero, 1986; Schiavini, 1994; Cruz et al., 2007, 2010; Barberena, 2008; Borella, 2010; Muñoz, 2011).

In contrast, ethnographic and archaeological evidence from southern Tierra del Fuego showed that the subsistence of human populations that inhabited the Beagle Channel and Cape Horn region was substantially based on marine resources, navigating intensively with canoes along the coasts but rarely on open ocean waters (Orquera and Piana, 2009). Abundant zooarchaeological data indicate the consumption of pinnipeds and mussels (e.g. Orquera and Piana, 1999; Orquera, 2005). The zooarchaeological studies of Tivoli and Zangrando (2011) in shellmiddens from the Beagle Channel also detected numerous types of fish (e.g. *Austrolycus* sp., *Patagonotothen* sp., *Paranotothenia magellanica*, *Thyrstites atun*, *Sprattus fueguensis*) and birds (e.g. *Spheniscus magellanicus*, *Eudyptes chrysocome*, *Phalacrocorax* sp., *Diomedea* sp., *Macronectes giganteus*, *Procellaria* sp., *Daption capense*). Accordingly, isotopic analyses support the highest exploitation of marine foods in this region (Tessone et al., 2003; Yesner et al., 2003; Panarello et al., 2006).

From a biological point of view, studies based on mitochondrial DNA suggest that continental and island groups shared common ancestors (Lalueza et al., 1997). Hernández et al. (1997) have shown that craniofacial morphological similarities among Fuegian groups are far more important than some differences between marine and terrestrial groups, regarded as a general adaptive response to a very harsh environment. However, some degree of craniofacial morphological variability was observed, tending to cluster the Fuegian groups together, differentiating them from continental

groups (Cocilovo and Guichón, 1986; Gonzalez-José et al., 2001). The causes of these differentiation patterns remain unclear, although some explanatory models suggest that development of marine and terrestrial strategies as well as the isolation of Tierra del Fuego due to the opening of Magellan Strait c. 8000 years BP (e.g. Borrero and McEwan, 1997) had a significant role in this evolutionary process (e.g. Gonzalez-José et al., 2002; Pérez et al., 2007).

Materials and Methods

For the purpose of this study, human remains recovered in the southern continental and insular territories located between 50° and 56° S (Figure 1) were considered. Taking into account the biocultural variation among human populations from southern Patagonia described above, only individuals with spatial, paleodietary and chronological information were included. Skulls at least 75% complete, well preserved, and with at least one orbit present were accepted. Based on these selection criteria, the study sample included 40 individuals from 36 different archaeological sites (Table 1), housed in museums and research institutions of Argentina (Museo del Fin del Mundo, Ushuaia; IMHICIHU, Buenos Aires; Museo Etnográfico J.B. Ambrosetti, Buenos Aires; CADIC, Ushuaia; and Laboratorio de Ecología Evolutiva Humana, Quequén) and Chile (Instituto de la Patagonia, Punta Arenas). Chronologically, the human remains correspond to the late Holocene, including skeletons dated from c. 3800 years BP to c. 100 years BP (Table 1), with the exception of the skeleton recovered from La Arcillosa 2 site, dated c. 5200 years BP (Santiago et al., 2011).

As pointed out by Guichón et al. (2001, 2006), the bioarchaeological record of southern Patagonia is characterized by its fragmentary condition, mainly due to the small number of human remains with spatial and chronological information. Moreover, most of the burials contain only one skeleton, since no cemeteries were reported from the pre-Columbian period (Guichón et al., 2001; Santiago et al., 2011). Consequently, the sample studied in this paper, although small, includes almost all the well-preserved skeletons which are spatially, paleodietary, and chronologically documented from the considered region.

Selected skeletons were sexed following the methods proposed in Buikstra and Ubelaker (1994) based on dimorphic structures of pelvis and skull. Non-adult individuals were not sexed, following Brickley and Mckinley (2004) and Lewis (2006). Age in adults was estimated according to the methods of Brooks and Suchey (1990), Todd (1921, in Buikstra and Ubelaker, 1994), and İşcan et al. (1984, in Bass, 1995), while in non-adults it was based on tooth formation and eruption (Ubelaker, 1989). The sample includes 32 adults (80%) between 20 and 50 years old, and 8 (20%) non-adults (as defined by Lewis, 2006), between 2.5 and 17 years old. Among adults, 22 (68.7%) are males and 10 (31.3%) are females.

The presence/absence of porotic hyperostosis and cribra orbitalia was macroscopically examined in all skulls with the aid of a 10× hand lens. The severity of both conditions was categorized as stage 1–4: 1, scattered fine foramina; 2, large and small isolated foramina; 3, foramina are linked

Table 1. Human skeletal remains included in the study sample.

