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The mandibulosphenoidal joint in penguins, albatrosses, and petrels: comparative anatomy and functional implications

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Abstract

We discuss the potential use of the mandibulosphenoidal joint structures to interpret the diet and trophic habits of penguins, albatrosses, and petrels. For this purpose, several species of these phylogenetically related groups, whose diet and feeding strategies are already known, were selected. After comparisons, we conclude that: 1 – the efficiency of the quadrate-articular primary articulation is decisive for the development of the secondary mandibulosphenoidal joint, 2 – the morphology of the mandibulosphenoidal joint is closely related to the trophic habits of specialist birds, and 3 – the use of the mandibulosphenoidal joint structures to infer dietary preferences has a limited use.

Key words

Functional morphology, medial brace, osteology, Procellariiformes, seabirds, secondary support, Sphenisciformes.

Introduction

The *lamina parasphenoidalis* is a largely expanded plate located on the cranium base and rostral to the area where the ventral neck muscles insert on the basioccipital bone in front of the *condylus occipitalis* (Fig. 1A). Also erroneously named as *lamina basitemporalis* (because it is not related to a temporal element or region of the cranium), the *lamina parasphenoidalis* is an ossification of the basiparasphenoid center. It assumes different configurations and carries structures (i.e. *processus medialis parasphenoidalis*, *processus lateralis parasphenoidalis*, *ala parasphenoidalis*, and *tuberculum basilare*) that are differentially developed in each group of birds. The *processus lateralis parasphenoidalis* can be completely merged (and indistinguishable) with the *processus medialis parasphenoidalis*, constituting wing-like structures in the margin of the external acoustic meatus (named *ala parasphenoidalis*). Otherwise, the *processus lateralis parasphenoidalis* can be developed as an independent process (Fig. 1A, Baumel & Witmer, 1993).

The development of a *tuberculum basilare* (Fig. 1A) increases the attachment area of the cranio-cervical *m. rectus capitis dorsalis*. This muscle is constituted by a series of discrete slips converging towards the insertion that originate from the cranio-lateral surface of the cervical vertebra C1, and the transverse processes of cervical vertebrae C1–C6. This muscle is in charge of the ventro-flexion of the head, relative to the neck (Snively & Russell, 2007a, 2007b), and is more voluminous in long-skulled birds (Baumel & Raikow, 1993).

The interaction between the *lamina parasphenoidalis* (Fig. 1A) and the articular region of the mandible (Fig. 1B) has functional implications related to the jaw

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opening (Bock, 1960). Basically, the caudal end of the mandible comprises three articular areas (*cotyla mandibularis lateralis*, *cotyla mandibularis caudalis*, and *cotyla mandibularis medialis*), and two processes (*processus medialis mandibularis* and *processus retroarticularis*) (Fig. 1B). The contact between any of the *lamina parasphenoidalis* processes or the lamina itself, and the *processus medialis mandibulae* (or particularly the *facies articularis parasphenoidalis* when developed, Fig. 1B) constitutes the mandibulosphenoidal joint ("medial brace" sensu Bock, 1960). This articulation works as a supplementary bony support of the mandible.

The first hypothesis was that this secondary support would prevent the caudal dislocation of the mandible when the condyles of the quadrate and the corresponding cotylae of the mandible do not strongly interlock (Bock, 1960). However, it was not completely accepted; and instead it was proposed that the elongation of the *processus medialis mandibulae* would modify the angle of action of the *m. depressor mandibulae* (Zusi, 1967). A few years later, during the examination of the ecthetmoidal-mandibular articulation in a particular family of passerines, a different function for this secondary joint was proposed. The medial brace would reduce the compressive forces exerted by the mandible on the quadrate (Bock & Morioka, 1971).

The mandibulosphenoidal articulation originated between the *processus medialis mandibulae* and the *lamina parasphenoidalis* or its processes stabilizes the mandible. This allows the mandible to be held in the proper position by the jaw muscles with the resulting force applied on the mandibulosphenoidal articulation rather than on the primary quadrate-squamosal joint (Bock & Morioka, 1971). Decreasing or annulling the destabilizing forces that the quadrate needs to resist and keeping the contact between the cranium and the mandible through the medial brace, the mandible is firmly held during opening of the bill along the wide range of positions (Bock & Morioka, 1971).

The mandibulosphenoidal articulation would have evolved many times in many different avian orders, and therefore the *processus medialis mandibulae* constitutes a preadaptation (Bock, 1960). The enlargement of this process originating a wider muscular attachment surface is originally related to the strengthening of two muscles that work on the cranial kinesis and the jaw movements: the *m. depressor mandibulae* and the *m. pterygoideus* (Bock, 1959, 1960).

The *m. depressor mandibulae* inserts along the posterior edge of the *processus medialis parasphenoidalis* and causes the protraction of the upper jaw and depression of the lower jaw (Zusi, 1967). The *m. pterygoideus* attaches to the anterior surface of the *processus medialis parasphenoidalis*, participates in closing the upper and lower jaws (Bock, 1959, 1960; Bühler, 1981) and has an important role in kinesis (Bock, 1964, 1999). The participation of the *processus medialis mandibulae* in the mandibulosphenoidal joint of the mandible constitutes a new advantage in the mandibular mechanism. This articulation, medial to the quadrate-articular joint, was described in birds that catch their prey or break the food by rapid movements of the head (Zusi, 1962), and according to our preliminary observations, it exists in many extinct and extant birds belonging to different groups. On the contrary, this abutment lacks in other species, condition that might be related with the anatomic and functional demands. When disrupting forces are strong and the primary quadrate-articular joint of the mandible is deficient, the medial brace compensates the articulation (Bock, 1960; Baumel & Raikow, 1993). Beyond a few pioneer contributions (Bock, 1960; Zusi, 1967; Bock & Morioka, 1971), the presence and configuration of the mandibulosphenoidal articulation was not deeply analyzed in many groups of birds.

The main goal of this study is the comparative analysis of the mandibulosphenoidal joint and the morphological variations of the elements involved. We discuss the potential use of these variations to interpret the diet and trophic habits of the analyzed birds. For this purpose, we selected several species of two phylogenetically related groups: Sphenisciformes and Procellariiformes, whose diet and feeding strategies are already known. References to our previous works on ontogeny and the variations found in fossil representatives are also included.

Feeding mechanisms and food preferences of the selected species

Adult seabirds (i.e. marine birds) feed both on the ocean surface and below it, or even on other seabirds. Preferred items for seabirds are fish, a wide range of planktonic crustaceans, cephalopods (mainly squid) and other molluscs. There is also a certain degree of variation between populations and along the time depending on the food availability, usually constrained by weather conditions (Furness & Monaghan, 1987). In Antarctic regions, for example, the Antarctic krill *Euphausia superba* is the most important source of food for pelagic birds, although carrion and offal constitute a significant item in the diet of many species (Ashmole, 1971; Croxall & Prince, 1980; Furness & Monaghan, 1987).

Considering this, we selected one penguin species of each extant genus to cover the broad morphological and dietary variations: *Aptenodytes forsteri*, *Spheniscus magellanicus*, *Pygoscelis antarcticus*, *Eudyptes sclateri*, *Megadyptes antipodes*, and *Eudyptula minor*. Penguins are often divided in three dietary categories, although a gradient in the proportion of the consumed items is observed between *A. forsteri*, the main catcher of medium and large fish (Cherel & Kooyman, 1998), and *Eudyptes sclateri*, the most crustaceavores (Cooper *et al.*, 1990). In the middle of this spectrum, the little *Eudyptula minor* also preys on fish, but small-sized. *Spheniscus magellanicus* and *M. antipodes* consume fish and a small portion of cephalopods (Van Heezik, 1990; Scolaro *et al.*, 1999); and finally, *P. antarcticus* is a filter-feeding penguin that mostly catches small crustaceans (Williams, 1995; Lynnes *et al.*, 2004).

