

Postcranial axial skeletal pathology in Commerson's dolphins *Cephalorhynchus c. commersonii* from Tierra del Fuego, Argentina

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ABSTRACT: Commerson's dolphins *Cephalorhynchus c. commersonii* are the small cetacean most frequently found stranded along the coast of Tierra del Fuego, Argentina, but little is known about their pathologies. We examined the postcranial axial skeleton of 425 Commerson's dolphins collected in the period 1974–2011 for the presence of pathologies. Miscellaneous lesions were detected in 107 (25.2%) of the specimens. Among them, idiopathic hyperostosis was the most frequent pathology (73.8%), followed by spondyloarthropathy (40.2%). Traumata (25.2%), spondylitis (10.3%) and osteoarthritis (11.2%) occurred less frequently. The type of lesion was statistically associated with the region of the vertebral column. Idiopathic hyperostosis occurred significantly more frequently in the lumbar vertebrae than in other parts of the vertebral column, while spondyloarthropathy was more frequent in the thoracic and caudal vertebrae. Both conditions were predominantly seen in mature dolphins. Osteoarthritis affected the transverse processes of the thoracic vertebrae of 6 males, 3 females and 3 individuals of undetermined sex, all mature. Healed and unhealed fractures were observed in the ribs of 27 specimens and in the transverse processes of 3 others. Spondylitis of various degrees of severity affected the cervical, thoracic, lumbar and caudal regions of 11 individuals. Together these data indicate that bone lesions and traumata commonly occur in Commerson's dolphins, likely causing pain and morbidity in severe cases.

KEY WORDS: Skeletal pathology · Idiopathic hyperostosis · Spondylitis · Osteoarthritis · Degenerative lesions · Traumata · Osteolysis · Commerson's dolphins · Cetacean

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1. INTRODUCTION

Vertebral lesions in cetaceans affect individuals from all age classes, causing severe functional limitations or even death (Kompanje 1999, Sweeny et al. 2005, Félix et al. 2007). Some are the result of degenerative processes associated with aging, while others are caused by trauma, mechanical stress, inflammatory processes and pathogens. Degenerative lesions

include osteoarthritis, 'idiopathic hyperostosis' and spondyloarthropathy among others. Osteoarthritis is a disorder of the synovial joints that may be caused by repeated and excessive mechanical stress and traumata (Salter 2002). It is characterized by a degeneration of the articular cartilage, leading to fissures and loss of the joint surface, and may be accompanied by osteophytes formation and thickening of the subchondral bone plate (Martel-Pelletier 2004).

Spondyloarthropathy refers to any joint diseases of the vertebral column and includes ankylosing spondylitis (Kompanje 1999). Spondyloarthropathy often results from the degeneration of the intervertebral discs and mostly occurs in adult animals (Kompanje 1995a, Galatius et al. 2009). Idiopathic hyperostosis of the vertebrae is characterized by excessive growth or thickening of the bone tissue that does not affect the cartilage and intervertebral discs and occurs in the absence of subchondral bone remodeling (Lagier 1989). It takes place mainly in the area of tendon and ligaments insertion, i.e. areas of strong muscle tension (de Smet 1977). Traumata, such as fractures, may be the result of intra- or inter-specific interactions or may be caused by anthropogenic factors, such as entanglement and ship strikes (Oremland et al. 2010, Groch et al. 2012). Spondylitis is an acute or chronic infection of the vertebrae characterized by bone destruction and new bone formation that may occur between several vertebrae and affect (spondylodiscitis) or not (spondylitis) the intervertebral disc (Kompanje 1995a,b, Groch et al. 2012). Other conditions include soft tissue ossification and intraspongious disc herniation (La Sala et al. 2012, Nganvongpanit et al. 2017). Though these bone lesions and traumata have been documented in cetaceans from several ocean provinces (Kompanje 1995a, 1996, 1999, Kompanje & García Hartmann 2001, Van Bressemer et al. 2006, 2007, Laeta et al. 2010, Oremland et al. 2010, Groch et al. 2012, Bertulli et al. 2015, San Martín et al. 2016), they have never been reported in the Commerson's dolphin *Cephalorhynchus c. commersonii*.

The Commerson's dolphin, including the subspecies *Cephalorhynchus c. commersonii* and *C. c. kerguelensis*, is one of the most common small cetaceans inhabiting the coastal waters of the Southwest Atlantic Ocean and is the species most frequently by-caught in artisanal coastal gill nets in the provinces of Santa Cruz and Tierra del Fuego, Argentina (Goodall & Schiavini 1994, Iñíguez et al. 2003). It is small and stout, with adults growing to ~145 cm. Sexes are easily distinguished by the form of the genital black patch. Shaped like a teardrop in males, this patch completely covers the genital slit. In females, the patch has 2 lateral lobed projections and only partially covers the genital slit (Goodall et al. 1988, Robineau et al. 2007). The total number of vertebrae in *Cephalorhynchus c. commersonii* varies between 63 and 66, including 7 cervical, 12 to 14 thoracic, 13 to 15 lumbar and 26 to 32 caudal vertebrae. There are 11–13 pairs of true ribs, 1 pair of floating ribs and 7 pairs of sternal ribs (Goodall et al. 1988).