Region	Skeleton/Site	Chronology (years BP)	Diet	Sex	Age (years)	PH	CO	Ref
Continental southern Patagonia	1. Cañadón misionero	70 ± 30	T	M	35–45	No	No	Suby et al., 2009
	2. San Gregorio 4	During-contact	T	U	10 ± 2	No	No	Prieto 1993–1994; Guichón 1994
	3. Rincón del buque	830 ± 42	T	M	35–40	No	No	Suby et al., 2009
	4. Punta entrada 3	1748 ± 45	T	U	8–11	No	No	Suby et al., 2009
	5. Cabo vírgenes 17	900 ± 40	Mix	M	20–34	No	No	L'Heureux et al., 2003
	6. Orejas de burro (sk.1)	3565 ± 45	T	M	20–25	Yes	No	L'Heureux and Barberena, 2008
	7. Orejas de burro (sk.2)	3565 ± 45	T	M	45–50	No	No	L'Heureux and Barberena, 2008
	8. Cerro Johnny	390 ± 60	T	M	30–40	Yes	No	Borrero and Barberena, 2006
	9. Juni Aike	During-contact	T	M	30–40	No	No	Borrero and Barberena, 2006
	10. Punta Daniel	1118 ± 43*	Mix	M	30–40	Yes	No	Borrero and Barberena, 2006
	11. Posesión Olimpia 2	19th century	T	M	30–40	No	No	Borrero and Barberena, 2006
Northern Tierra del Fuego	12. San Genaro 4	During-contact	Mix	F	25–39	No	No	Martin et al., 2004
	13. Estancia San Julio	350 ± 50	T	M	36–48	No	No	Suby and Guichón, 2010
	14. La Arcillosa 2	5208 ± 58	T	F	20–24	No	No	Santiago et al., 2011
	15. Chorrillos 2	265 ± 44	T	M	20–28	No	No	Santiago et al., 2011
	16. Las mandíbulas	19th century	T	M	20–24	Yes	No	Guichón et al., 2000
	17. Margen sur (sk. A)	897 ± 38	T	U	6–8	No	No	Santiago et al., 2011
	18. Margen sur (sk. B)	897 ± 38	T	U	6–8	No	No	Santiago et al., 2011
	19. Margen sur (sk. C)	897 ± 38	T	U	9–11	No	No	Santiago et al., 2011
	20. Margen sur (sk. D)	897 ± 38	T	U	9–11	No	No	Santiago et al., 2011
	21. Puesto pescador	335 ± 35	T	M	21–25	No	No	Suby et al., 2008
	22. Santana	269 ± 46	T	M	Adult	No	No	Santiago et al., 2011
	23. Bahía Felipe 1	1608 ± 45*	Mix	M	35–50	Yes	No	Schinder and Guichón, 2003
	24. Bahía Felipe 2	1608 ± 45	Mix	F	30–40	Yes	No	Schinder and Guichón, 2003
	25. Bahía gente grande	During-contact	T	M	30–40	No	No	Schinder and Guichón, 2003
	26. Lengua de vaca	251 ± 41*	Mix	F	30–40	No	No	Schinder and Guichón, 2003
	27. Myren 1	640 ± 20	Mix	M	18–23	Yes	No	Schinder and Guichón, 2003
	28. Laguna flamenco	During-contact	Mix	F	24–39	Yes	No	Schinder and Guichón, 2003
Southern Tierra del Fuego	29. Harberton cementerio	During-contact	Ma	M	25–35	Yes	No	Piana et al., 2006
	30. Imiwaia 1	640 ± 43	Ma	F	25–49	No	No	Piana et al., 2006
	31. Mischiwen 3	625 ± 25	Ma	U	13–17	Yes	No	Piana et al., 2006
	32. Paiashauaia	1504 ± 46	Ma	F	35–45	Yes	Yes	Piana et al., 2006
	33. Shamakush 6	1536 ± 46	Ma	M	35–45	Yes	No	Piana et al., 2006
	34. Lauta 2	Pre-contact	Ma	F	35–40	Yes	No	Schinder and Guichón, 2003
	35. Isla hoste 1	Pre-contact	Ma	F	Adult	No	No	Schinder and Guichón, 2003
	36. Isla hoste 2	Pre-contact	Ma	M	Adult	Yes	Yes	Schinder and Guichón, 2003
	37. Caleta Falsa site 7.2	820 ± 40	Ma	F	30–39	Yes	Yes	Guichón and Suby, 2011
	38. Caleta Falsa site 8.1	820 ± 40	Ma	M	18–23	Yes	No	Guichón and Suby, 2011
	39. Caleta Falsa site 8.4	820 ± 40	Ma	M	43–49	No	No	Guichón and Suby, 2011
	40. Caleta Falsa site 8.5	820 ± 40	Ma	U	2.5–5	No	No	Guichón and Suby, 2011

