

Ontogenetic variations of the head of *Aptenodytes forsteri* (Aves, Sphenisciformes): muscular and skull morphology

María Alejandra Sosa¹ · Carolina Acosta Hospitaleche^{1,2}

Received: 22 March 2017 / Revised: 13 July 2017 / Accepted: 14 July 2017 / Published online: 22 July 2017
© Springer-Verlag GmbH Germany 2017

Abstract The emperor penguin (*Aptenodytes forsteri*) is the largest extant penguin among living species breeding in winter, at Antarctic high latitudes. Despite several studies made on this species, musculature and skeletal anatomy are barely known, especially in non-adult specimens. To address this shortfall, dissections and comparative descriptions were made on crania and mandibles of individuals of different ontogenetic stages: chicks, juveniles, and adults. The results presented here show significant differences in musculature between the age groups, and the proportions between bill and cranium also change along postnatal ontogeny.

Keywords Anatomy · Cranium–mandible · Head muscles · Ontogeny · Spheniscidae · Antarctica

Introduction

The emperor penguin *Aptenodytes forsteri* Gray, 1844 (Aves, Sphenisciformes) has a circumpolar distribution restricted to Antarctica. It is the largest penguin regarding size and weight among current species, reaching 1.20 m height and 45 kg weight (Martínez 1992). It is listed as near threatened (NT) according to IUCN, estimating that within the next three generations, its population will decline rapidly

due to climate change. However, the status of current populations remains stable (BirdLife International 2012).

The emperor penguin is a species of marine and pelagic habits, feeding mainly on fish, but krill and cephalopods are also included in its diet (Klages 1989; Wienecke and Robertson 1997; Cherel and Kooyman 1998). *A. forsteri* is the only species that breeds and has an annual reproductive cycle which is well known (Stonehouse 1953; Prévost 1961; Isenmann and Jouventin 1970; Jouventin 1971).

Little is known about details of the osteo-muscular anatomy of *A. forsteri* (Sclater 1888; Zusi 1975; Saiff 1976; Welsch and Aschauer 1986; Osa et al. 1993); therefore any additional information is extremely valuable. The life cycle, together with its distribution at high latitudes, partly explains the scarceness of anatomical studies, particularly in the case of chicks and juveniles where samples are difficult to collect. In our study, the musculature and osteology of the cranium and mandible were compared among individuals of different ages, including chicks, juveniles, and adults, with the aim of improving the knowledge about *A. forsteri* anatomy.

Materials and methods

Crania and mandibles were collected by members of the Instituto Antártico Argentino (IAA) in Snow Hill Island (West Antarctica) during summer field trip of 2014. They are deposited in the Ornithology section of the Museo de La Plata (MLP-O), Argentina. Other skeletons consulted belong to the Naturhistoriska Riksmuseet (Nr), Sweden, and the Natural History Museum (NHM) in Tring, United Kingdom. Specimens were classified into the age categories: chicks ($n = 9$), juveniles ($n = 2$), and adults ($n = 2$) following (Stonehouse 1953) (Table 1).

✉ Carolina Acosta Hospitaleche
acostacar@fnym.unlp.edu.ar

María Alejandra Sosa
alesosa_15@hotmail.com

¹ División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina

² CONICET, Buenos Aires, Argentina

According to the available material, chicks and juveniles were dissected, identifying major muscle groups, and described from the most superficial to the deepest layers. The muscles in the adult were compared from Zusi (1975). Then, each cranium and mandible was prepared for osteological comparisons.

The descriptions follow Baumel et al. (1993), supplemented by George and Berger (1966), Zusi (1975), and Livezey and Zusi (2006) when necessary. Measurements were taken with a Vernier Caliper in increments of 0.1 mm.

Results

Comparative osteology

Cranium

In adults, the occipital region has a quadrangular shape in occipital view (Fig. 1a), while it is triangular in juveniles (Fig. 1b). All the elements that form this region are fused

in both cases. On the contrary, this region does not have a definite shape in chicks (Fig. 1c), and all its elements are individualized as independent structures.

The *Os supraoccipitale* is completely developed in the adult, but in juveniles it has an unossified dorsal longitudinal line (Fig. 1b), which is larger in chicks. The *Os epioticum* is observed at both sides of the *Os supraoccipitale* in chicks. The fusion degree between the *Os epioticum* and the *Os supraoccipitale* varies among specimens delimiting the *foramen veni occipitalis externa* (Fig. 1c).

The *Ossa exoccipitale*, at both sides of the *condyle occipitale* are individualized in chicks. In both, juvenile and adults, the *Ossa exoccipitale* constitute the *processi paraoccipitale*. These triangular processes are projected ventrolaterally, surpassing the *processi mediale parasphenoidale* in adults (Fig. 1a). The *processi mediale parasphenoidale* have angular outlines which are equally projected in juveniles (Fig. 1b). These processes are not yet defined in chicks, where the area remains cartilaginous (Fig. 1c).