Initiated in the 1970s by Dr. Goodall in Tierra del Fuego, the R. Natalie P. Goodall (RNP) program has been collecting stranded or incidentally caught cetaceans and pinnipeds for >50 yr. Currently the RNP marine mammal's collection has the world's largest number of Commerson's dolphin skeletal remains. To provide insight into the diseases affecting this species, we examined the postcranial axial skeleton of 425 individuals stranded along the coast of Tierra del Fuego between 1974 and 2011 for the presence of lesions and traumata and evaluated their correlation with sex, age and vertebral regions.

2. MATERIALS AND METHODS

2.1. Specimens

We studied the postcranial axial skeletal pathologies of 425 *Cephalorhynchus c. commersonii* from the RNP collection curated at the Museo Acatushún de Aves y Mamíferos Marinos Australes, Estancia Harberton, Tierra del Fuego, Argentina. All were collected in the period 1974 to 2011 during beach surveys carried out along the coast of northeastern Tierra del Fuego, from Cabo Espíritu Santo (52° 40' S, 68° 36' W) to Cabo San Pablo (54° 17' S, 66° 45' W) (Goodall 1978, Goodall & Schiavini 1994, Goodall et al. 2008; Fig. 1). Most specimens were found in an advanced state of decomposition and had been partially eaten by scavengers or cut by fisherman, and the skulls, pelvic bones and pectoral fins were often missing or severely damaged. To standardize the data, we decided to limit our analyses to the complete postcranial axial skeleton. Data on the collec-

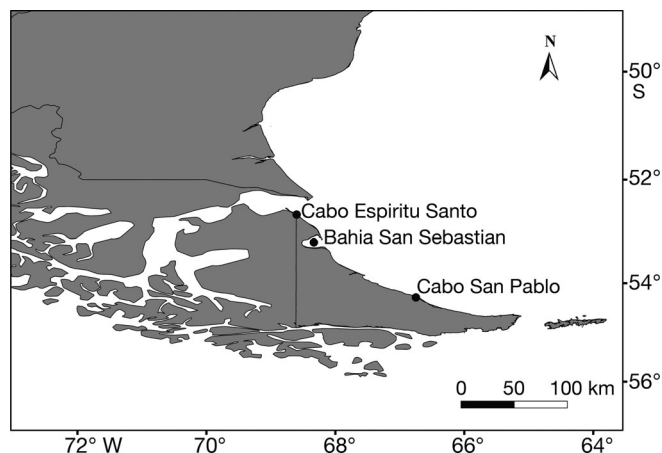


Fig. 1. Sites (●) where most of the investigated Commerson's dolphins *Cephalorhynchus c. commersonii* were found stranded along the coast of Tierra del Fuego Island, Argentina

tion date, stranding location, condition and type of skeleton (complete or incomplete) were available for all specimens. Sex was determined in 308 individuals, directly during necropsy or indirectly by examining the genital black patch of fresh specimens, by evaluating the form and size of the pelvic bones or by molecular testing using DNA amplified from teeth or bones (Pimper 2010, Pimper et al. 2010). Age was determined for 293 dolphins by counting the growth layer groups in dentin (Perrin & Myrick 1980). Physical maturity, based on the status of epiphyseal fusion of vertebrae, was determined for 411 specimens, as follows: 0—Fetus or newborn: unfused neural arch and vertebral discs; 1—young dolphins, calves and juveniles under 5 yr old: fusion of the neural arch but not of the vertebral discs; 2—Subadult: fusions of some vertebral discs; 3—Adult (physically mature): fusions of all vertebral discs (Perrin 1975, modified by Goodall et al. 1988). On the basis of the age and physical maturity, specimens were classified into an immature (6 mo to <5 yr; physical maturity 1) and a mature (from 5 yr onwards; physical maturity 2 & 3) category (Table 1).

2.2. Identification of bone lesions

All postcranial axial skeletons were macroscopically examined for the presence of pathologies and traumata. They were photographed, described and classified into 3 categories:

(1) Degenerative lesions. This category includes osteoarthritis, idiopathic hyperostosis of the spinal and transverse processes of the vertebrae and spondyloarthropathy.

(2) Traumatic lesions. This category includes healed and unhealed fractures.

(3) Spondylitis (spondylo-osteomyelitis) and spondylodiscitis. This condition is characterized by bone destruction (osteolysis), the development of cavities (cloacae) likely caused by the accumulation of pus, the formation of fistulae and new bone formation (Kompanje 1995b).