Notes: * ^{14}C presented in this paper. All the ^{14}C values are uncalibrated. Ma, marine diet; Mix, mixed diet; T, terrestrial diet; M, male; F, female; U, undetermined; PH, porotic hyperostosis; CO, cribra orbitalia.

into a trabecular structure; 4, outgrowth in trabecular form from the outer table surface (cf. Stuart-Macadam, 1985). The major stage observed in each individual has been considered as the final value. The degree of healing was coded as active vs. healed/healing. Although interobserver biases of these methods were remarked when normal bones are examined, a good level of agreement was observed when lesions are present (Jacobi and Danforth, 2002). Statistical differences of lesion frequencies between presence/absence, adults/non-adults, male/female, marine/mix/terrestrial diet, and pre-contact/during-contact groups were calculated by χ^2 test, with a statistical significance of $P < 0.05$.

In order to explore the variation of porotic hyperostosis and cribra orbitalia according to diet, the skeletons were grouped based on the stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$)

and nitrogen ($^{15}\text{N}/^{14}\text{N}$) results previously reported (see references in Table 1), following three proposed dietary classes (Barberena, 2002; Borrero and Barberena, 2006; Borrero et al., 2009): terrestrial, marine, and mixed (in which there is no predominance of one kind of consumed resources over the other). From these classifications, 20 (50%) of the selected skeletons have stable isotope values compatible with consumption of terrestrial resources; 12 (30%) are compatible with marine diets, and 8 (20%) with mixed diets.

Chronologically, individuals from previous (19/47.5%) and during (21/52.5%) periods of Native–European contact are included, considering remains prior to c. 600 years BP as precontact. Most of the skeletons have previously been dated by ^{14}C (see references in Table 1), although some of them were dated by association with the archaeological

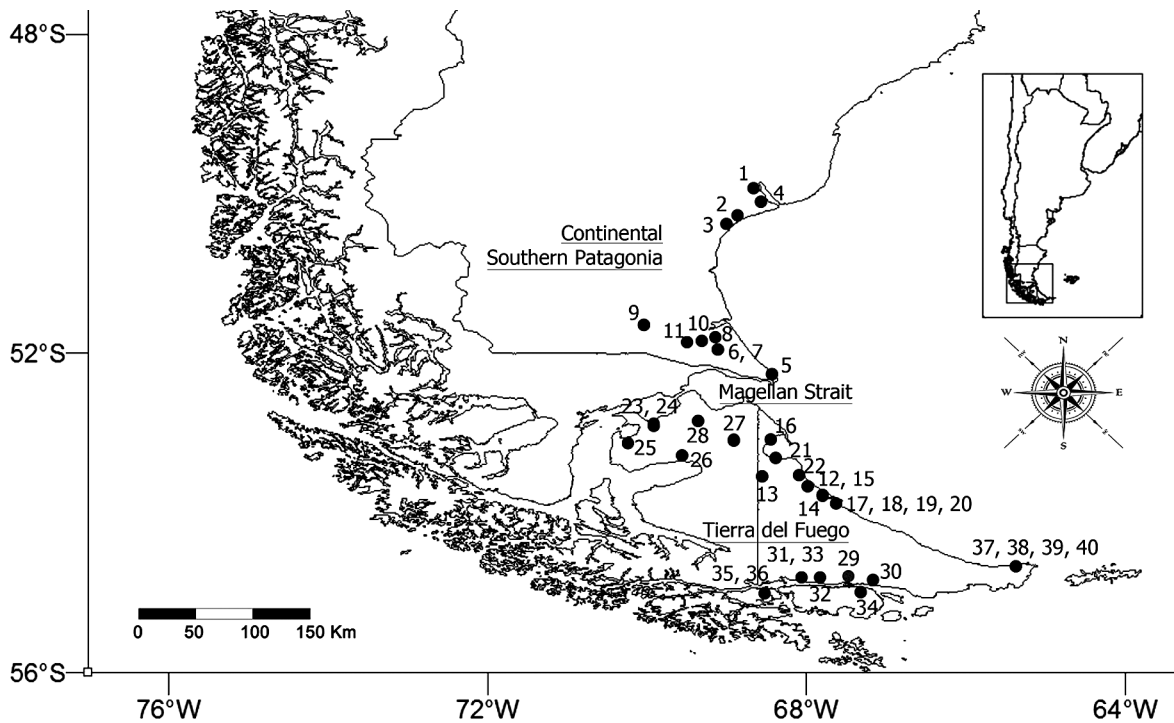


Figure 1. Map of southern Patagonia, showing the location of the sites (see references in Table 1) where the human remains studied were recovered.

context. Three new radiocarbon dates analyzed at the NSF-Arizona AMS Laboratory are presented, corresponding to human remains from Lengua de Vaca (AA94277), Bahía Felipe 1 (AA94278), and Punta Daniel (AA94279) archaeological sites (see Table 1 and Figure 1).