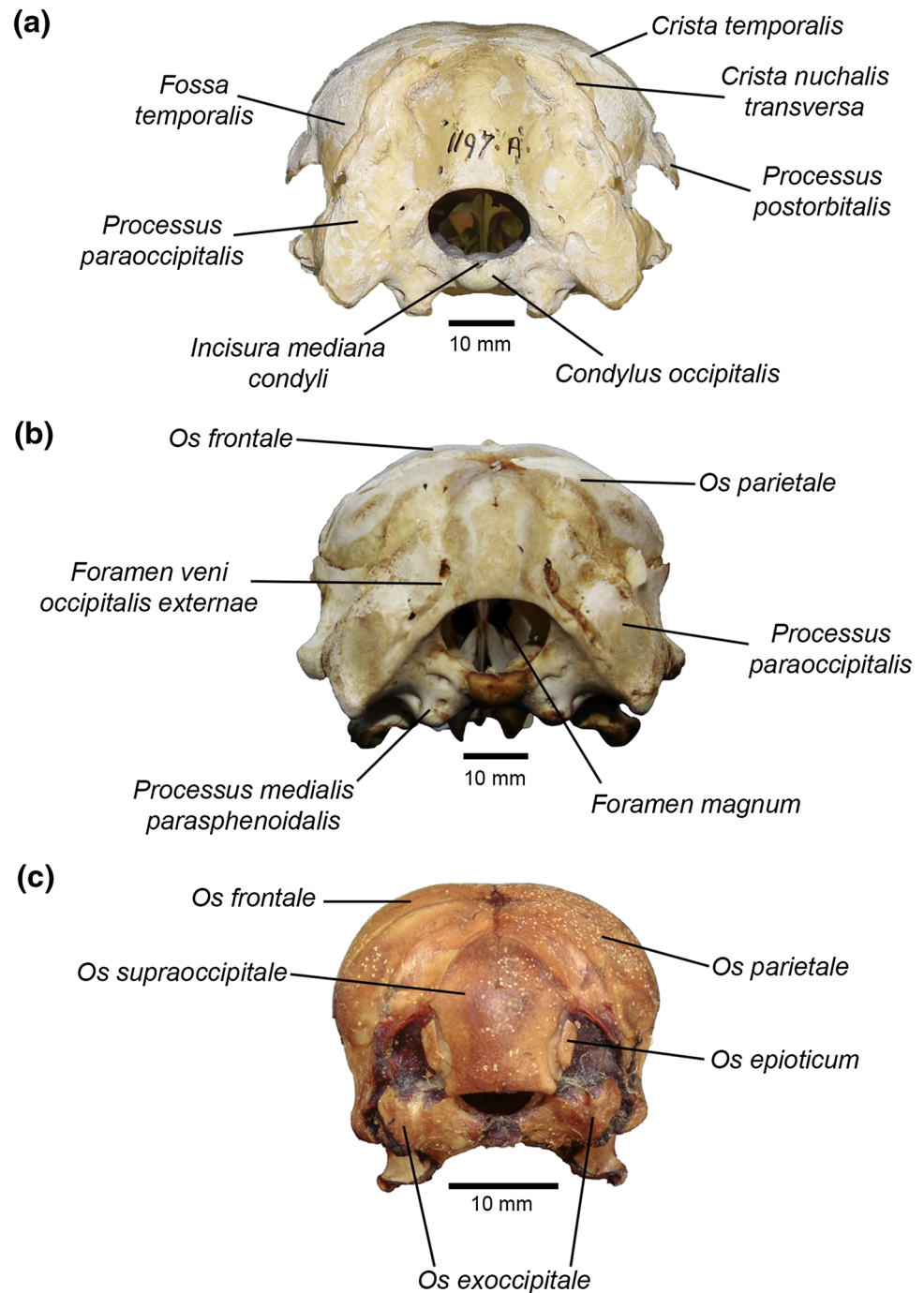
Table 1 Measurements (in mm) taken on the crania and mandibles of *Aptenodytes forsteri*

	Chicks								Juvenile MLP-O- 15035	Adults		
	MLP-O- 15026	MLP-O- 15027	MLP-O- 15028	MLP-O- 15029	MLP-O- 15030	MLP-O- 15031	MLP-O- 15032	MLP-O- 15033		NHM 1846.4.15.28	NHM 1846.4.15.26	
C	30.6	30.0	30.4	29.6	29.6	26.4	29.8	21.0	75.5	88.8	85.3	
BH	08.0	07.2	07.0	08.2	08.3	07.7	07.6	07.4	12.2	17.7	25.1	
BW	16.0	14.0	16.4	16.5	15.5	08.7	13.0	10.0	30.0	39.1	42.1	
NL	16.1	16.8	15.3	18.0	15.6	14.2	16.9	14.3	33.0	60.9	25.2	
PrW	09.0	09.4	07.8	09.6	10.7	08.6	09.6	07.2	19.4	25.2	30.8	
IW	08.9	08.1	09.9	08.9	10.2	08.4	07.4	06.4	13.2	19.2	25.7	
PoW	35.3	32.2	31.8	34.4	34.6	29.9	31.2	29.6	55.6	69.7	73.8	
FGL	27.1	26.0	24.7	30.4	29.8	24.1	26.7	25.5	49.8	55.8	58.1	
FGW	06.5	05.7	04.5	06.1	07.0	04.9	05.8	05.5	11.2	09.5	10.8	
SH	Cr	22.3	16.3	18.6	17.5	20.9	20.3	20.0	16.0	38.4	ca. 35.4	ca. 30.1
	Ca	30.2	26.5	25.2	26.3	27.5	23.9	27.2	21.8	42.5	ca. 50.5	ca. 52.5
FMW	10.6	09.0	09.5	10.2	10.1	08.6	10.3	09.3	15.9	–	15.8	
FMH	06.8	06.2	04.8	05.6	06.7	10.0	06.4	05.0	12.8	–	11.7	
CW	03.9	04.4	04.0	04.2	03.9	03.3	04.3	01.7	09.3	–	08.8	
CH	03.3	03.2	02.8	03.2	03.3	2.7	03.1	02.1	05.0	–	04.5	
TL	74.4	72.4	71.2	75.7	75.3	64.6	70.9	66.0	155.6	180.2	178.6	
CL	65.4	65.7	64.0	68.8	65.9	57.3	64.4	58.6	150.4	179.6	–	
ML	61.3	61.5	60.4	64.8	61.9	53.0	59.7	53.5	141.8	176.4	15.7	
MH	05.8	04.9	05.2	05.7	05.9	04.7	05.0	05.0	11.2	15.7	15.9	

Only complete specimens were measured

C culmen length, BH bill height, BW maximum width of the bill, NL apertura nasi ossea length, PrW preorbital width taken at the *Os lacrimale* level, IW interorbital minimum width taken dorsally, PoW width taken at the level of the *processus postorbitalis*, FGL length of the *fossa glandulae nasalis*, distance measured from the *Os lacrimale* to the *processus postorbitalis*, FGW maximum width of the *fossa glandula nasale*, SH height of the cranium (Cr taken at the contact between the *Os frontale* and the *processus frontalis nasalis*, Ca taken in the point of maximum height), FMW width of *foramen magnum*, FMH height of *foramen magnum*, CW width of *condylus occipitalis*, CH height of *condylus occipitalis*, TL total length of the cranium, CL length of the cranium taken from the *condylus occipitalis* to the tip of the bill, ML length of the *ramus mandibulae*, MH height of the *ramus mandibulae* taken caudally to the *fenestra rostralis mandibulae*

Fig. 1 Crania of *Aptenodytes forsteri* in occipital view showing the main features compared in the text: **a** adult, **b** juvenile, **c** chick



The *foramen magnum* presents an uninterrupted sub-circular outline in all ontogenetic stages examined. The *condylus occipitalis*, constituted by the *Ossa basioccipitalis*, is kidney shaped, with a pronounced *incisura mediana condyli* in the adults, which is less conspicuous in the juveniles. In chicks, the *condylus occipitalis* is not defined or, in some cases, is very small, oval shaped, and without the typical *incisura mediana condyli* that appears in juveniles (Fig. 1).