Table 1. Specimens of Commerson's dolphin (*Cephalorhynchus c. commersonii*) examined during the study

Age class	Males	Females	Unknown	Total
Immature	59	47	38	144
Mature	152	50	78	280
Unknown	0	0	1	1
Total	211	97	117	425

2.3. Data analysis

To evaluate the significance of sexual variation and of the region of the vertebral column in the prevalence of idiopathic hyperostosis and spondyloarthropathy, we used a Pearson's Chi-squared Test for Count Data, in R (R v.1.1.456, RStudio: Integrated Development Environment for R). We evaluated the relationships between the occurrence of bone lesions and biological variables using generalized linear mixed-effects models. Mixed models accounted for the non-independence of data among repeated measures (in this case, different column regions from the same specimen; Pinheiro & Bates 2000). We modeled only for idiopathic hyperostosis and spondyloarthropathy because the sample size for the other lesions was too small for statistical analysis.

The presence of vertebral pathologies was modeled as the response variable, while sex, age and the region of the vertebral column affected were modeled as fixed effects. The specimen identity (RNP number) was included in all the models as a random effect. For the analysis, we used only those specimens for which data on sex and age were available ($n = 249$). Five age categories were considered according to Lockyer et al. (1988): juvenile (6 mo to 2 yr), subadult (3–4 yr), early adult (5–8 yr), sexually adult (9–12 yr) and physically adult (>12 yr). Models were constructed by backwards selection, removing non-significant fixed terms (as a function of the approximate p-values). For analyses, we used models with a binomial error distribution and a logit link function, with the maximum likelihood method of parameter estimation, with the specific packages nlme4 and lme4 in the statistical package R (R v.2.9.2; R Development Core Team 2008). The significance of the random effect was assessed using a maximum likelihood method (Pinheiro & Bates 2000, Crawley 2007). Models were selected using Akaike's information criterion (AIC). The model with the lowest AIC value was taken to be the best approximating model, and subsequent models with an Akaike difference < 2 were considered to also have substantial support from data (Burnham & Anderson 2002).

3. RESULTS

The number of mature and immature individuals of each sex is provided in Table 1. The postcranial axial skeletons of 107 (25.2%) of 425 Commerson's dolphins *Cephalorhynchus c. commersonii* stranded

along the coast of Tierra del Fuego in the period 1974 to 2011 had bone lesions or traumata. Among the 107 affected dolphins, idiopathic hyperostosis was the most frequent pathology (73.8%), followed by spondyloarthropathy (40.2%). Traumata (25.2%), spondylitis and spondylodiscitis (10.3%) and osteoarthritis (11.2%) occurred less frequently (Fig. 2).

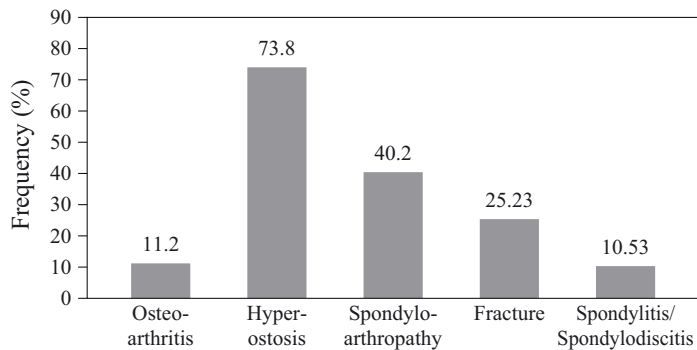


Fig. 2. Frequency of occurrence (%) of bone pathologies among 107 affected Commerson's dolphins *Cephalorhynchus c. commersonii* (of 425 ind. surveyed) from Tierra del Fuego, Argentina

3.1. Degenerative lesions

3.1.1. Osteoarthritis

Osteoarthritis affected the transverse processes of the thoracic vertebrae of 6 males, 3 females and 3 individuals of undetermined sex, all physically mature and 9 of them (6 males and 3 females) aged between 6 and 16 yr (Fig. 3a). The prevalence of this condition was 2.82% in the 425 *C. c. commersonii*.

3.1.2. Idiopathic hyperostosis

Idiopathic hyperostosis was detected in 79 mature specimens, including 52 males, 9 females and 18 dolphins of undetermined sex. This condition was characterized by bone overgrowth at the surface of the spinal and transverse processes (Fig. 3b). The prevalence was 18.6% in the 425 specimens. It was significantly ($\chi^2_1 = 9.879$, $p = 0.001672$) higher in males (24.6%, $n = 211$) than in females (9.2%, $n = 97$). The lumbar vertebrae were significantly ($\chi^2_3 = 132.08$, $p <$