Results

The results of presence/absence of porotic hyperostosis (Figure 2a) and cribra orbitalia (Figure 2b) per individual are presented in Table 1. Porotic hyperostosis involved mainly occipital and parietal bones and only two skulls showed lesions affecting temporal and frontal bones. The three individuals who showed cribra orbitalia, bilateral in all cases, also presented vault lesions. Total, sex, and age distributions of the lesions are presented in Table 2. Among the studied skulls, 40% showed porotic hyperostosis and 7.5% showed

cribra orbitalia. Adults presented higher frequency of porotic hyperostosis than non-adults ($\chi^2 = 3.78$, $P = 0.05$). On the contrary, the frequency of cribra orbitalia did not result in a significantly different between adults and non-adults ($\chi^2 = 0.81$, $P = 0.36$). The frequency of porotic hyperostosis in females showed no statistically significant difference with males ($\chi^2 = 0.06$, $P = 0.81$). Although the frequency of cribra orbitalia was higher in females than males, the difference was not significant ($\chi^2 = 1.93$, $P = 0.16$).

All individuals presented severity of porotic hyperostosis coded as stage 1 or 2 (Figure 3), while cribra orbitalia were coded as stage 1 in the three affected individuals. Among individuals with porotic hyperostosis, 75% (12 out of 16 individuals) showed the lowest level of lesions. The only non-adult which presented lesions was coded as stage 1. Moreover, males showed higher frequency (90%, 9 out of 10 individuals) with stage 1 ($\chi^2 = 4.26$, $P = 0.03$). On the contrary, females were more affected by stage 2 lesions than males ($\chi^2 = 4.26$, $P = 0.03$). In relation to degree of healing, the only non-adult affected presented active lesions (Figure 4). Ten out of 15 adult individuals (75%) showed healing/healed lesions. No statistically significant differences were observed between healed and healing/healed lesions in females ($\chi^2 = 0.4$, $P = 0.52$) or in males ($\chi^2 = 3.2$, $P = 0.07$).

When the association between diet and lesions was explored (Figure 5), individuals with terrestrial diet were significantly less affected by porotic hyperostosis than individuals with mixed ($\chi^2 = 6.32$, $P = 0.01$) and marine diets ($\chi^2 = 8.88$, $P = 0.002$). Between skeletons with mixed and marine diets no significant difference was observed ($\chi^2 = 0.04$, $P = 0.84$). For cribra orbitalia, all the recorded cases corresponded to marine diet. Considering chronological data

Table 2. Age and sex distribution of porotic hyperostosis and cribra orbitalia in southern Patagonia.

	Porotic hyperostosis			Cribra orbitalia		
	No. affected	No. observed	%	No. affected	No. observed	%
Total	16	40	40	3	40	7.5
Age						
Non-adult	1	8	12.5	0	8	0
Adult	15	32	46.9	3	32	9.4
Sex						
Female	5	10	50	2	10	20
Male	10	22	45.5	1	22	4.5
Unknown	1	8	12.5	0	0	0

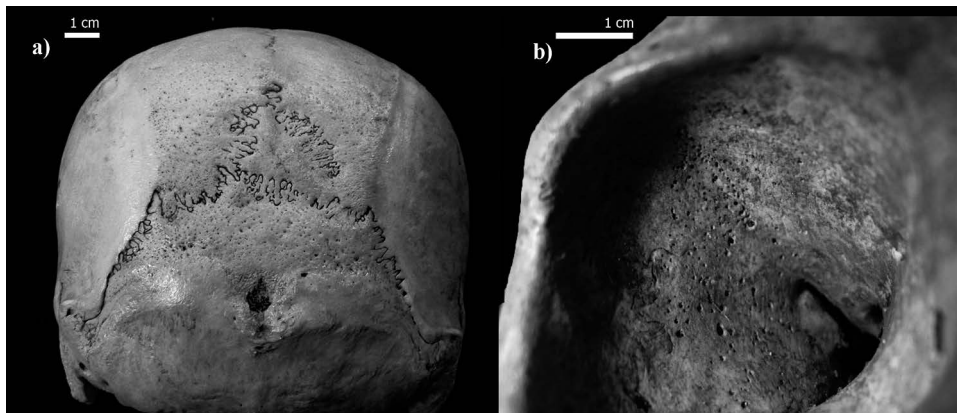


Figure 2. Vaults (a) and orbital (b) porotic lesion observed in skeletons recovered from the Cerro Johnny and Caleta Falsa 7.2 sites, respectively.