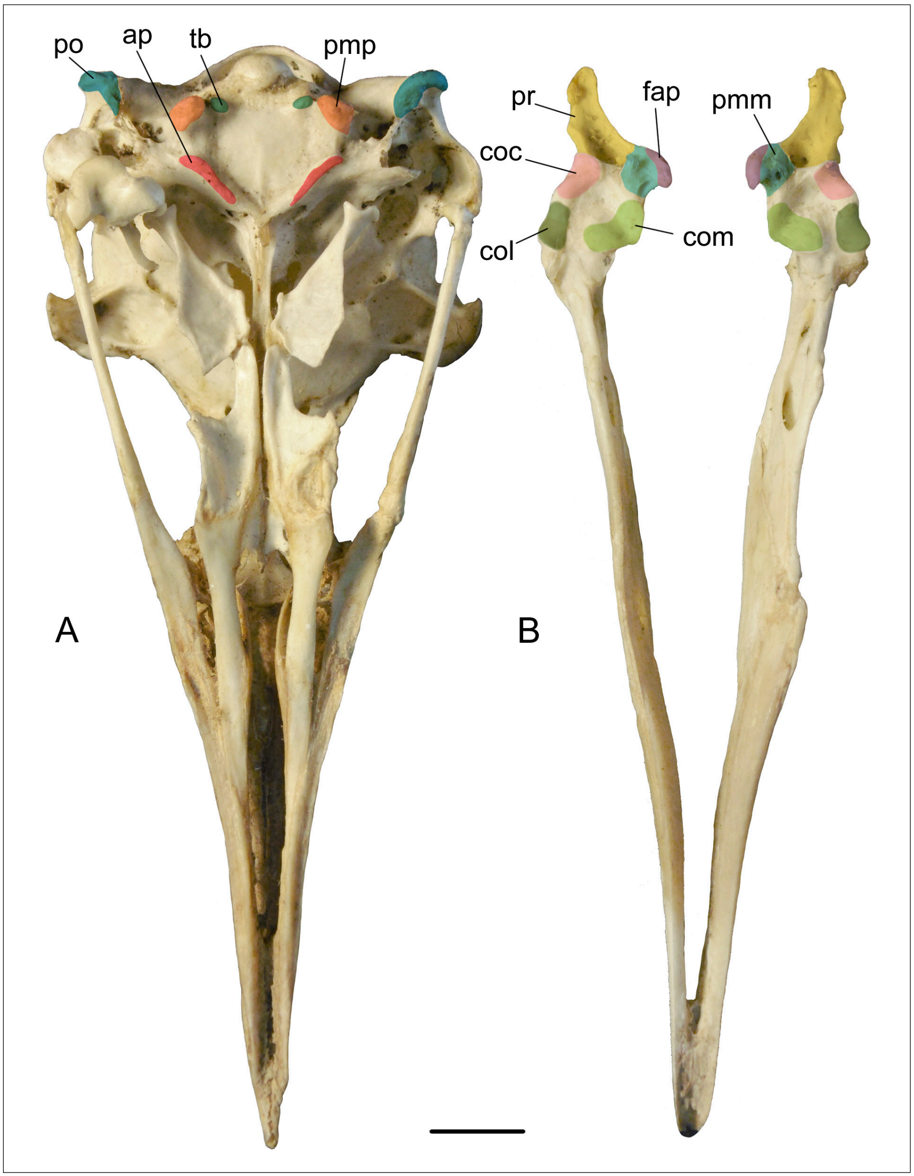


Fig. 1. Elements of the *lamina parasphenoidalis* in ventral view (**A**) and articular area of the mandible in dorsal view (**B**) compared in the selected species (the photographs correspond to *Spheniscus humboldti* MLP 686).

Abbreviations: (ap) *ala paraspheнidalis*, (coc) *cotyla caudalis*, (col) *cotyla lateralis*, (com) *cotyla medialis*, (fap) *facies articularis parasphenoidalis*, (pmm) *processus medialis mandibulae*, (pmp) *processus medialis parasphenoidalis*, (po) *processus paroccipitalis*, (pr) *processus retroarticularis*, (tb) *tuberculum basilaris*. Scale bar: 10 mm.

Within Procellariiformes, we choose the Oceanitidae *Oceanites oceanicus*, the Diomedeidae *Thalassarche melanophris*, the Procellariidae *Macronectes giganteus*, and due to the high variability observed within this family, we decided to include also *Fulmarus glacialoides*. Albatrosses and petrels have a diet based on crustaceans, cephalopods, fish, fur seals and other birds in different proportions depending on the resources availability. Among the largest species, *T. melanophris* feed mostly on crustaceans and fish (del Hoyo *et al*., 2020), whereas *M. giganteus* catches also young seabirds and ingests fur seals (Carboneras *et al*., 2020). *Fulmarus glacialoides* is another generalist and opportunistic medium-sized species that consumes crustaceans, cephalopods, and small fish (Carboneras *et al*., 2020b). In the other extreme of variation, *O. oceanicus* is a small bird that feeds mainly on planktonic crustaceans (*Euphausia sp.*) and fish (*Protomyctophum sp.*) and secondarily on squid, polychaetes, gastropods, and carrion (Drucker *et al*., 2020).

Material and methods

Specimen collections. The skeletons here examined (Appendix 1) belong to adult extant specimens. These material are deposited in the collections of the Ornithological Section of Vertebrates Zoology Division (MLP-O) and the Vertebrates Paleontology Division (MLP) of the Museo de La Plata, the Ornithological Section of the Museo Argentino de Ciencias Naturales (MACN), and the Azara Foundation (CFA-OR) of Ciudad Autónoma de Buenos Aires (Argentina); the Museo Nacional de Historia Natural de Uruguay (MNHU), and the Natural History Museum (NHM) in Tring (United Kingdom).

Methods. Descriptions of the elements involved in the mandibulosphenoidal articulation and the quadrate (implicated in the primary articulation) were selected according to Bock (1959, 1960) and Zusi (1962), and follow the terminology proposed by Baumel & Witmer (1993).

The description of each species includes the configuration of the *lamina parasphenoidalis* and its processes in ventral view, the articular area of the mandible in dorsal view (Figs. 1–3), and the general configuration of the quadrate (Fig. 4). After that, the opening/closing mechanism of the jaw (Fig. 5) was described for each species based on macerated specimens of the examined collections.

Results

Osteological descriptions

Sphenisciformes

In ***Aptenodytes forsteri*** (Fig. 2A), the *lamina parasphenoidalis* is rectangular (medio-laterally elongated). The *processi mediales parasphenoidales* are bulky and kidney-shaped, sub-parallel to the sagittal plane and diverging cranially. These processes are caudally located, occupying ⅔ of the cranio-caudal length of the plate. The *alae parasphenoidales* are merged to the cranial edge of the *lamina parasphenoidalis*, and project caudo-laterally. The *processus medialis mandibulae* (Fig. 2B) is hook-shaped and points cranially. The *facies articularis parasphenoidalis* is oval and oblique and occupies the entire *processus medialis*. The *cotyla medialis* is oval and larger than the other cotylae. This cotyla is oblique to the *ramus mandibulae*, and its lateral wall is inclined giving an irregular aspect to the articular area. The *cotyla lateralis* is cranio-caudally elongated and fused with the less differentiated and inclined *cotyla caudalis*. A rounded and non-prominent *sulcus intercotylaris* divides the *cotyla medalis* from the *cotyla lateralis*.

Three condyles of the quadrate (Fig. 4A–C) articulate with the mandible and develop a medio-lateral elongated configuration. The *condylus medialis* represents most of the articulation area, it is elongated and well-defined. A sulcus in the middle of the condyle divides a caudal half-moon shaped part from the most lateral and irregular one. The *condylus caudalis* and the *condylus lateralis* are merged and not completely differentiated. This condition is accentuated in sub-adults. The *condyli medialis* and *lateralis* are co-planar, whereas the *condylus caudalis* is more caudo-dorsally located.

In ***Pygoscelis antarcticus*** (Fig. 2C), the *lamina parasphenoidalis* is kidney-shaped and delimited by cranial edges. The *processi mediales parasphenoidales* are prominent and oval, with their main axis caudally convergent. These processes are located at the caudalmost part of the lamina and cranio-lateral to the smaller and slightly developed *tubercula basilaria*. The *ala parasphenoidalis* originates laterally on the cranial half of the lamina and expands latero-caudally.

In the mandible (Fig. 2D), the *processus medialis mandibulae* is hook-shaped and points cranially. The *facies articularis parasphenoidalis* runs on the entire medial border of the *processus medialis mandibulae*. The *cotyla lateralis* and *cotyla caudalis* are merged and undifferentiated. The *cotyla medialis* presents a horseshoe shape, laterally opened.

The configuration of the quadrate is also three-condylar. The *condylus lateralis* is slightly differentiated from the *condylus caudalis*, and both are oval. The former is located in the same plane that the *condylus medialis*, whereas the *condylus caudalis* is caudo-dorsally positioned. The *condylus medialis* is elongated and oblique to the sagittal plane, divided by a sulcus into two parts.