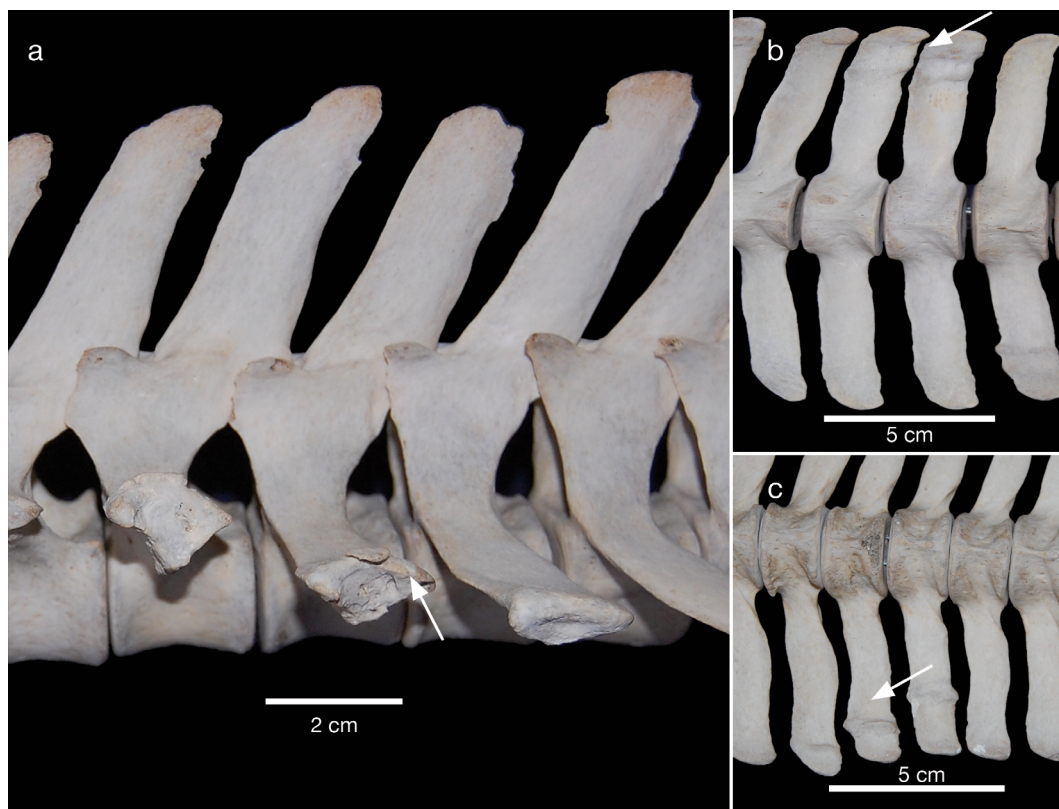


Fig. 3. (a) Osteoarthritis in the thoracic vertebra of a Commerson's dolphin *Cephalorhynchus c. commersonii* RNP 2310, as evidenced by bone overgrowth (arrow) on the extremity of the transverse processes; (b) and (c) idiopathic hyperostosis on the transverse process of lumbar vertebrae (ventral view) of RNP 2244 and RNP 2336 (the arrows indicate the overgrowth)

0.0001) more frequently (77.2%, n = 61) affected than the other parts of the vertebral column, followed by the thoracic vertebrae (48.1%, n = 38).

3.1.3. Spondyloarthropathy

Spondyloarthropathy was detected in 43 (10.11%) of the 425 *C. c. commersonii*, including 3 immature and 40 mature specimens. Eight of them had severe ankylosis of ≥ 2 cervical and/or thoracic vertebrae (Table 2, Fig. 4).

No significant ($\chi^2_1 = 0.057987$, $p = 0.8097$) differences in prevalence were found between males (10.4%, n = 211) and females (11.34%, n = 97), and sexes were grouped for subsequent analysis. The disease occurred significantly ($\chi^2_1 = 15.538$, $p < 0.0001$) more frequently in mature (14.3%, n = 40) than in immature (2.08%, n = 3) specimens. Though it af-

ected all regions of the vertebral column, it occurred significantly ($\chi^2_3 = 31.702$, $p < 0.0001$) more frequently in the thoracic (88.4%, n = 38) and caudal (69.8%, n = 30) vertebrae than in the cervical (34.9%, n = 15) and lumbar regions (44.2%, n = 19) in the 43 affected dolphins.

3.1.4. Traumata

A total of 27 specimens, most of them (89%) adults, had different types of fractures (Fig. 5). Among males, 9 had fractures of the ribs, 1 had an unhealed fracture of the transverse process of the thoracic vertebra, and 2 had healed and unhealed fractures of the transverse process of a lumbar vertebra. The 8 positive females and 7 specimens of undetermined sex had fractures of the ribs. Global fracture prevalence was 6.35% in the 425 Commerson's dolphins.