The *Ossa supraoccipitale*, *Ossa parietale*, *Ossa frontale*, and *processus frontalis nasalis* are fused in the adult,

whereas the joints are still visible in juveniles and chicks (Fig. 2). An unossified area of variable extension appears between the *Ossa parietale* and the *Ossa frontale* in all chicks, with increasing ossification of the cranial roof. This opening is completely closed in juveniles.

The *prominentia cerebellaris*, formed by the *Ossa supraoccipitalis*, is projected caudally beyond the occipital region, both in adults and juveniles (Fig. 2a, b). In the chick, this caudal projection does not differ as a separate structure or it is poorly differentiated (Fig. 2c).

The *Ossa frontale* have a triangular shape, covering a large area of the cranial roof in chicks (Fig. 2c). The *fossae glandulae nasale* reach their major development in adults, and the *Ossa frontale* cover a proportionally smaller surface.

In all stages the *fossae glandulae nasale* begin on the *Os lacrimale* and extend caudally to the *processi postorbitale*, widening caudally (Fig. 2). There is not a supraorbital edge, the *fossa* remains laterally open, and only a well-defined rim runs medially.

In the adult, the *fossae glandulae nasale* are fenestrated and projected ventrolaterally at the cranial-most end. In the juvenile, the *fossae glandulae nasale* have a notable medial ridge in their rostral portion that becomes weaker caudally (Fig. 2b). The *fossae glandulae nasale*

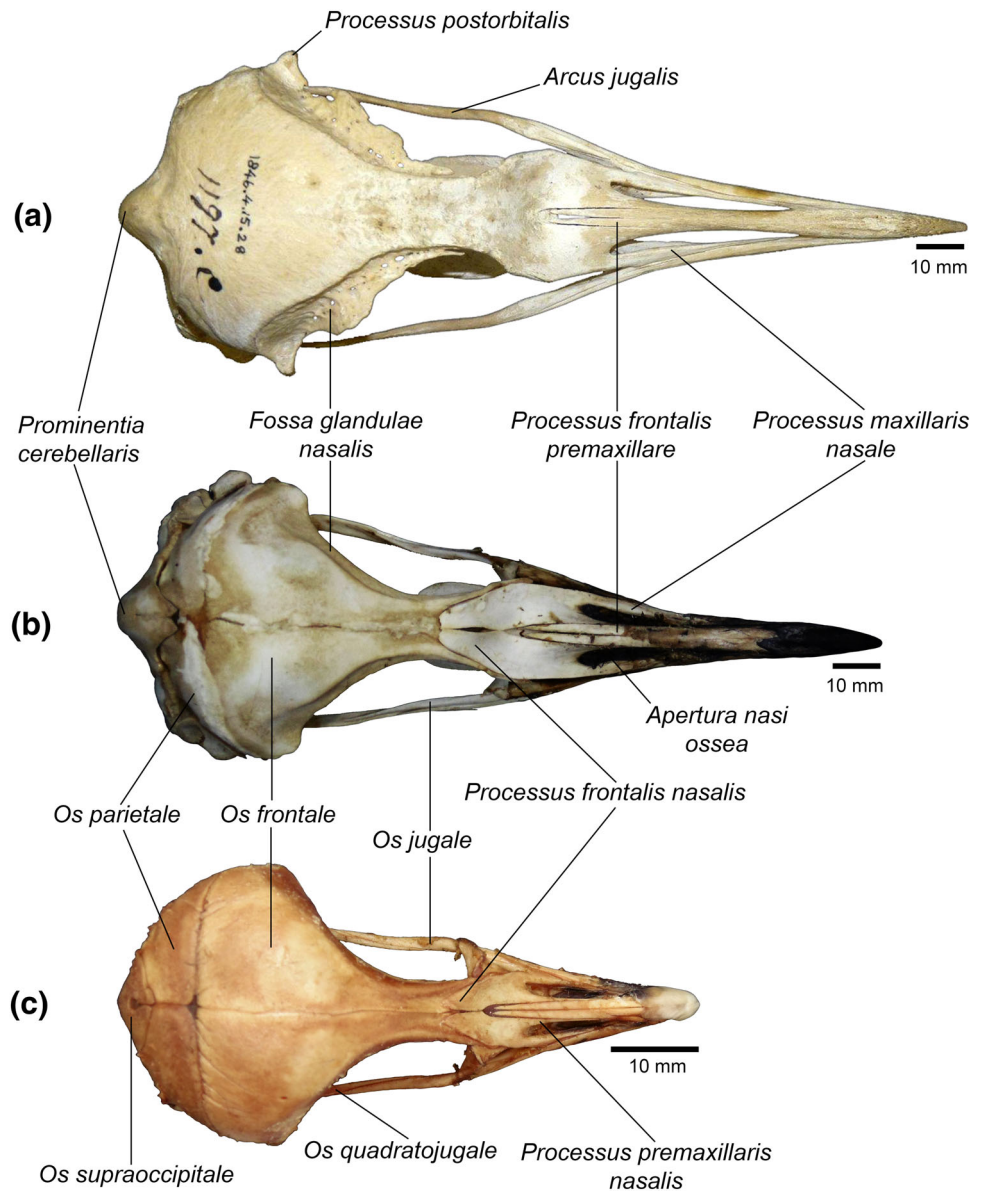
are still cartilaginous in chicks (Fig. 2c), and only a marked ridge in the rostral half of each *fossa* is observed. The *Os frontale* constitute a sagittal ridge, which is proportionally broader in the adults than in the juveniles and chicks.

The *processi postorbitale* are projected laterally in the adult (Fig. 2a), whereas in juveniles and chicks (Fig. 2b, c) they are not developed and the portion of the *Os laterosphenoidale* that contribute to their formation, remains cartilaginous.

The *processi frontale premaxillare* are parallel to each other up to the contact area with the *processi frontale nasale*. A similar condition is shared with juveniles and chicks.

The lateral wall of the braincase is completely fused in adults (Fig. 3a). On the contrary, in juveniles and chicks, the

Fig. 2 Crania of *Aptenodytes forsteri* in dorsal view, displaying the elements described in the text: **a** adult, **b** juvenile, **c** chick



Os supraoccipitale, *Os quadratum*, *Os parietale*, *Os laterosphenoidale*, and *Os frontale* are observed as independent elements (Fig. 3b, c). What is more, in chicks, a portion between the *Os parietale*, *Os frontale*, *Os laterosphenoidale*, and *Os squamosus* remains cartilaginous.

The *crista nuchalis temporalis* and the *crista nuchalis transversa* are well developed in the adult, although they are not conspicuous structures (Fig. 3a). The *crista temporalis* is not developed in juveniles because the *Os parietale* and the *Os frontale* are not fused and the *crista nuchalis transversa* is being sketched (Fig. 3b). None of these *cristae* are defined in chicks (Fig. 3c).