In ***Spheniscus magellanicus*** (Fig. 2E), the *lamina parasphenoidalis* is triangular and cranially delimited by strong edges that project ventrally. The *processi mediales parasphenoidales*, on the caudal vertices of the plate, are bulky and diverge cranially. On the sagittal line, a weak crest extends caudally until it disappears. The *ala parasphenoidalis* is triangular and caudo-laterally widen, reaching the *processus medialis parasphenoidalis* location.

In the mandible (Fig. 2F), the *processus medialis mandibulae* is well developed and projects dorso-medially with a hooked tip pointing cranially. The *facies articularis parasphenoidalis* is oval and its main axis is cranio-caudally oriented. The *cotyla lateralis* and the *cotyla medialis* are differentiated but continuous, constituting a sigmoid surface. The *cotyla medialis*, that occupies 1/3 of the articular area of the mandible, is large and kidney-shaped, with the cranial half more elevated than the caudal one.

The quadrate presents the typical three-condylar configuration with the *condylus lateralis* and the *condylus caudalis* merged. The *condylus medialis* and the *condylus lateralis* are coplanar, whereas the *condylus caudalis* is more caudo-dorsally located. The *condylus medialis* is irregular and elongated; the main axis is oblique and diverges cranially. The *condylus caudalis* is latero-medially elongated and the *condylus lateralis* is irregular.

In ***Eudyptes sclateri*** (Fig. 2G), the *lamina parasphenoidalis* is sub-rounded, and the cranial margins are demarcated by edges ventrally projected. The *processi mediales parasphenoidales* are elongated and oblique. The *ala parasphenoidalis* originates cranial to the lamina and widens latero-caudally becoming triangular.

In the mandible (Fig. 2H), the *processus medialis* is quadrangular and projects dorso-medially, the tip is hook-like. The *facies articularis parasphenoidalis* is rectangular, with its main axis cranio-caudally oriented. The *cotyla lateralis* is rounded and continuous with the *cotyla caudalis*, which is elongated and oblique. The *cotyla medialis* is concave and kidney-shaped.

The quadrate presents a three-condylar condition. The *condylus medialis* and the *condylus lateralis* are coplanar, whereas the *condylus caudalis* is more caudo-dorsal. The *condylus medialis* is elongated, with its main axis almost transversal to the sagittal plane. The *condylus*

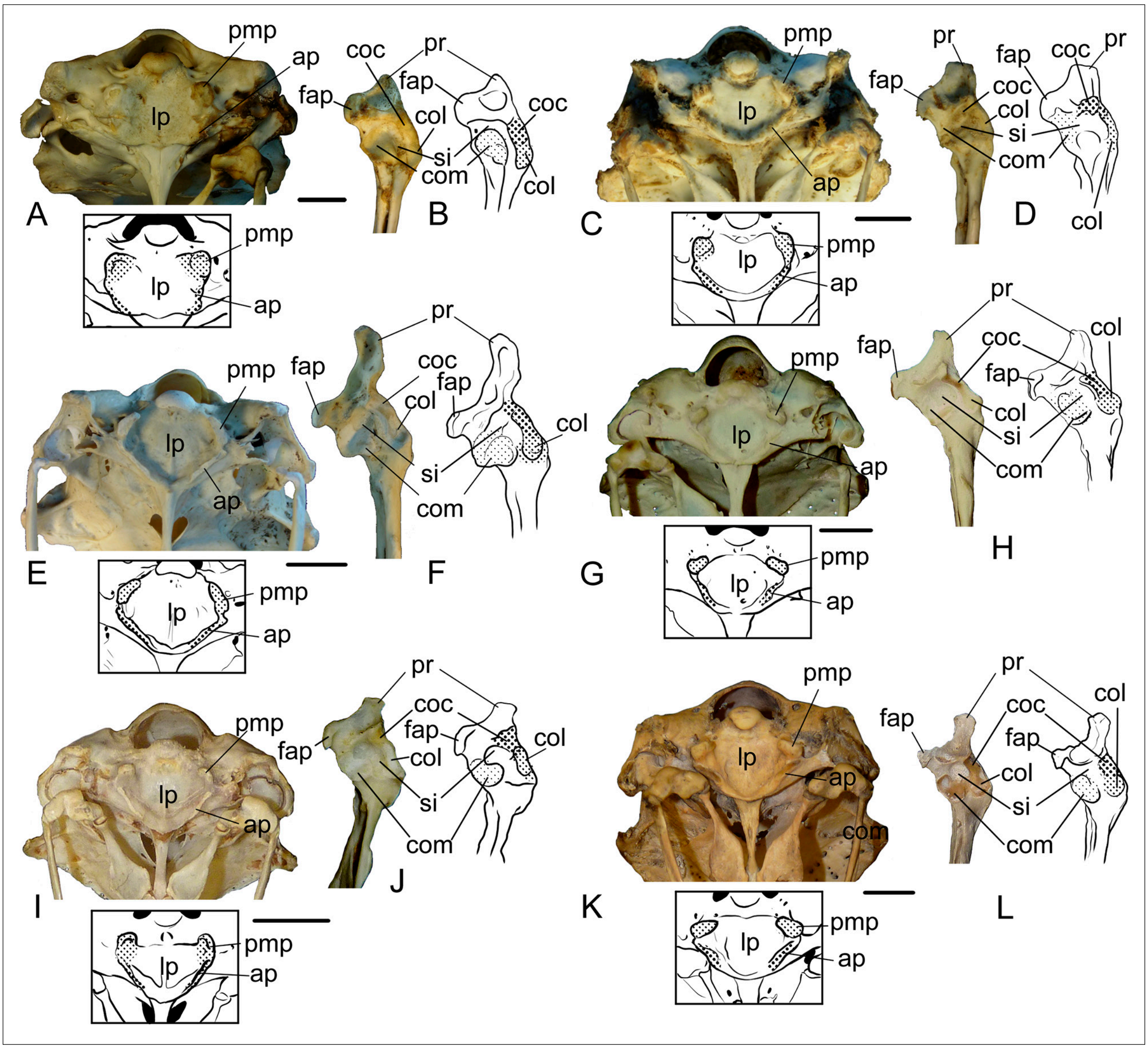


Fig. 2. Configuration of the *lamina parasphenoidalis* in ventral view (A, C, E, G, I, K) and the articular area of the left mandible in dorsal view (B, D, F, H, J, L) of penguins. Schematic draws show the elements described in the text: (**A–B**) *Aptenodytes forsteri*, (**C–D**) *Pygoscelis antarcticus*, (**E–F**) *Spheniscus magellanicus*, (**G–H**) *Eudyptes sclateri*, (**I–J**) *Eudyptula minor*, (**K–L**) *Megadyptes antipodes*. Abbreviations: (ap) *ala parasphenidalis*, (coc) *cotyla caudalis*, (col) *cotyla lateralis*, (com) *cotyla medialis*, (fap) *facies articularis parasphenoidalis*, (lp) *lamina parasphenoidalis*, (pmm) *processus medialis mandibulae*, (pmp) *processus medialis parasphenoidalis*, (pr) processus retroarticularis, (si) *sulcus intercotylaris*, (tb) *tuberculum basilaris*. Scale bar: 10 mm.

lateralis is rounded and separated from the *condylus caudalis* by a sulcus.

In ***Eudyptula minor*** (Fig. 2I), the *lamina parasphenoidalis* is kidney-shaped, and its cranial edges are cranioventrally projected. The *processi mediales parasphenoidales* are oval and oblique, with their main axis diverging cranially. The *ala parasphenoidalis* becomes triangular and extends latero-caudally toward the cranial end of the *processi mediales parasphenoidales*.

The *processus medialis mandibulae* (Fig. 2J) is short and caudo-dorsally extended, with the tip cranially hooked. The *facies articularis parasphenoidalis* is kidney-shaped and oblique. The *cotyla medialis* is concave and kidney-shaped. The *cotyla lateralis* and the *cotyla caudalis* are fused constituting a single and elongated articular surface.

The quadrate has a three-condylar configuration, the *condylus medialis* and the *condylus lateralis* are coplanar. The *condylus medialis* is irregular and a sulcus divides it in two portions. The *condylus lateralis* is rounded, whereas the *condylus caudalis* is latero-medially elongated.