Table 2. Spondyloarthropathy with ankylosis in Commerson's dolphin *Cephalorhynchus c. commersonii* from Tierra del Fuego, Argentina. Specimen numbers refer to the R. Natalie P. Goodall collection

Specimen	Sex	Age (yr)	Age class	Date found	Description
1054	M	4	2	18 Jan 1983	Fusions of 2 lumbar (L9–10) vertebrae
1858	M	11	3	25 Feb 1995	Fusion of all cervical vertebrae
1872	U	U	2	25 Feb 1995	Fusion of 6 thoracic (Th6–11) vertebrae
1924	F	6	2	19 Apr 1995	Fusion of 2 cervical (Cv6–7) vertebrae
1991	U	U	3	22 Feb 1997	Fusion of 2 thoracic (Th5–6) vertebrae; formation of marginal osteophytes in all thoracic vertebrae
2173	F	6	3	14 Nov 2000	Fusion of 3 (Cv3–5) cervical and 3 thoracic (Th6–8) vertebrae; formation of osteophytes in all cervical and thoracic vertebrae
2245	M	U	3	10 Mar 2002	Partial fusion of 2 cervical vertebrae (Cv4–5)
2268	F	13	3	06 Jan 2003	Fusion of 2 (Cv3–4) cervical vertebrae; osteophytes on the ventral side of at least another cervical vertebra

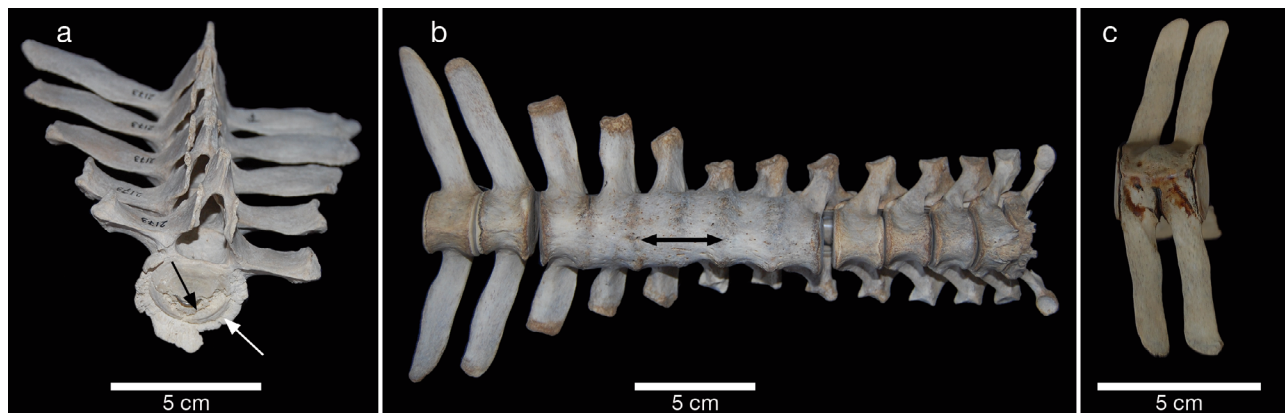


Fig. 4. Spondyloarthropathy in Commerson's dolphins *Cephalorhynchus c. commersonii*: (a) thoracic vertebral body (Th1) with disc erosion (black arrow) and marginal osteophytes (white arrow) in mature female (RNP 2173); (b) overgrowth of the osteophytes in contiguous vertebrae and ventral ankylosis of the thoracic vertebrae 6–11 (double arrow) in mature specimen (RNP 1872) and (c) 2 lumbar (L9–10) vertebrae with ventral ankylosis in mature male (RNP 1054)

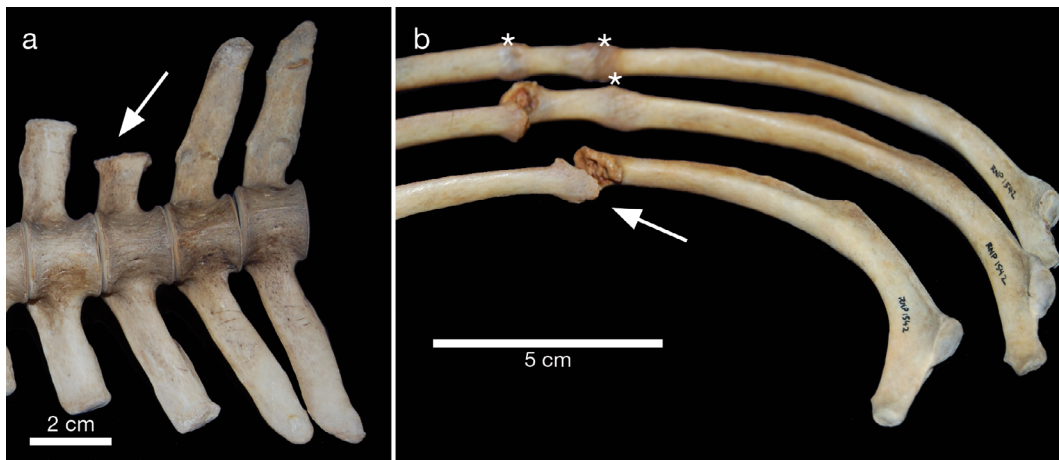


Fig. 5. Fractures in Commerson's dolphins *Cephalorhynchus c. commersonii*: (a) complete fracture (arrow) of the transverse process of the tenth thoracic vertebra in a male mature RNP 2708; (b) healed (asterisk) and unhealed fractures of the ribs of male mature RNP 1542