In the adults, the *fossa temporalis* is delimited rostrally by the *crista temporalis* and caudally by the *crista nuchalis transversa* (Fig. 3a). Its dorsal edge is sharp and does not reach the sagittal line. This fossa is shallow and presents a convex wall, following the contour of the cranium,

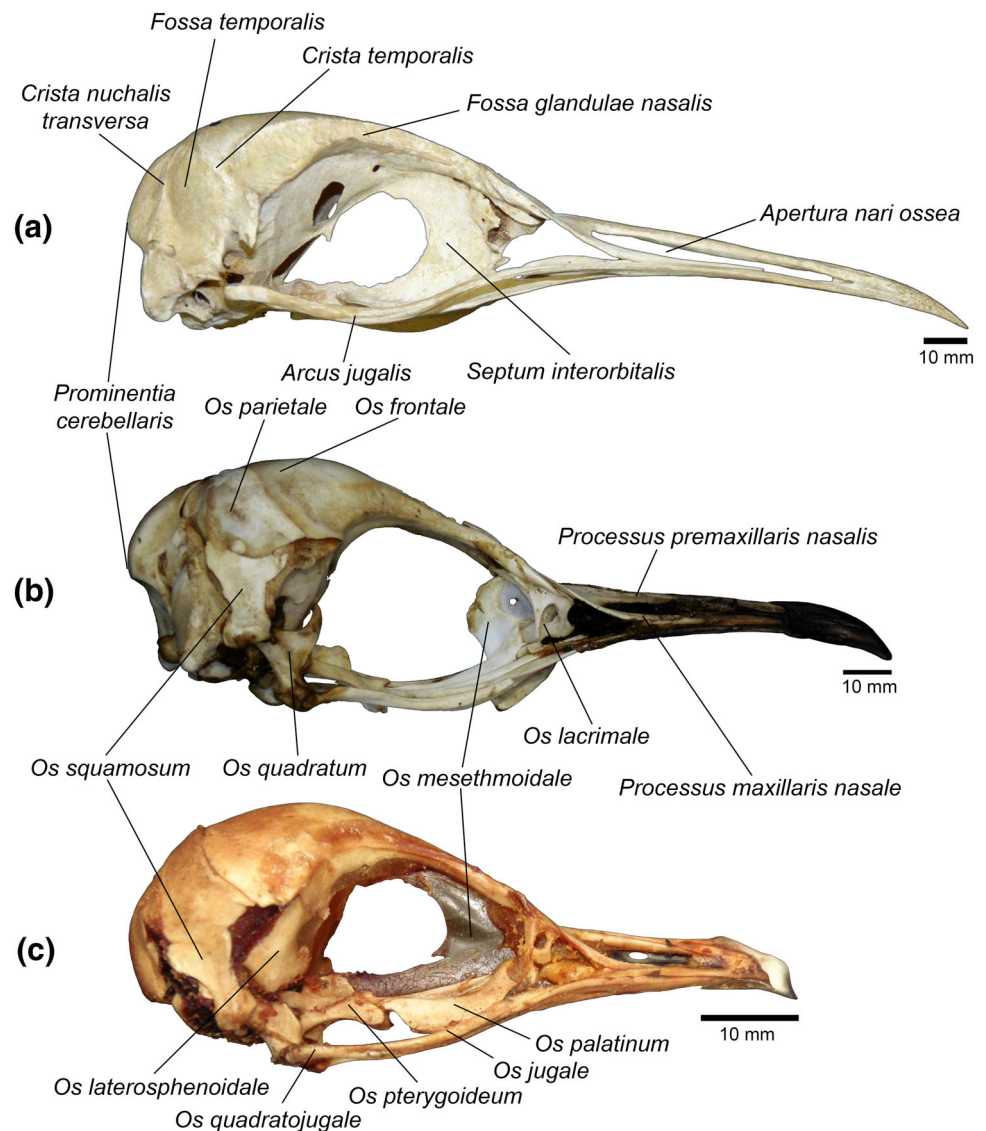
becoming slightly deeper toward its caudal portion. In juveniles and chicks, the *fossa temporalis* is not differentiated in the lateral wall of the cranium (Fig. 3b, c).

The *Ossa frontalia* are convex in all their extension, this convexity is stronger in juveniles and even more in chicks, determining a globus braincase. The rostral portion of the *Os frontale* descends toward the contact to the *Os lacrimale* and the *processus nasalis frontalis*.

The *Os mesethmoidale* is ossified in adults, forming the *septum interorbitale* (Fig. 3a). Only the rostral portion is ossified in juveniles (Fig. 3b), whereas this area remains totally cartilaginous in chicks (Fig. 3c).

The sigmoid *arcus jugalis* is constituted by the fusion of the *processus jugalis* of the *Os maxillare*, *Os jugale*, and *Os quadratojugale* in adults. All these bones are unfused in juveniles and chicks, appearing as separate elements. The ventral curvature surpasses the *lamina parasphenoidalis* in

Fig. 3 Crania of *Aptenodytes forsteri* in lateral right view, elements compared are pointed out: **a** adult, **b** juvenile, **c** chick



adults (Fig. 3a) and it is less pronounced in juveniles and chicks (Fig. 3b, c).

The rostrum is formed by the fusion of the *Ossa premaxillaria*, *Ossa maxillaria*, and *Ossa nasalia* in adults, constituting approximately one half of the total length and height of the cranium (see Table 1). These proportions are clearly different in juveniles and chicks, in which the rostrum is proportionally smaller.

The *apertura nasi ossea* are elongated and constant in width. They open laterally at the rostral portion, and dorsally at the caudal end. These openings are proportionally shorter in chicks.

The base of the cranium is constituted by the complete fusion of elements in adults and juveniles, whereas the *Os basioccipitale*, *Os exoccipitale*, *Os parasphenoidale*, and *rostrum parasphenoidale* are still independent elements in chicks. The *rostrum parasphenoidale* is proportionally larger in adults than in juveniles and chicks, extending rostrally until it contacts with the *Os pterygoideum* and *Os palatinum*.

The *Os pterygoideum* widens rostrally in adults and juveniles, forming the *pars palatina* (Fig. 4a, b). In chicks, these bones have a marked concavity at their lateral margin (Fig. 4c). The *Os palatinum* is flattened in the adult, with the *pars lateralis* well developed. A similar condition is observed in juveniles, whereas in chicks the *Os palatinum* has a similar width throughout, but the *pars lateralis* does not extend laterally.