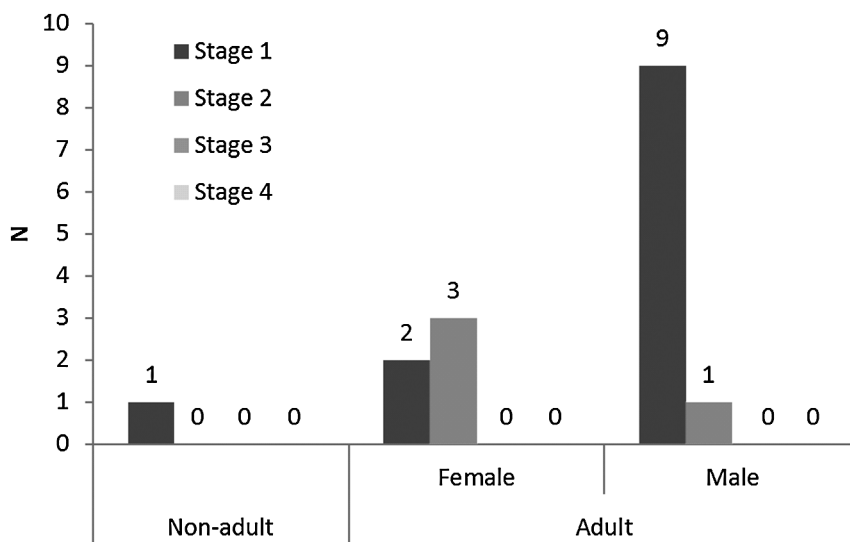


Figure 3. Severity of porotic hyperostosis in southern Patagonia.

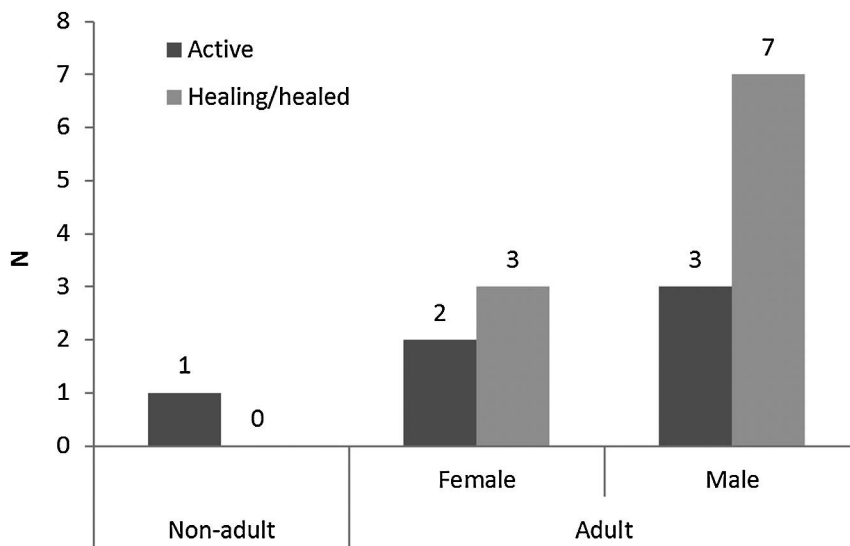


Figure 4. Degree of healing of porotic hyperostosis in southern Patagonia.

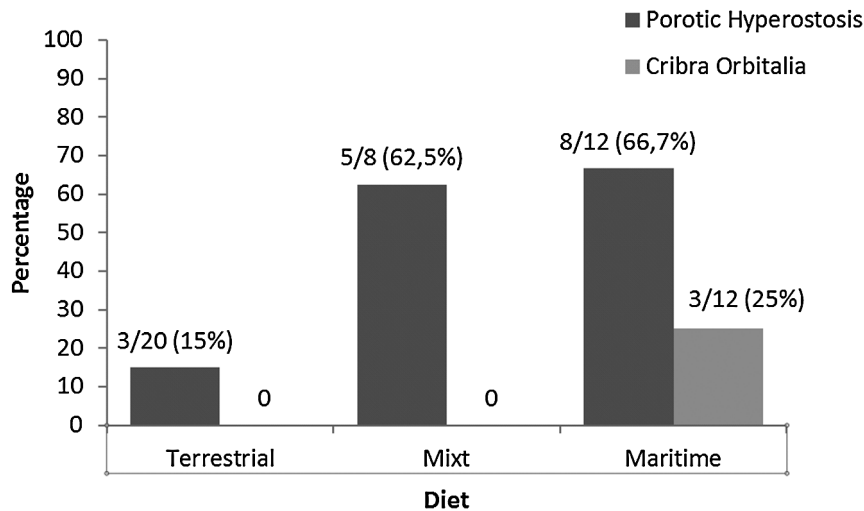


Figure 5. Diet distribution of porotic hyperostosis and cribra orbitalia in southern Patagonia.