In ***Megadyptes antipodes*** (Fig. 2K), the *lamina parasphenoidalis* is kidney-shaped and presents strong cranial edges that project ventrally. The *processi mediales parasphenoidales* are oval and prominent, their main axis are oblique and diverge cranially. These processes are located on the latero-caudal margins of the *lamina par-*

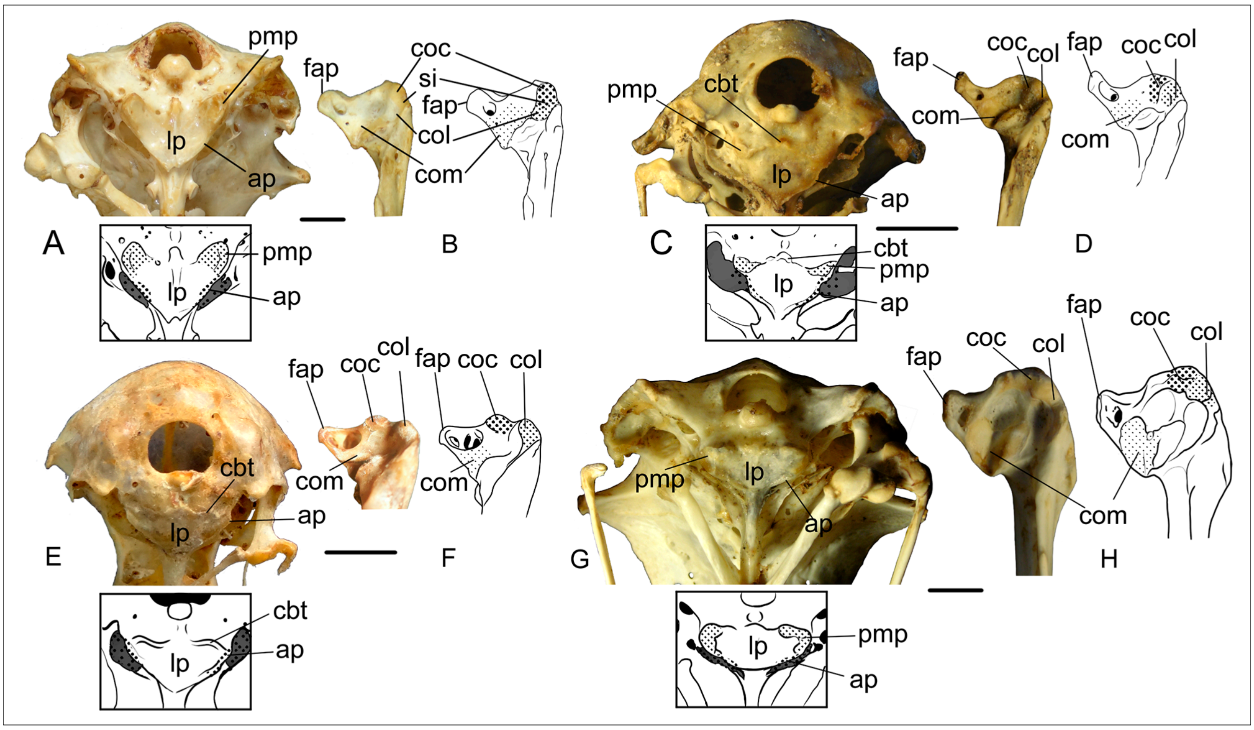


Fig. 3. Configuration of the *lamina parasphenoidalis* in ventral view (A, C, E, G) and the articular area of the left mandible in dorsal view (B, D, F, H) of albatrosses and petrels: Schematic draws show the elements described in the text: (**A–B**) *Macronectes giganteus*, (**C–D**) *Fulmarus glacialoides*, (**E–F**) *Oceanites ocanicus*, (**G–H**) *Thalassarche melanophris*. Abbreviations: (ap) *ala parasphenidalis*, (cbt) *crista basilaria transversa*, (coc) *cotyla caudalis*, (col) *cotyla lateralis*, (com) *cotyla medialis*, (fap) *facies articularis parasphenoidalis*, (lp) *lamina parasphenoidalis*, (pmm) *processus medialis mandibulae*, (pmp) *processus medialis parasphenoidalis*, (si) *sulcus intercotylaris*. Scale bar: 10 mm (A–D, G–H), 4 mm (E) and 2 mm (F).

asphenoidalis, except by the *ala parasphenoidalis* that originates on the cranial end and extends latero-caudally acquiring a rectangular shape.

In the mandible (Fig. 2L), the *processus medialis mandibulae* is poorly developed, and is represented by a weak quadrangular edge. The *cotyla medialis* is kidney-shaped and oblique. The *cotyla lateralis* is rounded and merged to the irregular *cotyla caudalis*.

The quadrate has a three-condylar configuration. The *condylus medialis* and the *condylus lateralis* are in the same plane. The *condylus caudalis* is dorsal and extends caudally. The *condylus medialis* is oval and oblique, with a sulcus in the middle. The *condylus lateralis* is robust and rounded, and the *condylus caudalis* is latero-medially elongated.

Procellariiformes

In ***Macronectes giganteus*** (Fig. 3A), the *lamina parasphenoidalis* is triangular and bears prominent and sharp *processi mediales parasphenoidales* that extend caudally. In the sagittal line, a tubercle continues with a crest that becomes weaker cranially disappearing without reaching the cranial end of the plate. The *ala parasphenoidalis* is represented by an edge laterally interrupted that turns into irregular sulcus and crests.

The articular area of the mandible (Fig. 3B) presents a sub-quadrangular configuration, which is the result of the latero-medial extension of the *cotyla medialis*. A crest divides this cotyla in two parts: a medial portion and a lateral and medially inclined one. The *cotyla lateralis* and the *cotyla caudalis* are partially merged, with the *sulcus intercotylaris* in-between. The *processus medialis mandibulae* is quadrangular and projects medio-caudally. A large *foramen pneumaticum articulare* opens laterally to the *facies articularis parasphenoidalis*.

The quadrate has a three-condylar configuration, with each condyle well differentiated. The *condylus medialis* projects more ventrally than the others. The *condylus medialis* is laterally elongated and presents a sulcus that divides a rounded ventral portion from a compressed latero-cranial one. The *condylus caudalis* is cranio-caudally compressed and separated from the rounded and blunt *condylus lateralis* by a sulcus.

In ***Fulmarus glacialoides*** (Fig. 3C), the *lamina parasphenoidalis* is triangular and delimited by strong crests: the caudal *cristae basilaria transversa*, the continuous and lateral *processi mediales paraspheoidales*, and the cranio-lateral *alae parasphenoidales*. The *processus mediales parasphenoidales* is small and low, and the *ala parasphenoidalis* is developed as a ventral discontinued crest, that turns into irregular sulcus and crests.

In the mandible (Fig. 3D), the *cotyla medialis* is laterally well-defined. The *cotyla lateralis* is stronger than the *cotyla caudalis*. A deep fossa is in the middle of the three