3.1.5. Spondylitis and spondylodiscitis

Spondylitis and spondylodiscitis were detected in the cervical, thoracic, lumbar and caudal regions of 11 individuals (Fig. 6), 6 of them immature. Prevalence of these conditions was 2.6% in the 425 specimens. The lesions were limited to 1 or 2 vertebrae in 5 dolphins. In 4 others, they were more severe, with large areas of bone destruction and new bone formation affecting 2 to 10 vertebrae (Fig. 6a,b). In another individual, an immature male (RNP 1338), >50% of the vertebrae were affected. Localized osteolysis and cloacae were seen in 5 thoracic vertebrae (6–8 and 10–11). Bone destruction and new bone formation were observed in all lumbar vertebrae and in most of the caudal vertebrae. Finally, in a mature female (RNP 1875) osteolysis and new formation were observed on the transverse processes of 3 lumbar vertebrae.

3.1.6. Undetermined

Extensive bone remodeling and limited osteolysis were observed on 4 caudal vertebrae of a 4 yr old immature female (Fig. 7). Though these lesions may have been related to osteomyelitis, they may also have had a metabolic etiology.

3.2. Statistics and model analysis

The best-supported model to explain the occurrence of idiopathic hyperostosis included the region of the vertebral column as the only explanatory vari-

able. This model indicated that the prevalence of idiopathic hyperostosis is higher in the thoracic and lumbar vertebrae than in those in the caudal and cervical regions (Table 3). The variability explained by the random effect was significant in the final model ($p \leq 0.001$).

Similar results were observed for spondyloarthropathy, with the region of the vertebral column being the only significant explanatory variable in the model with the lowest AIC score. This model suggested that the probability of having spondyloarthropathy is lower in the lumbar region than in the other regions (Table 4). The variability explained by the identity (ID number) of the specimens was significant in the final model ($p \leq 0.001$). Sex and age did not significantly affect the occurrence of this condition.

4. DISCUSSION

During this study, we observed spondylitis and spondylodiscitis, degenerative lesions and traumata in the postcranial axial skeletal of 107 Commerson's dolphins *Cephalorhynchus c. commersonii* stranded or by-caught along the coast of Tierra del Fuego in the period 1974 to 2011, with a global prevalence of 25.2% ($n = 425$). In comparison, the prevalence of postcranial axial skeletal pathologies was 41% in 78 sympatric Peale's dolphins *Lagenorhynchus australis* (San Martín et al. 2016). The large number ($n = 249$) of Commerson's dolphin specimens for which the age was determined allowed the use of generalized linear mixed-effects models to explore the relation between prevalence and biological variables, such as