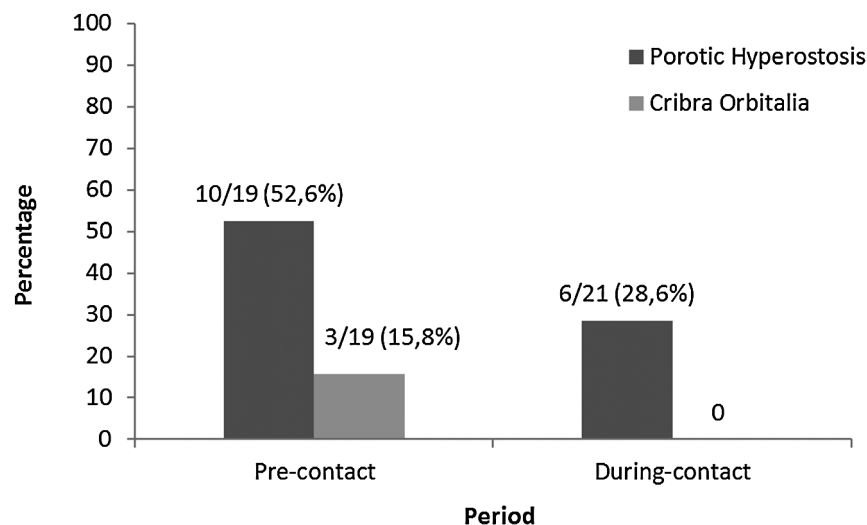


Figure 6. Chronological distribution of porotic hyperostosis and cribra orbitalia in southern Patagonia.

(Figure 6), no significant differences between remains from precontact and during-contact periods were observed for both porotic hyperostosis ($\chi^2 = 2.41$, $P = 0.12$) and cribra orbitalia ($\chi^2 = 3.58$, $P = 0.06$).

Discussion

From the sample studied in this paper, a higher prevalence of porotic hyperostosis rather than cribra orbitalia has been recorded, following the same tendencies previously reported in Tierra del Fuego (Pérez-Pérez and Lalueza-Fox, 1992; Guichón, 1994; Schinder and Guichón, 2003; Suby and Guichón, 2010). The higher frequency of vault lesions over orbital lesions is in general contrary to the results informed in other ancient populations, in which cribra orbitalia was more prevalent (e.g. Lovell, 1997; Stuart-Macadam, 1998; Keenleyside and Panayotova, 2006). Although an exact relationship between lesions in both anatomical areas is not completely understood, it is recognized that cribra orbitalia

is an early expression of porotic hyperostosis, while vault lesion could indicate long-term cases of anemia (e.g. Stuart-Macadam, 1985, 1998; Walker, 1986; Blom et al., 2005). Moreover, skulls with both areas affected have been associated with more severe cases of anemia (Stuart-Macadam, 1989). Since most of the skulls studied here show low-severity and healed lesions, the higher frequency of vault lesions could be explained as the result of chronic long-term anemia. However, it cannot be excluded that orbital lesions gradually vanish during life, disappearing in adults through bone remodeling, as was previously suggested (Walker, 1986).

Non-adults showed lower frequencies of porotic hyperostosis and cribra orbitalia than adults, although the difference among ages was not significant. This result is again contrary to others reported in past populations (e.g. Walker, 1986; Blom et al., 2005; Facchini et al., 2004; Keenleyside and Panayotova, 2006), though lower prevalence in non-adults was also observed in some cases (e.g. Grauer, 1993).

Subrepresentation of non-adults could not be excluded as a possible cause of lower prevalence in this age group. As an alternative hypothesis, a low severity of anemia could not increase the mortality of afflicted non-adults (Blom et al., 2005), and as a consequence they could have survived until adulthood. As was noted by Stuart-Macadam (1985), porotic hyperostosis in adults most probably represent healed lesions from marrow hyperplasia occurring during childhood, since children have greater bone plasticity and iron requirements than adults. Thus, the higher frequency of mild healed lesions observed in the sample studied here could support this hypothesis. Moreover, anemia persisted in some adults, since lesions in these cases remained active until the time of death.

The presented data indicate no difference in the frequency of both porotic hyperostosis and cribra orbitalia between adult males and females. While some studies reported similar results (e.g. Stuart-Macadam, 1989, 1998; Keenleyside and Panayotova, 2006), others have noted a higher frequency of porotic lesions in women, considering menstruation, childbirth, and lactation as factors that increase the risk of anemia (Ryan, 1997; Stuart-Macadam, 1998). Nevertheless, since porotic hyperostosis is probably developed during childhood, the results are only informative about that period and possibly indicate that girls and boys were not exposed to differential factors that produced anemia. No difference in the frequency of active lesions was observed between males and females, which do not support the idea of sex as a risk factor predictive of anemia in human populations from southern Patagonia.