The *Os quadratum* is similarly developed in adults and juveniles (Fig. 5g, h). The *corpus ossi quadrati* connects with the *processus oticum*, *processus orbitalis*, and *processus mandibularis*, which are all ossified. The *processus oticum* is projected laterally and articulates dorsally with the *Os squamosum*. The *capitulum oticum* and *capitulum squamosum* are well defined, separated by the *incisura intercapularis*. The slender and rectangular *processus orbitalis* projects dorsomedially. The strong *processus mandibularis* projects ventrally, and presents a *condylus pterigoideus*, a *condylus medialis*, and a *condylus caudalis* well developed. The *foramen pneumaticum* is constituted by a very small opening observed in caudomedial view, between the *processus orbitalis* and the *processus mandibularis*. In chicks, the *Os quadratum* has the *corpus Ossi quadrati* well ossified, the *processus oticum* and the *processus mandibularis* only partially ossified, and the *processus orbitalis* cartilaginous.

Mandible

Each ramus is curved caudoventrally at its middle part, and both ends are straight in adults (Fig. 5b). This curvature is smaller in juveniles (Fig. 5d) and the rostral third is inclined ventrally, producing a sigmoid shape. In chicks,

the jaw is almost straight (Fig. 5f), the curvature is minimal and the rostral portion is directed ventrally.

All the elements of the rami, i.e., *Os dentale*, *Os prearticular*, *Os coronoideum*, *Os spleniale*, *Os supra-angulare*, and *Os articulare* are still individualized in juveniles and chicks (Fig. 5). In adults they are almost completely fused (Fig. 5a, b).

The *fenestra caudalis mandibularis* and the *fenestra rostralis mandibularis* open laterally. The first one has a rounded contour in adults (Fig. 5b) and an oval one in juveniles and chicks (Fig. 5d, f), with its major axis cranio-caudally developed. The *fenestra rostralis mandibularis* is elongated, with the major axis parallel to the edges of the mandible in all of the stages analyzed, including in the chick.

The *processus retroarticularis* is projected caudoventrally only in the adult (Fig. 5a, b); in juveniles it is placed at the same plane as the rami (Fig. 5c). The *incisura retroarticularis* is well developed in adults and juveniles. The complete articular region remains cartilaginous and indistinguishable in chicks (Fig. 5e, f), and only the *processus retroarticularis* is barely developed and projected caudally.

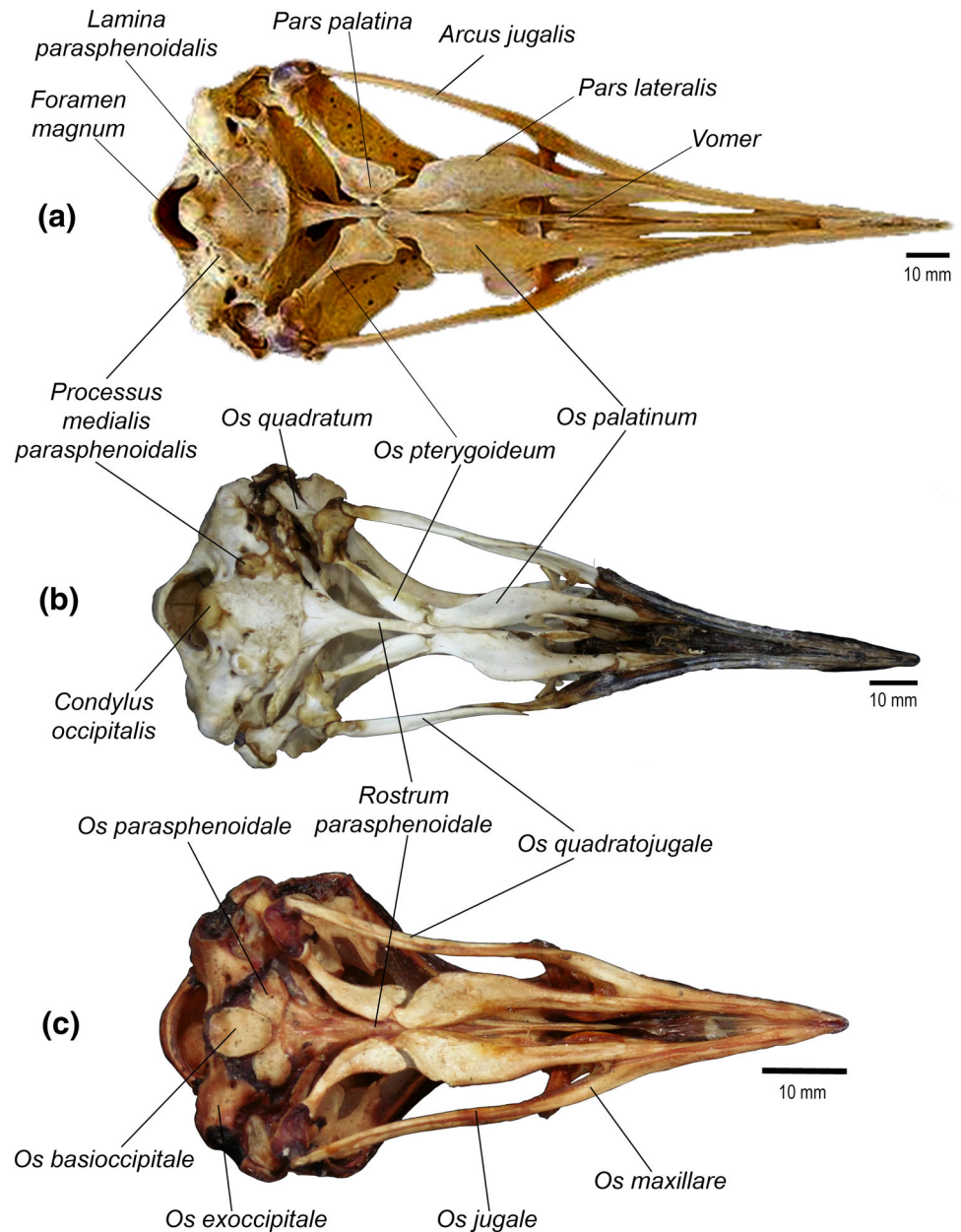
The *processus coronoideus*, located dorsally in relation to the rostral border of the *fenestra caudalis mandibularis*, is presented as an outstanding structure in the adult (Fig. 5b), whereas in the juvenile it appears as a scarcely marked ridge and it is absent in chicks. Even though the *cotyla medialis*, *cotyla lateralis*, and *cotyla caudalis* are well defined in adults, they are hardly differentiated in juveniles (Fig. 5a, c). Among these structures, the *cotyla medialis* develops first in early stages.