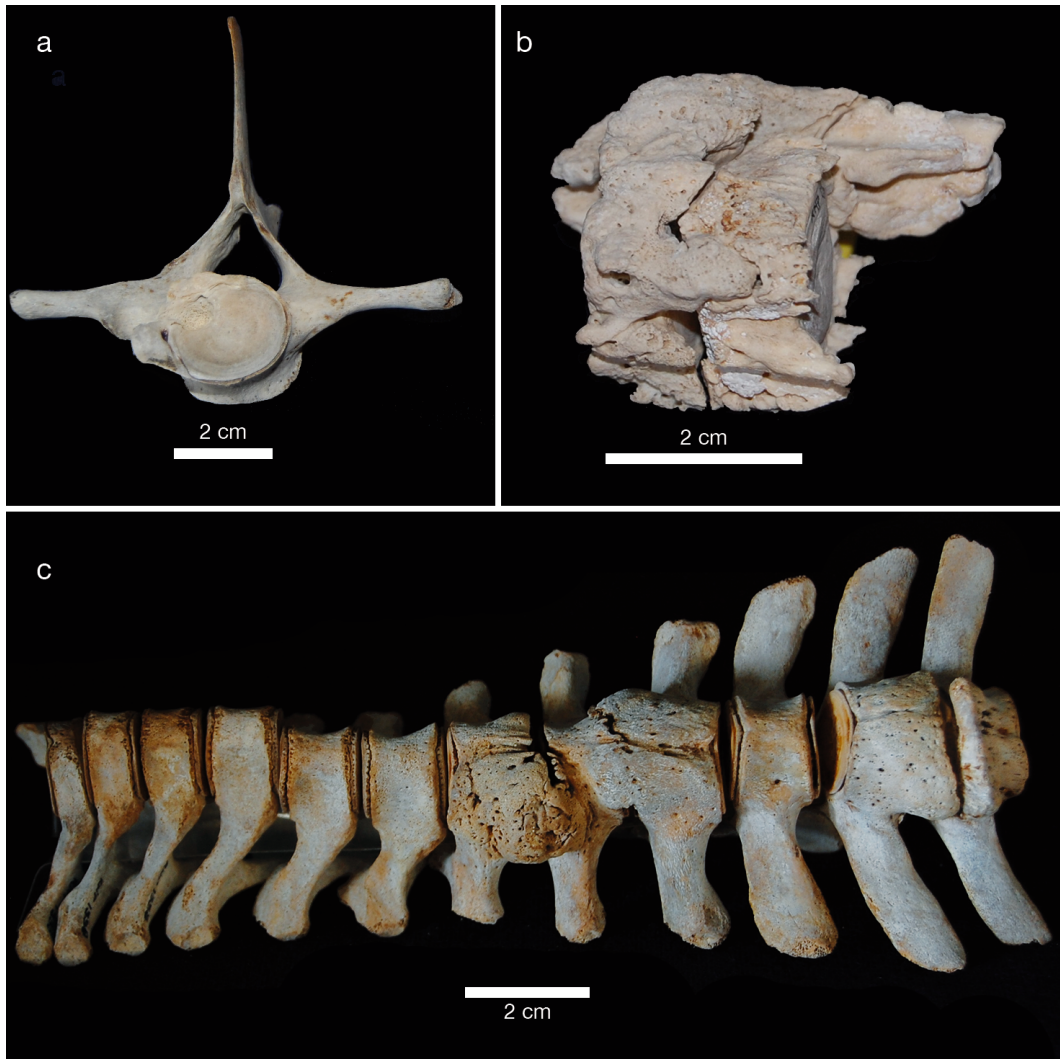


Fig. 6. (a) Osteolysis in an intervertebral disc and new bone formation in the thoracic vertebrae of immature male RNP 1691 (spondylodiscitis); (b) lysis and bone remodeling in several caudal vertebrae of mature female RNP 2254 (spondylodiscitis); (c) osteomyelitis in 5 thoracic vertebrae (spondylitis) of immature male RNP 1338

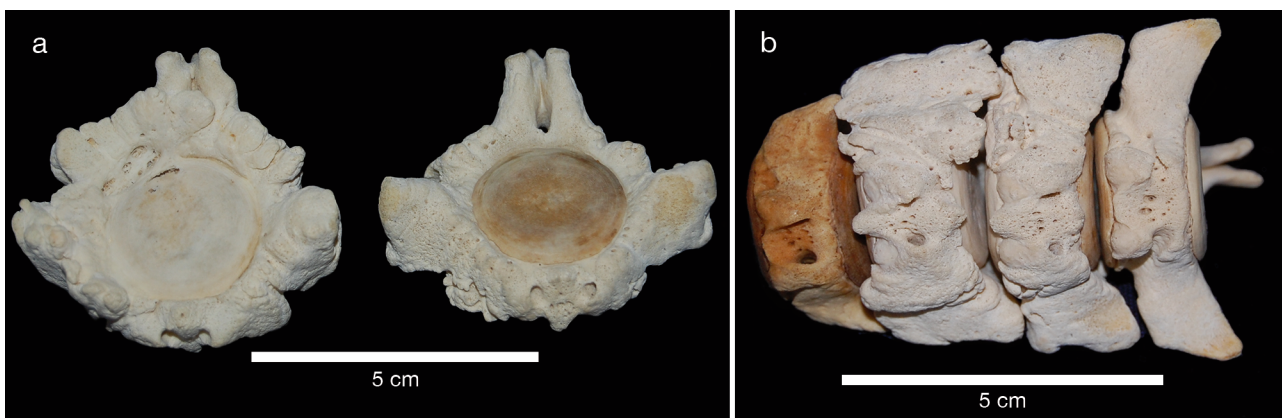


Fig. 7. Undetermined bone disease in immature female Commerson's dolphin RNP-1894: (a) new bone formation and presence of cloaca in caudal vertebrae (Ca 9) (b) bone destruction and new bone formation in 4 caudal vertebrae (Ca 8-11)

Table 3. Final model for the presence of idiopathic hyperostosis. The identity (RNP number) of the animal was included as a random effect. SE: standard error. Significant p-values in **bold**

Fixed effect	Coefficient (± 1 SE)	p
Intercept	14.0 (± 2.21)	<<0.001
Cervical region	0.75 (± 1.31)	0.57
Thoracic region	4.39 (± 1.43)	0.002
Lumbar region	5.52 (± 1.48)	0.0002

Table 4. Final model for the presence of spondyloarthropathy. The identity (RNP number) of the animal was included as a random effect. SE: standard error. Significant p-values in **bold**

Fixed effect	Coefficient (± 1 SE)	p
Intercept	-14.84 (± 20.9)	0.477
Age	0.80 (± 4.25)	0.84
Cervical region	-1.78 (± 1.10)	0.10
Thoracic region	0.59 (± 1.19)	0.65
Lumbar region	-2.99 (± 1.32)	0.012
Sex	2.22 (± 8.60)	0.79

sex, age classes and regions of the vertebral column. The best-supported model to explain the occurrence of idiopathic hyperostosis and spondyloarthropathy in these specimens included the region of the vertebral column as the only explanatory variable, with a higher probability of idiopathic hyperostosis in the thoracic and lumbar vertebrae than in the cervical and caudal ones but a lower probability of spondyloarthropathy in the lumbar region than in the other ones.