Discriminating between the causes of anemia in human skeletons is frequently difficult (Brickley and Ives, 2008). Porotic hyperostosis has been widely recognized as being caused by marrow hyperplasia, most commonly in response to iron-deficiency anemia (Stuart-Macadam, 1985, 1998; Ortner, 2003). In contrast to this assumption, Walker et al. (2009) recently claimed that clinical evidence indicates that megaloblastic anemia is a more probable cause of marrow hyperplasia. Concerning this new argument, Mays (2012) suggested that not all the biomedical literature supports this hypothesis and diploic hyperplasia can also occur in iron-deficiency anemia. Therefore, at least for now, iron-deficiency anemia is accepted as a probable cause of marrow hyperplasia responsible for porotic hyperostosis. As was remarked by Stuart-Macadam (1998), iron-deficiency anemia has to be considered as a symptom and not a disease, the possible origins of which include inadequate diet, poor iron absorption, increased iron utilization, blood loss, or infection. The possible causes of anemia in past populations from southern Patagonia are discussed below, taking into account the results presented here.

Diet and nutrition

Individuals with terrestrial diet showed lower frequencies of vault and orbital lesions than skeletons with marine and mixed diet in the studied sample. Thus, incorporation of marine resources could be one of the possible causes associated with a high prevalence of anemia. On the contrary, Gómez Otero and Novellino (2011) reported a lower frequency of porotic hyperostosis and cribra orbitalia in indi-

viduals with mixed diet in southern Patagonia, suggesting that it could have been nutritionally more complete than exclusively terrestrial and marine diets. However, Gómez Otero and Novellino (2011) included skeletons without isotopic analyses as a mixed-diet sample, based on ethnographical and geographical data (e.g. skeletons from Valentin Bay site), which could be the reason for that difference.

As was described above, archaeological data indicate that terrestrial diets were based mainly on the consumption of guanaco, while marine resources incorporated by southern Patagonian populations include mostly mollusks, sea mammals, seabirds, and fish. In both cases, as consumed foods provide a rich source of proteins (Draper, 1977), iron-deficient intake is not expected, although other diseases produced by excess protein consumption with marine diets, such as ammonia intoxication, were suggested (Noli and Avery, 1988).

Nonetheless, dietary consumption of iron is not necessarily absorbed. Iron absorption is determined by the content of heme and nonheme iron, their bioavailability and the relationship with other dietary components (Hallberg and Björn-Rasmussen, 1981). For example, several dietary factors (e.g. ascorbic acid, meat and fish) enhance iron absorption, whereas others (e.g. phosphates, calcium and low levels of vitamin C) inhibit iron absorption (Hallberg and Hulthén, 2000). Thus, high phosphate contents consumed with marine diets could have reduced the iron absorption, explaining the high frequency of porotic hyperostosis in marine hunter-gatherers. Similar patterns were previously proposed for other marine-based populations (Lallo et al., 1977; Walker, 1986; Blom et al., 2005). Despite the high frequency observed, anemia associated with marine diets could not have had severe physiological effects, since Suby and Guichón (2009) showed higher mechanical demand on the femoral diaphysis of both males and females with a diet that relied upon marine resources rather than those with terrestrial and mixed diets.

Parasite infections

The exposure to gastrointestinal parasite infection may also induce blood-loss and anemia. The effects of soil-transmitted helminthes (e.g. *Ascaris lumbricoides*, *Trichuris trichiura*, and hookworms), schistosomiasis (*Schistosoma haematobium*, *S. mansoni* and *S. japonicum*), and malaria, which cause or aggravate malnutrition and chronic blood-loss, are well documented (Crompton and Nesheim, 2002; Hotez et al., 2004; Pullan and Brooker, 2008). Moreover, it was claimed that polyparasitism may have a greater impact on morbidity than single-species infection (Pullan and Brooker, 2008). Some soil-transmitted parasites, specifically *T. trichiura*, *Capillaria* spp., *Eimeria macusaniensis*, and *A. lumbricoides*, were recently identified in archaeological sites of southern Patagonia, all of which have terrestrial hosts (Fugassa et al., 2008a, b). Consequently, some of these species could be responsible for anemia in populations that subsist on terrestrial diets. However, the mentioned species of parasites so far detected in archaeological sites of southern Patagonia do not explain the higher frequency of porotic hyperostosis on individuals with marine diets.

Parasites of the genus *Diphyllobothrium*, generally report-

ed from areas where fish are eaten raw, marinated, or undercooked (Butt et al., 2004), have been associated with the development of anemia in ancient marine-dependent societies (Walker, 1986; Blom et al., 2005) and reported in archaeological coprolites from the Peruvian coasts (e.g. Ferreira et al., 1984). Since *Diphyllobothrium* has South American sea lions and several species of marine fishes as hosts (Butt et al., 2004), it could have been an infectious agent in the past in southern Patagonia. Currently, these parasites are prevalent in the southwest Atlantic, affecting many marine fishes (Timi, 2007). Moreover, several species of helminths have been identified in current populations of Magellan penguin (Pazos et al., 2003). Although zooarchaeological researches suggest scarce exploitation of this marine bird by hunter-gatherers (Cruz et al., 2010), their consumption could have been a source of parasitic infection.