Comparative myology

Musculus depressor mandibulae

This muscle is divided into two parts: *M. depressor mandibulae pars superficialis*, and *M. depressor mandibulae pars profunda* (sensu Livezey and Zusi 2006). The *M. depressor mandibulae pars superficialis* has its origin by fleshy fibers on the *Ossa parietalia*, on both sides of the *prominentia cerebellaris*. It is directed ventrally, passes over the *Os exoccipitale* and inserts by fleshy fibers on the *processus retroarticularis* of the mandible in the chicks (Fig. 6b), whereas in the juveniles, it passes on the lateral surface of the *processus paraoccipitale* and inserts by an aponeurosis on the *processus retroarticularis* (Fig. 6a). It is an important muscle that, although already individualized in chicks, becomes bulkier in juveniles. In chicks, the *M. depressor mandibulae pars profunda* (Fig. 6c) originates behind the *meatus acusticus externus*. It is ventrally directed and inserted by fleshy fibers on the

Fig. 4 Crania of *Aptenodytes forsteri* in palatal (ventral) view, pointing out the elements described: **a** adult, **b** juvenile, **c** chick



processus retroarticularis, rostral to the insertion of the *M. depressor mandibulae pars superficialis*.

Musculus adductor mandibulae externus

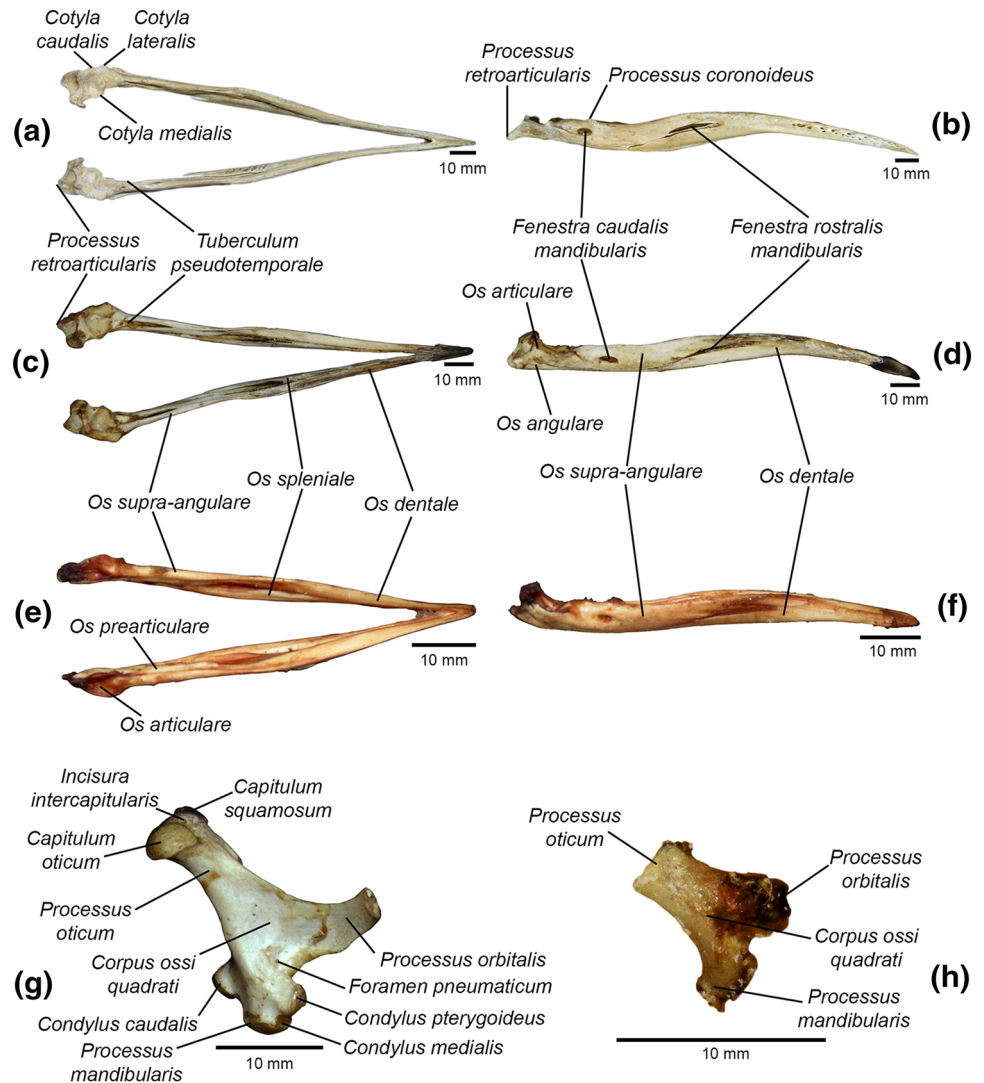
It is divided into three parts in adults: *M. adductor mandibulae externus pars rostralis*, *M. adductor mandibulae externus pars ventralis*, and *M. adductor mandibulae externus pars profunda* (Baumel et al. 1993). This differentiation is not so marked in the chicks, probably because the musculature is not completely developed. Therefore, it is treated without subdivisions. It is inserted by fleshy fibers on the dorsal edge and on the lateral surface

of the mandible in chicks and juveniles. This muscle is barely developed in chicks, as a very thin sheet, especially in its origin on the *fossa temporalis*, (Fig. 6b, c) then it is directed cranioventrally, passing under the *processus postorbitalis* and behind the *arcus jugalis*. In juveniles, the *M. adductor mandibulae externus* is notably bulkier, covering a more extensive area on the lateral wall of the cranium (Fig. 6a).

Musculus pseudotemporalis superficialis

This is an elongated and thin muscle in chicks (Fig. 6d, e) that originates in the caudal wall of the orbit, on the *Os*

Fig. 5 Mandibles and quadrates of *Aptenodytes forsteri*: mandible of **a** adult in dorsal view, **b** adult in lateral view, **c** juvenile in dorsal view, **d** juvenile in lateral view, **e** chick in dorsal view, **f** chick in lateral view; left quadrate of **g** juvenile in medial view, **h** chick in medial view



laterosphenoidale, adjacent to the *processus postorbitalis*. It is directed ventrally to inserts through a tendon on the medial surface of the mandible, caudal to the *fenestra mandibularis caudalis*. In juveniles and adults, this muscle originates on the *Os laterosphenoidale* and inserts on the *tuberculum pseudotemporale* of the mandible.