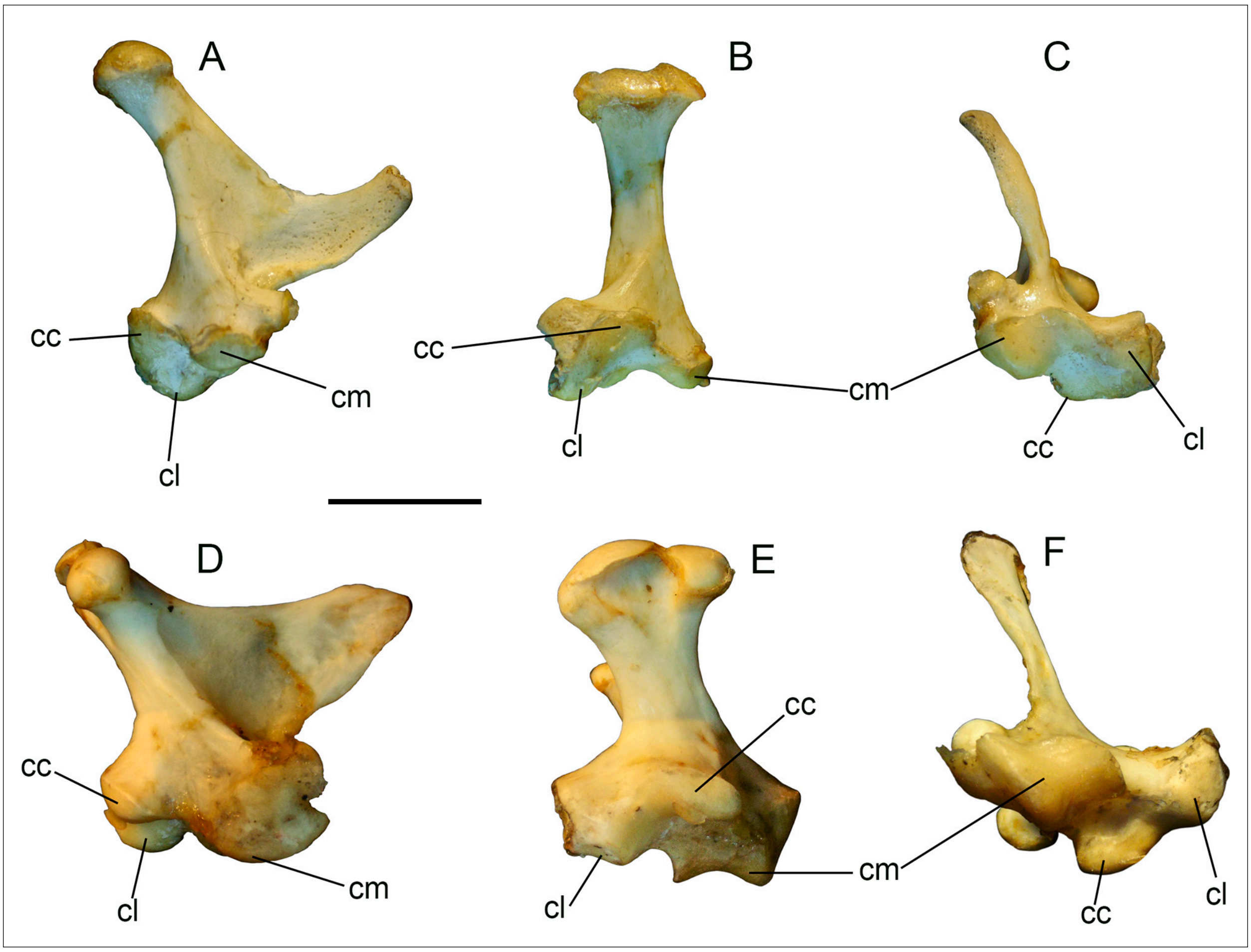


Fig. 4. Left quadrates of: *Aptenodytes forsteri* (**A–C**) in medial (**A**), caudal (**B**), and ventral (**C**) views; *Thalassarche melanophris* (**D–F**) in medial (**D**), caudal (**E**), and ventral (**F**) views. Abbreviations: (cc) *condylus caudalis*, (cl) *condylus lateralis*, (cm) *condylus medialis*. Scale bar: 10 mm.

cotylae. The *processus medialis mandibulae* is well-developed and medio-caudally projected.

The quadrate has a three-condylar configuration, with each condyle well differentiated. The *condylus medialis* is laterally elongated and projects ventrally. This condyle has a pulley-like structure with two crests and a sulcus in the middle. The *condylus caudalis* is cranio-caudally compressed and separated from the rounded and blunt *condylus lateralis* by a sulcus.

In ***Oceanites oceanicus*** (Fig. 3E)**,** the *lamina parasphenoidalis* is sub-triangular, with undefined boundaries. The *ala parasphenoidalis* is narrow and the *processi mediales parasphenoidales* are absent. Caudally, the *cristae basilaria transversa* constitute the only structures of the *lamina parasphenoidalis*. The *ala parasphenoidalis* ossifies as a lateral edge dorsally discontinued.

In the mandible (Fig. 3F), the *cotyla medialis* is deep, laterally delimited by a tubercle and poorly delimited medially. The *cotyla lateralis* is more cranially located and merges with the latero-caudal *cotyla caudalis* constituting a single and extended articular facet dorsal to the *cotyla medialis*. The *processus medialis mandibulae* is triangular and projects medio-caudally.

The quadrate presents also a three-condylar configuration. The *condylus medialis* is elongated and medio-ventrally inclined. In cranial view, the *condylus lateralis* is ventro-laterally projected. Ventrally, the *condylus caudalis* is displaced ventro-medially and has a caudal facet.

In ***Thalassarche melanophris*** (Fig. 3G), the *lamina parasphenoidalis* is oval and cranio-caudally compressed due to the reduction of the cranialmost portion. The *ala parasphenoidalis* is narrow and close to the *processi mediales parasphenoidales* that occupy the entire lateral of the *lamina parasphenoidalis*. Cranial to the *fossa subcondylaris*, a sagittal crest gradually become weaker and disappears before reaching the cranial end of the lamina. The *ala parasphenoidalis* is only represented by a lateral edge dorsally discontinued.

In the mandible (Fig. 3H), the cotylae are well differentiated. The *cotyla lateralis* and the *cotyla caudalis* are continuous but divided by a small tubercle. The *cotyla medialis* is wider and separated from the others by a deep and broad *sulcus intercotylaris*. The *processus medialis mandibulae* projects medio-caudally.

The quadrate (Fig. 4D–F) has a three-condylar configuration, with each condylus well differentiated. In the middle, there is a well-defined fossa. The *condylus medialis* projects more ventrally than the others and bears a pulley-like structure with two sharp crests. The *condylus caudalis* is rounded and prominent, delimited caudally by a crest. This is separated from the *condylus lateralis* by a sulcus.

General mechanism of the mandibulosphenoidal joint

In general terms, the secondary support of the mandible is an accessory articulation that supplements the quadrate-articular primary articulation, avoiding the disarticulation of the jaw during sudden or strong movements. In penguins (Fig. 5A–F), during the opening of the bill, the *facies articularis parasphenoidalis* slides on the lateral side of the *processus medialis parasphenoidalis*, and the *ramus mandibulae* slightly diverge from the sagittal line (Fig. 5A, D). The opening continues to the point where the *facies articularis parasphenoidalis* contacts with the *ala parasphenoidalis* (if developed), or with the lateral surface of the *processus medialis parasphenoidalis* (Fig. 5B, E). The *processus retroarticularis* (if developed) makes a stop with the *processus paroccipitalis* located in the caudal portion of the cranium (Fig. 5C, F).

In albatrosses and petrels (Fig. 5G–L), the *processus medialis mandibularis* is less extended and the *facies articularis parasphenoidalis* is not developed, determining a slightly different mechanism. In general, the *processus medialis mandibulae* does not contact any process of the *lamina parasphenoidalis* during the opening of the bill (Fig. 5G, J), with the exception of *Thalassarche melanophris*, in which it slides laterally on the *processus medialis parasphenoidalis*. Besides, the caudal border of the mandible (the *processus retroarticularis* is not developed) does not stop against the *processus paroccipitalis* at the maximum opening point (Fig. 5I, L). Another difference is that in penguins the *ala parasphenoidalis* is continuous with the *tuba auditiva* that encloses the ear region of the skull, whereas in albatrosses and petrels, the *ala parasphenoidalis* is less ossified and the ear zone is not covered by a bony layer.

Discussion

Available information about the development of the elements involved in the quadrate-articular and mandibulosphenoidal articulations during ontogeny is limited (Starck, 1998; Bhullar *et al*., 2012, 2016). Our own previous studies provide morphological data on the postnatal development in those penguin *Aptenodytes forsteri* (Sosa & Acosta Hospitaleche, 2017) and the petrel *Macronectes giganteus* (Piro & Acosta Hospitaleche, 2019).