Other parasites, such as *Anisakis*, which are responsible for the most common human nematode infection associated with consumption of seafood (Sakanari and McKerrow, 1989), is widely distributed in modern sea mammals and fishes in South American Atlantic waters (Timi, 2007), and has been reported in paleoparasitological contexts (e.g. Arriaza et al., 2010). So far none of these types of parasites have been recorded in archaeological sites or human remains from southern Patagonia. Nevertheless, it cannot be excluded that some of them affected human populations in the past, explaining the high prevalence of anemia associated with marine diets. Further explorations will probably offer new evidence about the zoonotic impact of a high consumption of seafood.

Since many microorganisms require iron for their metabolism, the host's immune system reduces the available serum iron and the iron absorbed from food, provoking a state of hypoferrremia. For that reason, some infections can lead to an immune-induced anemia (Stuart-Macadam, 1998; Wessling-Resnick, 2008). In the studied skeletons, non-parasitic infectious diseases are improbable causes of the high frequency of anemia registered, due to the low prevalence of new bone formation, as well as in other samples reported earlier in Tierra del Fuego (e.g. Guichón, 1994; Schinder and Guichón, 2003; Suby et al., 2009, 2011; Santiago et al., 2011), although they cannot be excluded.

Congenital and metabolic causes

Congenital forms, scurvy, and rickets were also proposed as causes of porotic hyperostosis (Ortner, 2003). Congenital anemia seems not to be a probable cause of the lesions recorded in the studied sample, since postcranial lesions, enlargement of the cranial bones, and cortical destruction and expansion of the ribs (Aufderheide and Rodríguez Martín, 1998; Ortner, 2003) are absent in these particular skeletons.

Because diet in southern Patagonia is probably reduced in vitamin C, scurvy could not be completely discounted. However, no evidence of porosities of the maxillary and sphenoid bones, suggested by this pathology (Ortner et al., 2001; Ortner, 2003; Brickley and Ives, 2008), were found. Lesions described in rickets (Ortner, 2003) were also not observed. In addition, vitamin D deficiency associated with high latitudes is not expected, since hunter-gatherers are frequently exposed to sunlight (Ortner, 2003). In fact, Oliveri et

al. (2000) showed that low vitamin D levels do not affect young modern populations of Ushuaia (Tierra del Fuego, Argentina), despite the reduced hours of light during winter.

Temporal differences

Skeletons from the pre-contact period show a higher frequency of porotic hyperostosis and cribra orbitalia than those from the during-contact period, although the results are not statistically significant. Thus, chronological variation seems not to be a predictable factor for anemia. Nonetheless, during-contact skeletons included in this study were recovered from burials not associated with missions established in southern Patagonia. In contrast, previous research on skeletons buried at the cemetery of the Salesian mission 'La Candelaria,' in the north of Tierra del Fuego, showed that 67% of the individuals were affected by porotic hyperostosis and 22% by cribra orbitalia, higher frequencies than those observed in this paper (García Laborde et al., 2010). In this sense, individuals who lived in missions could have suffered lower health status than individuals from other during-contact contexts, such as the ones included in the sample studied here.

Conclusions

Detailed information about sex- and age-related anemia, severity of lesions, and association with diet and nutrition was presented. The results showed a high prevalence of porotic hyperostosis in individuals with a marine-based diet, mainly of low severity. They also indicate no difference between males and females; thus, sex seems not to be biologically or socially related to the anemia in these populations.

Due to the small size of the studied sample, it is necessary to be cautious about the results. However, a paleopathological approach and the well-documented remains suggest that iron-deficiency anemia is the most probable cause of the high prevalence of porotic hyperostosis in individuals whose diet includes marine resources. Nutritional and zoonotic factors are proposed as possible explanations of anemia being most prevalent in populations subsisting on a marine diet, based on clinical and paleopathological research and biological data of modern marine parasites. However, direct paleodietary and paleoparasitological evidence is currently unavailable, since marine parasites have not yet been recovered from archaeological sites.

As was noted previously (Guichón, 1994; García Laborde et al., 2010), the lifestyle of native individuals in the post-Columbian period could have increased the risk of developing some diseases, especially in people who lived in missions. A diet rich in carbohydrates with low protein intake, infections, and the crowded environments described for the missions in Tierra del Fuego (Casali et al., 2006) could be responsible of the high levels of anemia observed in missionary contexts. In contrast, individuals who were not housed in missions, as is probably the case for the skeletons studied here, presented less evidence of anemia. These results suggest heterogeneous patterns of health in the post-contact period, possibly associated with differences in diet and living conditions.

The hypotheses presented here need to be tested by addi-

tional studies on more numerous archaeological samples from museum collections and the systematic recovery of new burials. In addition, new researches are needed in order to find evidence of possible parasite infections from marine sources in past populations from southern Patagonia.

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