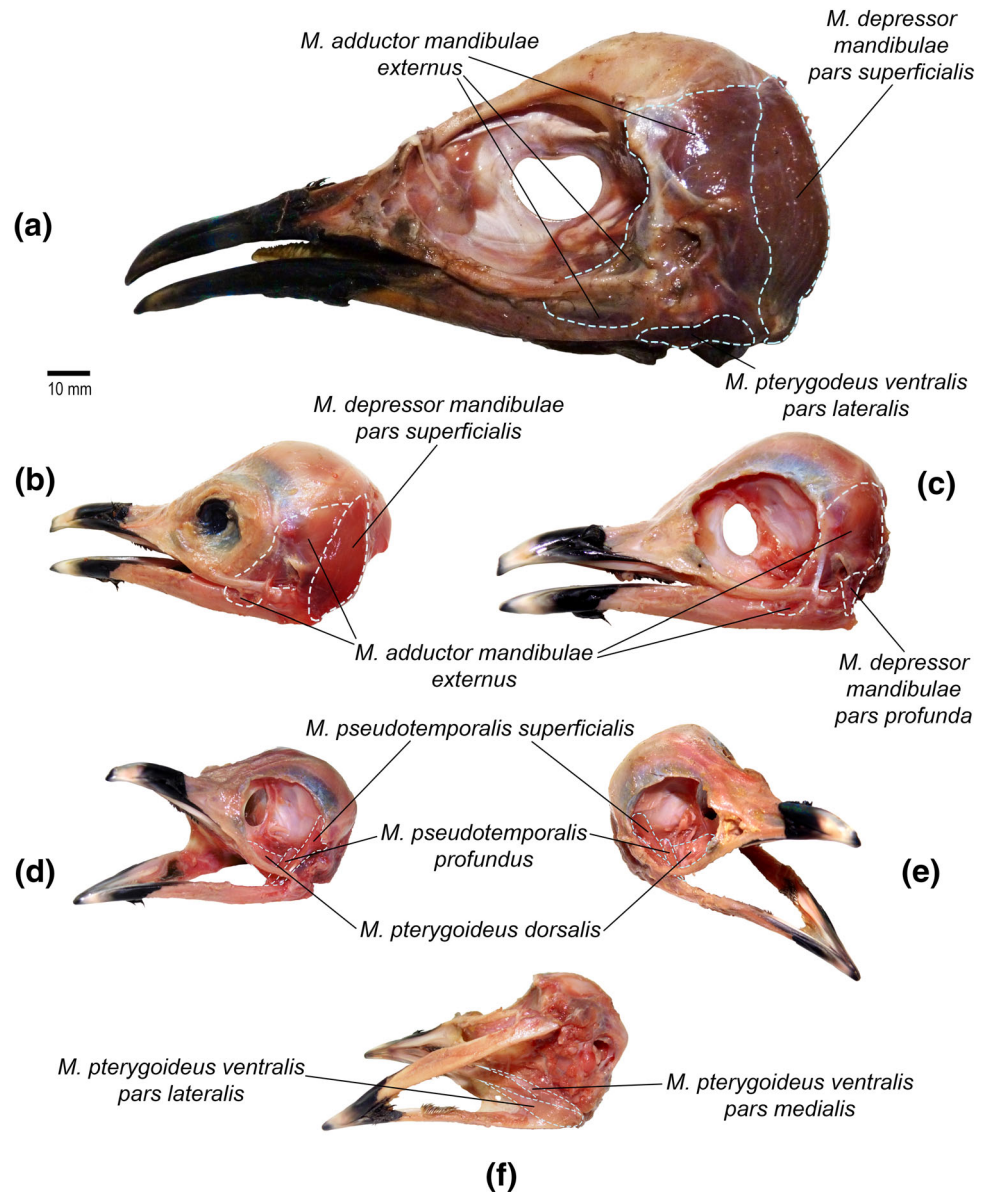
Musculus pseudotemporalis profundus

Although not very large, it is already well developed in chicks (Fig. 6d, e). This muscle originates by fleshy fibers on the rostral surface of the *processus orbitalis quadrati*; it is directed anteroventrally and inserts into the medial surface of the mandible, rostral to the insertion of the *M. pseudotemporalis superficialis* and ventral to the insertion of the *M. adductor mandibulae externus*.

Musculus pterygoideus ventralis

It can be subdivided into a lateral and a medial portion in chicks (Fig. 6f). The *M. pterygoideus ventralis pars lateralis* originates from an aponeurosis that extends caudally along the entire lateral border of the *Os palatinum*. Its fibers widen caudally up to its fleshy insertion on the posteromedial portion of the mandible, behind the articulation area. In juveniles, this muscle extends ventral and laterally, and occupies part of the posterolateral region of the mandible (Fig. 6a). The *M. pterygoideus ventralis pars medialis* has its origin through an aponeurosis on the posteromedial border of the *Os palatinum*. It extends caudo-laterally on the ventral side of the *Os pterygoideum*, widened by fleshy fibers to be inserted on the medial border of the mandible, dorsal to the insertion of the *M. pterygoideus ventralis pars lateralis*.

Fig. 6 Muscles of cranium and mandible of *Aptenodytes forsteri*: **a** juvenile in lateral view, **b** chick in caudo-lateral view, **c** chick in lateral view, **d**, **e** chick in cranio-lateral view, **f** chick in caudo-palatal view



Musculus pterygoideus dorsalis

This muscle can be divided in two parts in chicks. The *M. pterygoideus pars lateralis* originates on the dorsal edge of the *Os palatinum*, while the *M. pterygoideus pars medialis* originates on the *Os pterygoideum*. Both parts are directed caudo-laterally to insert in the medial surface of the jaw, dorsal to its contact with the *Os quadratum* (Fig. 6d, e).

Musculus protractor pterygoidei et quadrati

This is a very small muscle in chicks. It originates on the caudoventral region of the *septum interorbitalis* and inserts into the posterior face of the *corpus Os quadratum*.

Discussion and final remarks

As expected, the development of the musculature is closely related to the degree of ossification of the skull and mandible. Cartilaginous structures hardly support muscle attachment. The following muscles were identified in all the ontogenetic stages analyzed: *M. depressor mandibulae*, *M. adductor mandibulae externus*, *M. pseudotemporalis superficialis*, *M. pseudotemporalis profundus*, *M. pterygoideus ventralis*, *M. pterygoideus dorsalis*, and *M. protractor pterygoidei et quadrati*. However, the development degree is clearly different in chicks, juveniles, and adults.