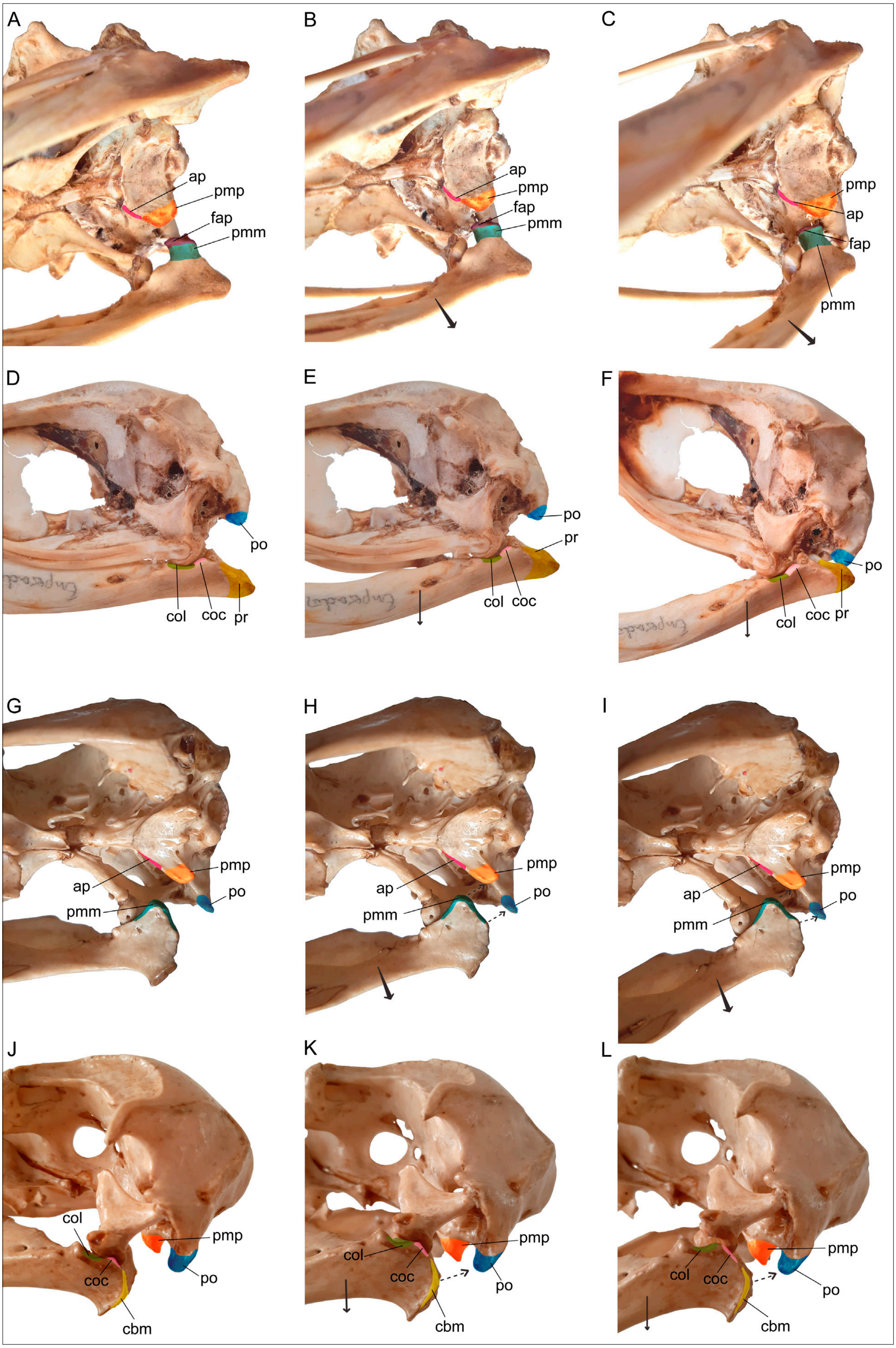
Here, we restricted the comparisons among the different species of penguins and albatrosses/petrels to adult specimens because the ossification is incomplete in immature skulls. Whereas the configuration of the quadrate is similar in juveniles and adults, in chicks some areas remain cartilaginous (Sosa & Acosta Hospitaleche, 2017: Fig. 5g–h). The *lamina parasphenoidalis* is not developed as such in the chicks, as the *os basioccipitale*, *os exoccipitale*, *os parasphenoidale*, and *rostrum parasphenoidale* are still independent elements in *A. forsteri* (Sosa & Acosta Hospitaleche, 2017: Fig. 4c), and *M. giganteus* (Piro & Acosta Hospitaleche, 2019: Fig. 3c). Similarly, in juveniles, is equivalent to that in adults, whereas the cotylae and processes of the chicks are still cartilaginous (Sosa & Acosta Hospitaleche, 2017: Fig. 5a–f; Piro & Acosta Hospitaleche: Fig. 8m, n).

In all the examined adult penguin species, the quadrate is three-condylar (Fig. 3A–C), but only the *condylus medialis* is well defined. This condylus is elongated (irregular in *Spheniscus magellanicus*) and represents the main articulation area. The three-condylar condition is already present in fossil penguins, although with some variations. The Neogene and extant species exhibit a similar pattern, whereas the Paleogene taxa develop stronger and massive quadrates (Ksepka *et al*., 2008, 2012; Acosta Hospitaleche *et al*., 2019)

In albatrosses and petrels, the general configuration is also three-condylar (Fig. 3D–F), but every condyle is well-defined as a separate and more complex structure. In addition, the shape and definition of the *cotylae mandibulares laterales* and the *cotylae mandibulares caudales* are better defined and consistent with the quadrate morphology.

These differences determine a more efficient primary mandibular articulation in tubenoses with respect to that of penguins and therefore, different requirements for the mandibulosphenoidal joint. Few fossil procellariforms preserve the *lamina parasphenoidalis*. As most of them corresponds to extant (Sallaberry *et al*., 2010), or closely related genera (Seguí *et al*., 2001), their morphological configurations are very similar to those observed in the species described here. Something similar is observed with the Neogene penguins (e.g. Stucchi *et al*., 2003; Acosta Hospitaleche *et al*., 2007), but unlike the procellariforms, the sphenisciforms have a vast fossil record that begins in the Paleocene with species having a different skeletal pattern. During the Paleocene and Eocene, penguins developed a *lamina parasphenoidalis* characterized by strong processes and tubercles (Acosta Hospitaleche *et al*., 2019a, b) proportionally larger than in the living taxa.

→ **Fig. 5.** Different stages during the opening of the jaw in the penguin *Aptenodytes forsteri* (**A–F**) and the petrel *Macronectes giganteus* (**G–L**) in latero-ventral (**A–C**, **G–I**) and lateral (**D–F**, **J–L**) views. Abbreviations: (ap) *ala parasphenidalis*, (cbm) caudal border of the mandible (the *processus retroarticularis* is absent here), (coc) *cotyla caudalis*, (col) *cotyla lateralis*, (pmm) *processus medialis mandibulae*, (pmp) *processus medialis parasphenoidalis*, (po) processus paroccipitalis, (pr) *processus retroarticularis*. The arrows indicate the movement direction. Scale bar: 10 mm.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Main inter-specific differences in the elements involved in the mandibulosphenoidal joint of the extant specimens here compared are in the shape of the *lamina parasphenoidalis*, the extension and position of the *processi mediales parasphenoidales*, the development degree of the *alae parasphenoidales*, the presence of the *tubercula basilaria* as independent structures, and the extension and orientation of the *processi mediales mandibulae*.

The shape, extension, and boundaries of the *lamina parasphenoidalis* are related to the structures it develops on. It is rectangular in *Aptenodyptes forsteri*, sub-rounded to oval in *Eudyptes sclateri* and *Thalassarche melanophris*, kidney-shaped in *Pygoscelis antarcticus*, *Eudyptula minor* and *Megadyptes antipodes*, triangular in *M. giganteus* and *Fulmarus glacialoides*, and sub-triangular in *Oceanites oceanicus*. It is also triangular but delimited by cranial edges in *S. magellanicus*, whereas the boundaries are indistinct in *O. oceanicus*.

The *processi mediales parasphenoidales* are absent in *O. oceanicus*, are moderately defined in *Eudyptes sclateri* and *Eudyptula minor*, well-defined in *P. antarcticus*, *M. antipodes*, and *T. melanophris*, sharp and elongated in *M. giganteus*, and bulky in *A. forsteri* and *S. magellanicus*. In *F. glacialoides*, these processes are continuous with the *cristae basilaria transversa*, also developed in *O. oceanicus*. Small *tubercula basilaria* developed as separate structures are only in *P. antarcticus*. *The alae parasphenoidales* are not completely ossified in *M. giganteus*, moderately developed in *A. forsteri*, *O. oceanicus*, and *T. melanophris*, and well-defined in *S. magellanicus*, *M. antipodes*, and *F. glacialoides*.

Within this spectrum of variation, the species with the less defined and most precarious structures are *O. oceanicus* among tubenoses and *Eudyptes sclateri* among penguins. These species are the most crustaceavores, they catch prey by filter-feeding mechanisms and do not struggle with live prey during diving. Destabilizing forces might be weaker than in the most piscivorous species such as *A. forsteri*. In this penguin species, like in *S. magellanicus*, the processes are prominent and the demands on the mandibulosphenoidal joint is higher. *M. giganteus*, which also preys on young alive birds, develop the strongest *lamina parasphenoidalis* processes among the albatrosses.

Other generalist and opportunistic species exhibit intermediate and mixed morphological conditions. For instance, *Eudyptula minor* presents barely defined *processi mediales parasphenoidales* and prey on small fish, and contrarily, *P. antarcticus* is a filter-feeding penguin (Lynnes *et al*., 2004) that develops well defined structures on the *lamina parasphenoidalis* as in *M. antipodes* that consumes fish and cephalopods (Van Heezik, 1990). The diet of *T. melanophris* and *F. glacialoides* is varied and the structures on the *lamina parasphenoidalis* are present but not well delimited like in the most piscivorous birds.

These morphological variations described, that can only be directly related with the trophic habits in the most strictly piscivorous and crustaceavores species, determine differences in the mandibulosphenoidal joint mechanism. This was unexpected given the previous observations made by Bock (1960) and his subsequent hypotheses about functional morphology of the secondary articulation of the mandible (Bock, 1960; Bock & Morioka, 1971).