Idiopathic hyperostosis was the lesion most frequently observed in Commerson's dolphins, mostly affecting adults and often occurring in the thoracic and lumbar vertebrae. Similarly, San Martín et al. (2016) found idiopathic hyperostosis in the thoracic vertebrae of 25% of the 78 Peale's dolphins examined. There are only a few papers on the occurrence of this pathology in the axial skeleton of cetaceans (Van Bressemer et al. 2007, San Martín et al. 2016). In offshore common bottlenose dolphins *Tursiops truncatus* from Peru, idiopathic hyperostosis seemed to be linked to the development of ankylosing spondylitis (Van Bressemer et al. 2007), a form of spondyloarthropathy (Kompanje 1999).

Spondyloarthropathy was the second most commonly detected pathology in Commerson's dolphins, affecting the whole vertebral column, though with a higher occurrence in the thoracic and caudal regions. Similarly, this condition mostly affected the thoracic vertebrae of Peale's dolphins from the same ocean

province (San Martín et al. 2016). The typical behavior of these species, including high-speed swimming and abrupt changes in direction that require high maneuverability and, likely, a greater mobility of the cervical-thoracic region (Goodall & Schiavini 1994, Marchesi et al. 2017), may be at the origin of this pathology. Spondyloarthropathy has also been described in the humpback whale *Megaptera novaeangliae* (Hellier et al. 2011), fin whale *Baleanoptera physalus* and the white-beaked *Lagenorhynchus albirostris* (Kompanje 1999) among other species. Factors such as a bulky body, elevated vertebrae number and age are suspected to play a role in its etiology (Kompanje 1993, Galatius et al. 2009). Related to intervertebral cartilage wear, bone overgrowth worsens with age and occurs more frequently in older specimens (Kompanje 1993).

Osteoarthritis mostly affected the thoracic vertebrae in adult males and females. Several factors have been implicated in the pathogenesis of this degenerative disease, including increasing age, excessive joint stress and decreased joint lubrication (McKeag 1992, Lane & Buckwalter 1993, O'Connor & Brandt 1993). However, as cetaceans live in a weight-supporting medium and do not bear excessive weight on their joints, joint stress likely did not play a major role in the development of this condition (Turnbull & Cowan 1999). As osteoarthritis was only reported in mature individuals, it is possible that age also represents a risk factor in the development of this pathology in the Commerson's dolphin.

The healed and unhealed fractures of the ribs observed in 27 dolphins may have been the results of ship strikes and of inter- and intraspecific interactions (Duignan et al. 2003, Van Bressemer et al. 2007, Van Waerebeek et al. 2007). Commerson's dolphins are often observed close to ferries or bow riding in the Magellan Strait (Goodall et al. 1988). They also regularly interact with Peale's dolphins and southern sea lions *Otaria flavescens*, though aggressions have not been reported (Goodall et al. 1988). Aggressive interactions between bottlenose dolphins and Commerson's dolphins were described in Bahía Engaño, Patagonia, Argentina, in November 2001, but seem infrequent (Coscarella & Crespo 2010).

During this study, we observed spondylitis and spondylodiscitis in 11 specimens. The lesions often occurred in the caudal region and were in some cases accompanied by ankylosis. They affected 1, 2 or more vertebrae. Deformation, lysis of the intervertebral discs and osteolysis of the vertebrae were observed in all cases. The origin of these lesions is unknown, but bacteria, such as *Brucella* spp., might be the culprit

(Kompanje 1996, Sweeny et al. 2005, Félix et al. 2007, Goertz et al. 2011). Unfortunately, the cleaning process of the skeletons for the Museum collection prevented any attempt to isolate the etiologic agent(s).

Together these data indicate that bone lesions and traumata commonly occur in Commerson's dolphins, likely causing severe pain and morbidity in severe cases, as described in humans and other mammals (Ragetly 2008, Lascelles 2010, van Weeren & Grauw 2010). This paper provides the first insight into the bone pathologies of Commerson's dolphins from Argentina and contributes to baseline data on the biology of and threats affecting this species. It also lays the basis for comparative studies with other coastal and oceanic cetacean species from the South-west Atlantic Ocean and other ocean provinces.

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