The *M. depressor mandibulae* is a voluminous muscle that occupies a large area on the back of the cranium. Although it is already defined in chicks, the proportional

volume increases significantly in adults, which is coherent with their behavior because chicks are only fed by adults. The *M. adductor mandibulae externus* showed the greatest differences during postnatal ontogeny. It can typically be divided into three parts in adults: *pars rostralis*, *pars ventralis*, and *pars profunda* (Baumel et al. 1993). However, in chicks, it appears as a single and small muscle originated on the *fossa temporalis* and inserted on the mandible. Although each part remains still indistinguishable, this muscle is more voluminous in juveniles and occupies a larger area into the *fossa temporalis*, rostral to the origin of the *M. depressor mandibulae pars superficialis*.

The *M. pterygoideus ventralis* is clearly different in each stage. It is thin and inserts on the caudomedial surface of the mandible in chicks, whereas its volume increases in juveniles, in which the fibers reach the caudo-lateral surface of the mandible, to finally insert underneath the articulation with the *Os quadratum*. An increment in volume during growing is observed in the *M. pseudotemporalis superficialis*, *M. pseudotemporalis profundus*, *M. pterygoideus dorsalis*, and *M. protractor pterygoidei et quadrati* as the only visible change.

Crania of young chicks are weak, and ossification centers remain independent for each bone. Most of the elements complete their ossification and fusion with other bones during juvenile stages, whereas sutures between elements disappear partially or completely exclusively in adults.

The major osteological differences throughout ontogeny were found in the occipital region and the base of the cranium. These are the regions with the largest cartilaginous areas and unfused elements. The *Os epioticum* is independent and the degree of fusion with the *Os supraoccipitale* is variable. The fusion is complete in juveniles, stage in which the *foramen veni occipitalis externa* is completed.

Maximum development of the *prominentia cerebellaris* is reached in adults, but an outstanding structure is already present in chicks. In juveniles, the *prominentia cerebellaris* already projects caudally beyond the *condylus occipitalis*.

The *Os exoccipitale* is completely fused with other occipital bones in juveniles and adults, but in chicks they remain separated at both sides of the *foramen magnum*. The *condylus occipitalis* is cartilaginous, small, and very poorly defined in chicks, acquiring the adult configuration in juveniles, except for the *incisura mediana condyli* that appears in adults.

Most of the surface of the *fossa glandulae nasale* is cartilaginous in chicks, constituting a slightly concave structure on the dorsal margin of the orbits. In juveniles, these *fossae* are better defined, although their caudal ends are not completely differentiated. Only in adults a well-

marked medial rim differentiates each fossa from the *Os frontale*. The *fossa temporalis* as well as the *cristae occipitalis* are only well defined in adults.

At the base of the cranium, chicks have the *Os basioccipitale*, *Os exoccipitale*, *Os parasphenoidale*, and *rostrum parasphenoidale* separated from each other. In juveniles these bones are fused and the general configuration is reminiscent of adults. The *Os mesethmoidale* is completely cartilaginous in chicks, and in juveniles it contributes to the formation of the *septum interorbitalis*.

The only element of the mandible that appears cartilaginous in chicks is the *processus retroarticularis*. All the other elements remain individualized. The *cotyloae* are not completely differentiated in juveniles, and the *tuberculum pseudotemporale* is barely developed.

Finally, the proportions also change along postnatal ontogeny, particularly the relative extension of the bill and the globosity of the cranium. Chicks have more globous crania with shorter and deeper bills (at least at the base). In juveniles the bill reaches half of the length of the cranium, similar to the adult condition. The depth of the beak also increases with age, and the cranium loses globosity, becoming dorsoventrally depressed.

Acknowledgements We mainly thanks to the Instituto Antártico Argentino (Dirección Nacional del Antártico) for supporting the field trip. Dr. Leopoldo Soibelzon and Dra. Marcela Libertelli for the collected material, and Dr. Diego Montalti for the access to the material. María Florencia Sosa who improved the English grammar. To Julian Hume and two anonymous reviewers for their comments that improve the manuscript.

References

- Baumel JJ, King JE, Breazile HE, Vanden Berge JC (1993) Handbook of avian anatomy: nomina anatomica avium, 2nd edn. Publications of the Nuttall Ornithological Club, Cambridge
- BirdLife International (2012) *Aptenodytes forsteri*. The IUCN red list of threatened species 2012:e.T22697752A40172193. <http://dx.doi.org/10.2305/IUCN.UK.2012-1.RLTS.T22697752A40172193.en>. Accessed 21 Nov 2016
- Cherel Y, Kooyman GL (1998) Food of emperor penguins (*Aptenodytes forsteri*) in the Western Ross Sea, Antarctica. Mar Biol 130:335–344
- George JC, Berger AJ (1966) Avian myology. Academic, New York
- Isenmann P, Jouventin P (1970) Eco-éthologie du Manchot empereur (*Aptenodytes forsteri*) et comparaison avec le Manchot Adélie (*Pygoscelis adeliae*) et le Manchot royal (*Aptenodytes paragonica*). Expéditions Polaires Françaises
- Jouventin P (1971) Comportement et structure sociale chez le manchot empereur. La Terre et la Vie 25:510–586
- Klages N (1989) Food and feeding ecology of emperor penguins in the Eastern Weddell Sea. Pol Biol 9:385–390
- Livezey BC, Zusi RL (2006) Phylogeny of Neornithes. Bull Carnegie Mus Nat Hist 37:1–544
- Martínez I (1992) Order Sphenisciformes. In: del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the world, vol 1. Ostrich to ducks. Lynx Edicions, Barcelona, pp 140–160

- Osa Y, Kuramochi T, Wataniku Y, Naito Y, Murano M, Hayama S, Orima H, Fujita M (1993) Application of computed tomography to morphological study of emperor and Adélie penguins. *Auk* 110:651–653
- Prévost J (1961) *Ecologie du manchot empereur. Expéditions polaires francaises*. Hermann Press, Paris, pp 1–204
- Saiff E (1976) Anatomy of the middle ear region of the avian skull: Sphenisciformes. *Auk* 93:749–759
- Sclater PL (1888) Notes on the emperor penguin (*Aptenodytes forsteri*). *Ibis* 30:325–334
- Stonehouse B. (1953). The emperor penguin (*Aptenodytes forsteri*, Gray): I. Breeding behaviour and development. (Vol. 6). HMSO, London
- Welsch U, Aschauer B (1986) Ultrastructural observations on the lung of the emperor penguin (*Aptenodytes forsteri*). *Cell Tissue Res* 243:137–144
- Wienecke BC, Robertson G (1997) Foraging space of emperor penguins *Aptenodytes forsteri* in Antarctic shelf waters in winter. *Mar Ecol Prog Ser* 159:249–263
- Zusi RL (1975) An interpretation of skull structure in penguins. In: Stonehouse B (ed) *The biology of penguins*. Macmillan, London, pp 59–84