In all penguin species, the *processi mediales mandibulae* are aligned with the *processi mediales parasphenoidales* when the bill is closed. However, in *A. forsteri* and *M. antipodes*, the *facies articularis parasphenoidalis* laterally slides on the *processus medialis parasphenoidalis* when the opening starts, and the stop at the maximum opening point is against the *ala parasphenoidalis*. The difference with *P. antarcticus* is that the *facies articularis parasphenoidalis* contacts with the cranial edge of the *processus medialis parasphenoidalis* (not the lateral surface) during the opening of the bill until making the stop against the *ala parasphenoidalis*. At the maximum opening of the bill, the *processus retroarticularis* stops against the *processus paraoccipitalis*. In *S. magellanicus*, *Eudyptula minor*, and *Eudyptes sclateri*, the *facies articularis parasphenoidalis* slip on the cranio-lateral surface of the *processus medialis parasphenoidalis* and reaches the *ala parasphenoidalis*. When the bill is completely opened, the elongated *processus retroarticularis* stop against the *processus paraoccipitalis* in *S. magellanicus*, but not in *Eudyptes sclateri* and *Eudyptula minor*.

In Procellariiformes, this mechanism is slightly different; when the bill is closed, the *processus medialis mandibulae* is cranio-lateral to the *processus medialis parasphenoidalis*. In *M. giganteus*, during the opening of the beak, the mandible displaces lateralo-caudally making contact only with the *processus medialis parasphenoidalis*. The *processus retroarticularis* is not developed, and the *processus paroccipitalis* does not make a stop against any part of the mandible during the maximum opening point of the bill. On the contrary, in *O. oceanicus*, the *processus medialis mandibulae* remains cranially to the *ala parasphenoidalis* when the bill is closed. During the opening of the bill, the *processus medialis mandibulae* slides caudo-laterally on the *ala parasphenoidalis*. The difference with *F. glacialoides* is that the *processus medialis mandibulae* is cranio-lateral to the *processus medialis parasphenoidalis* when the bill is closed. When the opening of the bill starts, the *ramus mandibulae* diverge from the sagittal line without making any contact between the *processus medialis mandibulae* and the processes of the *lamina parasphenoidalis*. The *processus retroarticularis* is not developed. In a similar way, in *T. melanophris*, the *processus medialis mandibulae* approaches the *processus medialis parasphenoidalis* without making any contact during the opening of the bill.

Conclusions

The integrative analysis of the anatomy and functionality of the mandibulosphenoidal complex and other elements involved in this joint, allowed us to evaluate the magnitude of the variation within and between groups. The selection of different sized penguins and tubenoses, two phylogenetically related groups of seabirds that feed on a variety of trophic items and present different foraging strategies, gave us the opportunity to evaluate these variations in regard to each trophic demand and their primary quadrate-articular joint.

Given the previous analyses made by Bock (1960) and Zusi (1962), we expected to find the main variations in relation with the catching food strategies of each species. However, we observed that the configuration of the primary quadrate-articular joint was decisive in the secondary support development. It means that the mandibulosphenoidal and the quadrate-articular joints need to be integrally analyzed to understand the kind and relative magnitude that these structures are able to support. For that reason, the use of these elements to infer diet and trophic strategies is limited.

Morphological differences between the quadrate of Sphenisciformes and Procellariiformes were greater than among each group. This was decisive for the analysis of the mandibulosphenoidal joint, due to the quadrate-articular of both groups was not equally efficient, and therefore, the need to relieve stress and avoid disarticulation of the jaw was either not the same.

A more efficient primary quadrate-articular joint is ensured when the condyles of the quadrate are rounded and well delimited, and the mandibular cotylae are separated and well-defined like it was observed in adult Procellariiformes. This kind of joint allows a wider range of movements and a stronger destabilizing effort without dislocation.

On the contrary, in Sphenisciformes the quadrate has condyles barely defined, and the mandibulosphenoidal articulation acquires a stronger development. For the same reasons, the processes of the *lamina parasphenoidalis* and the mechanisms of stops between the mandible and the cranium are better developed in penguins. This is undoubtedly related to the poor development of the quadrate and the catching food strategies. Adult penguins capture live prey, during diving (Williams, 1995), applying higher forces in the jaw articulations, whereas albatrosses and petrels also consume carrion and offal (Furness &Monaghan, 1987).

In sub-adult specimens, however, the structures involved in the quadrate-articular and mandibulosphenoidal joints are even less defined (Sosa & Acosta Hospitaleche, 2017; Piro & Acosta Hospitaleche, 2019). This is not rare considering that penguins and tubenoses are semi-altricial birds (Starck & Ricklefts, 1998) that depend on their parents to be fed after hatching.

The use of the mandibulosphenoidal and quadrate-articular joints morphology as an interpretative tool is valid, although the scope of the inferences will depend on the particular case. For that reason, we must be cautions using this in fossil specimens. We demonstrated that the weaker mandibulosphenoidal joints appears in the crustaceavores species (*e.g. Oceanites oceanicus*), whereas stronger structures are developed in the most strictly piscivorous (*e.g. Aptenodytes forsteri*). However, the accuracy of the inferences becomes weaker in opportunistic and generalist seabirds.

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References

Acosta Hospitaleche, C., Haidr, N., Paulina-Carabajal, A. & Reguero, M. (2019). The first skull of *Anthropornis grandis* (Aves, Sphenisciformes) associated with postcranial elements. *Comptes Rendus Palevol*, **18**, 599–617.

Acosta Hospitaleche, C. Piro, A. & Sosa, M. A. (2019). Desarrollo de la articulación mandibular secundaria en pingüinos del eoceno de Antártida. *Reunión de Comunicaciones de la Asociación Paleontológica Argentina*, *Libro de Resumenes*, 21.

Acosta Hospitaleche, C., Tambussi, C., Donato, M. & Cozzuol, M. (2007). A new Miocene penguin from Patagonia and its phylogenetic relationships. *Acta Palaeontologica Polonica*, **52**, 299–314.

Ashmole, N. P. (1971). Seabird ecology and the marine environment, pp. 223–286 *in:* Farner, D.S. & King J.R. (eds) *Avian Biology*, vol. **1**. London, Academic Press.

Baumel, J. J. & Raikow, R. J. (1993). Arthrologia, pp. 133–187 *in*: Baumel, J. J., King, S. A ., Breazile, J. E., Evans, H. E. & Berge, J. C. (eds) H*andbook of Avian Anatomy: Nomina anatomica avium*. Cambridge, MA, Publications of the Nuttall Ornithological Club.

Baumel, J. J. & Witmer, L. M. (1993). Osteologia, pp 45–132 *in*: Baumel, J. J., King, S. A ., Breazile, J. E., Evans, H. E. & Berge, J. C. (eds) *Handbook of Avian Anatomy: Nomina anatomica avium*. Cambridge, MA, Publications of the Nuttall Ornithological Club.

Bock, W. J. (1959). Preadaptation and multiple evolutionary pathways. *Evolution*, **13**, 194 –211.

Bock, W. J. (1960). Secondary articulation of the avian mandible. *The Auk*, **77**, 19–55.

Bock, W. J. (1964). Kinetics of the avian skull. *Journal of Morphology*, **114**, 1–41.

Bock, W. J. & Morioka, H. (1971). Morphology and evolution of the ectethmoid-mandibular articulation in the Meliphagidae (Aves). *Journal of Morphology*, **135**, 13–50.

Bhullar, B. A. S., Hanson, M., Fabbri, M., Pritchard, A., Bever, G. S. & Hoffman, E. (2016). How to make a bird skull: Major transitions in the evolution of the avian cranium, paedomorphosis, and the beak as a surrogate hand. *Integrative and Comparative Biology*, **56**, 389–403.

Bhullar, B. A. S., Marugán-Lobón, J., Racimo, F., Bever, G. S., Rowe, T. B., Norell, M. A. & Abzhanov, A. (2012). Birds have paedomorphic dinosaur skulls. *Nature*, **487**, 223–226.

Bühler, P. (1981). Functional anatomy of the avian jaw apparatus, pp. 439–468 *in*: King, A.S. & McLelland, J. (eds). *Form and Function in Birds*, vol. **2**,. London, Academic Press.

Bock, W. J. (1999). Cranial kinesis revisited. *Zoologischer Anzeiger*, **238**, 27–40.

Carboneras, C., Jutglar, F. & Kirwan, G. M. (2020). Southern Giant-Petrel (*Macronectes giganteus*), version 1.0 *in* del Hoyo, J. Elliott, A. Sargatal, J., Christie, D. A. & de Juana, E. (eds) *Birds of the World*. Ithaca, NY, USA, Cornell Lab of Ornithology. https://doi.org/10.2173/bow.angpet1.01

Carboneras, C., Jutglar, F. & Kirwan, G. M. (2020b). Southern Fulmar (*Fulmarus glacialoides*), version 1.0. *in* del Hoyo, J. Elliott, A. Sargatal, J., Christie, D. A. & de Juana, E. (eds) *Birds of the World*. Ithaca, NY, Cornell Lab of Ornithology, https://doi.org/10.2173/bow.souful1.01

Drucker, J., Carboneras, C. Jutglar, F. & Kirwan, G. M. (2020). Wilson's Storm-Petrel (*Oceanites oceanicus*), version 1.0 *in* Billerman, S. M. (ed) *Birds of the World* Ithaca, NY, USA, Cornell Lab of Ornithology. https://doi.org/10.2173/bow.wispet.01

Cherel, Y. & Kooyman, G. L. (1998). Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. *Marine Biology*, **130**, 335–344.

Cooper, J., Brown, C. R., Gales, R. P., Hindell, M. A., Klages, N. T. W., Moors, P. J., Pemberton, V.R., Thompson, K.R. & Van Heezik, Y. M. (1990). Diets and Dietary Segregation of Crested Penguins, pp. 131–156 *in*: Davis, L.S. & Darby J.T. (eds) *Penguin Biology*. San Diego, Academic Press.

Croxall, J. P. & Prince, P. A. (1980). Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological journal of the Linnean Society*, **14**, 103–131.

del Hoyo, J., Carboneras, C. Jutglar, F. Collar, N. & Kirwan, G. M. (2020). Black-browed Albatross (*Thalassarche melanophris*), version 1.0 *in*: Billerman, S. M., Keeney, B. K., Rodewald, P. G. & Schulenberg, T. S. (Eds). *Birds of the World*. Ithaca, NY, USA, Cornell Lab of Ornithology. https://doi.org/10.2173/bow.bkbalb.01

Furness, R. W. & Monaghan, P. (1987). *Seabird Ecology*. New York, Chapman and Hall.

Ksepka, D. T., Clarke, J. A., DeVries, T. J. & Urbina, M. (2008). Osteology of *Icadyptes salasi*, a giant penguin from the Eocene of Peru. *Journal of Anatomy*, **213**, 131–147.

Ksepka, D. T., Fordyce, R. E., Ando, T. & Jones, C. M. (2012). New fossil penguins (Aves, Sphenisciformes) from the Oligocene of New Zealand reveal the skeletal plan of stem penguins. *Journal of Vertebrate Paleontology*, **32**, 235–254.

Lynnes, A. S., Reid, K. & Croxall, J. P. (2004). Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biology*, **27**, 544–554.

Piro, A. & Acosta Hospitaleche, C. (2019). Skull morphology and ontogenetic variation of the Southern Giant Petrel *Macronectes giganteus* (Aves: Procellariiformes). *Polar Biology*, **42**, 27–45.

Sallaberry, M., Rubilar-Rogers, D., Suárez, M. E. & Gutstein, C. S. (2010). The skull of a fossil Prion (Aves: Procellariiformes) from the Neogene (Late Miocene) of northern Chile. *Andean Geology*, **34**, 147–154.

Seguí, B., Quintana, J., Fornós, J. J. & Alcover, J. A. (2001). A new fulmarine petrel (Aves: Procellariiformes) from the upper Miocene of the Western Mediterranean. *Palaeontology*, **44**, 933–948.

Scolaro, J. A., Wilson, R. P., Laurenti, S., Kierspel, M., Gallelli, H. & Upton, J. A. (1999). Feeding preferences of the Magellanic penguin over its breeding range in Argentina. *Waterbirds*, **22**, 104–110.

Snively, E. & Russell, A. P. (2007a). Functional variation of neck muscles and their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs. *Anatomical Record*, **290**, 934–957.

Snively, E. & Russell, A. P. (2007b). Functional morphology of neck musculature in the Tyrannosauridae (Dinosauria, Theropoda) as determined via a hierarchical inferential approach. *Zoological Journal of the Linnean Society of London*, **151**, 759–808.

Sosa, M. A. & Acosta Hospitaleche, C. A. (2018). Ontogenetic variations of the head of *Aptenodytes forsteri* (Aves, Sphenisciformes): muscular and skull morphology. *Polar Biology*, **41**, 225–235.

Starck, J. M. (1998). Structural variants and invariants in avian embryonic and postnatal development. *Oxford Ornithology Series*, **8**, 59–88.

Starck, J. M. & Ricklefs, R. (1998). Patterns of development: the altricial-precocial spectrum, pp. 3–30 *in*: Starck, J. M. & Ricklefs, R. (eds) *Avian Growth and Development*, *Evolution between the Altricial-Precocial Spectrum*. New York, Oxford University Press.

Stucchi, M., Urbina, M. & Giraldo, A. (2003). Una nueva especie de Spheniscidae del Mioceno tardío de la Formación Pisco, Perú. *Bulletin de l'Institut français d'études andines*, **32**, 361–375.

Van Heezik, Y. (1990). Seasonal, geographical, and age-related variations in the diet of the yellow-eyed penguin (*Megadyptes antipodes*). *New Zealand Journal of Zoology*, **17**, 201–212.

Williams, T. D. (1995). *The Penguins: Spheniscidae*. Oxford, UK, Oxford University Press.

Zusi, R. L. (1962). Structural adaptations of the head and neck in the black skimmer *Rynchops nigra* Linnaeus. *Publication Nuttall Ornithological Club*, **3**, 1–101.

Zusi, R. L. (1967). The role of the depressor mandibulae muscle in kinesis of the avian skull. *Proceedings of the United States National Museum*, **123**, 1–28.

Appendix 1

Osteological material used for descriptions: *Aptenodytes forsteri* MLP-O-15035, MLP-O-15188, NHM 1850.9.7.2, NHM 1846.4.15.26, NHM 1846.4.15.27, NHM 1846.4.15.28, MNH 5/2011.14.1, NHM 5/1972.1.25, MNH 1905.12.30.419; *Eudyptes sclateri*: NHM 5/1952.1.38; *Eudyptula minor*: NHM 1896.2-16.38, NHM 5/1952.1.41, NHM 1881.1.17.105, NHM 5/1952.3.143; *Megadyptes antipodes*: NHM 1852.1.17.11, 5/2006.31.26, NHM 1852; *Pygoscelis antarcticus*: MLP-O-14670, MLP-O-14671, MLP-O-14672, MLP-O-14673, MLP-O-14674, MLP-O-14675, MLP-O-14676, MLP-O-14677, MLP-O-14678, MLP-O-14679, MLP-O-14703, MLP-O-14704, MLP-O-14705, MLP-O-14706, MLP-O-14707, MLP-O-14708, MLP-O-14709, MLP-O-14710, MLP-O-14717, MLP-O-14737, MLP-O-14831, MLP-O-14905, MLP-O-14916, MLP-O-14947, MLP-O-15189, MLP-O-15190, MLP-O- 15191, MLP-O-15211; *Spheniscus magellanicus*: MLP-597, MLP-611, MLP-614, MLP-642, MLP-643, MLP- O-14357, MLP-O-14439, MLP-O-14464, MLP-O-14894, MLP-O-14895, MLP-O-15091, MLP-O-15184, MLP-O-15185, MLP-O-15186, MLP-O-15187; *Spheniscus humboldti* MLP 686; *Macronectes giganteus*: CFA-OR-024, CFA-OR-1189, CFA-OR-1555, CFA-OR-1574, CFA-OR-1607, CFA-OR-1766, CFA-OR-299, MACN-26856, MACN-68029, MACN-68977, MLP-812, MLP-949, MLP-O-14500, MLP-O-14509, MLP-O-14510, MLP-O-14869, MLP-O-14898, MNHN-5804; *Thalassarche melanophris*: CFA-OR-1573, CFA-OR-1182, CFA-OR-1767, CFA-OR-503, CFA-OR-1219, MLP-928, MLP-O-14546, MLP-O-14681, MNHN-5928, MNHN-5478; *Fulmarus glacialoides*: CFA-OR-1191, MACN-2330, MACN-54741, MLP-O-15370, MNHN-7006, MNHN-5666; *Oceanites oceanicus*: MACN-68489, MLP-480, MLP-O-14538, MLP-O-14883, MNHN-5725.