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Osteology of the feeding apparatus of Magnificent Frigatebird *Fregata magnificens* and Brown Booby *Sula leucogaster* (Aves: Suliformes)

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ABSTRACT

In this paper, we describe the skulls of Magnificent Frigatebird Fregata magnificens *(Fregatidae) and Brown Booby (Sulidae)* Sula leucogaster, *with focus on the structures associated with the* Musculi mandibulae. *We discuss the results in the context of the feeding biology of the two species, which feed mainly on flying fish and squids. Frigatebirds capture prey from just above, or just below, the water surface in flight. The hook-shaped* Apex maxillae *in* F. magnificens *can be viewed as an adaptation for grasping prey from near the water surface. Boobies catch prey by plunging; thus, the dorsoventrally flattened skull and conical bill of* S. leucogaster *may reduce water resistance when it dives, or swims underwater. The bill is long in both species, such that it is on average 70% of the whole skull length in* F. magnificens *and 60% in* S. leucogaster. *Consequently, the* Mm. mandibulae *in the two species are more posteriorly positioned relative to the* Apex rostri. *This results in low mechanical advantage for the mandible opening-closing lever, indicating adaptations for a fast, rather than a strong, bite. Fast-moving mandibles would be advantageous for 'mandibulating' prey while swallowing. The* Fossa musculorum temporalium *and the* Palatum osseum *in both species provide a broad area for origins of the* Musculus adductor mandibulae externus *(all parts) and the* Musculus pterygoideus. *The* Processus orbitalis quadrati *is longer and thicker in* F. magnificens *than in* S. leucogaster, *and so is the* Musculus pseudotemporalis profundus. *We suggest that* Mm. adductores mandibulae *are relatively well developed in the two species; therefore, their* mandibulae *are still probably capable of a powerful adduction. In both species there is a mechanisms that contribute to protect the jaws from disarticulation and damage. Such mechanism involves the incorporation of a 'flange-like'* Crista intercotylare *on the* Margo medialis cotylae medialis fossae articularis quadratica *that grips the* Condylus medialis quadrati. *In* S. leucogaster, *the retractor-stop 'notch' formed by* Ossa lacrimale et nasale *also serves to protect the jaws against sudden external forces when birds are diving or swimming underwater for prey. A more detailed*

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hypothesis for the jaw movements and strength in F. magnificens *and in* S. leucogaster *and their relation with feeding habits should necessarily incorporate data on the jaw and anterior neck musculatures.*

Key-Words: Functional anatomy; Jaw apparatus; Mandible musculature; Seabirds; Syncranium.

INTRODUCTION

Suliformes is the clade containing Fregatidae (frigatebirds), Sulidae (boobies and gannets), Phalacrocoracidae (cormorants), and Anhingidae (anhingas). This assemblage includes some 60 living species (and a number of fossil ones) of medium to large-sized waterbirds distributed worldwide (del Hoyo *et al.,* 1992; Chesser *et al.,* 2010; Mayr, 2010). Formerly, the families of Suliformes have been grouped with Pelecanidae (pelicans) and Phaethontidae (tropicbirds) in the 'traditional' Pelecaniformes (del Hoyo *et al.,* 1992); however, most recent cladistic analyses have found it to be polyphyletic. Pelecaniformes, as often currently defined, consists of two clusters; one composed of Pelecanidae, Balaenicipitidae (shoebill), and Scopidae (hamerkop), the other of Threskiornithidae (ibises and spoonbills) and Ardeidae (herons). Phaethontidae has been proposed not to be closely related to the other members of the group (*e.g.,* Hackett *et al.,* 2008; Mayr, 2010; Smith, 2010; Jarvis *et al.,* 2014; Carlos, 2015).

In the late 1800s and early 1900s, anatomy and morphology have been extensively used in ornithological systematics (for an overview, see Livezey & Zusi, 2006b, 2007). As to Suliformes (then in Pelecaniformes), the most comprehensive works are those by Shufeldt (1888, 1902), Beddard (1897), and Pycraft (1898). These authors relied primarily on skeletal evidence to formulate hypotheses about inter-familiar relationships within the group. Today, osteology continues to be an essential part of avian systematics. In Livezey & Zusi's (2006b, 2007) cladistic analysis of 150 taxa of Neornithes, for example, 85% of the 2,954 characters are osteological.

Relatively less studied is the role of skeletal structures in the processes by which birds obtain their food. The avian skull and jaws are most intimately involved in feeding; therefore, morphological adaptations for this purpose are more likely to be found there (Burton, 1974; Burger, 1978; Donatelli *et al.,* 2014). In Suliformes, descriptions of cranial osteology as related to prey capture are available for Phalacrocoracidae and Anhingidae (Owre, 1967; Burger, 1978); however, there are no studies of comparable scope dealing with both Fregatidae and Sulidae. Thus, our aim here is to describe the skull of one species each of these families, namely, Magnificent Frigatebird *Fregata magnificens* and Brown Booby *Sula leucogaster,* with focus on those structures associated with the muscles responsible for opening and closing the jaws (the *Musculi mandibulae*). We shall discuss our results in the context of the feeding biology of these two species.

MATERIAL AND METHODS

We examined 15 adult skulls of *F. magnificens* and seven of *S. leucogaster* from the collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Sul (MCEMAV); and Museu de Ciências Naturais, Centro de Estudos Costeiros, Limnológicos e Marinhos do Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Imbé (MUCIN). The following specimens were used: *F. magnificens* – MZUSP 88433, 88434; MCEMAV 9, 10, 11, 48, 49, 182, 186, 215, 222, 223, 225, 240; MUCIN 386; and *S. leucogaster* – MCEMAV 247, 248, 319, 320; MUCIN 001, 384, 385.

We described a syncranium of *F. magnificens* (MUCIN 386) and took it as reference for comparisons, initially to conspecifics, and later to *S. leucogaster.* We observed the specimens under a 10-160X magnifying Opton TIM-2B stereomicroscope and photographed them with a Nikon D7000 digital camera with 60 mm 2.8 Nikon macro lens. For each specimen, we took the following measurements (after Burger, 1978) with digital calipers to the nearest 0.01 mm: cranium depth, cranium width, skull (syncranium) length, and upper jaw (*Maxilla*) length.

We mostly followed the anatomical nomenclature of the *Nomina Anatomica Avium* (Baumel & Witmer, 1993; Vanden Berge & Zweers, 1993). The main exceptions included following Cracraft (1968) with regard to the *Partes ossis lacrimalis* and Livezey & Zusi (2006a) for terms pertaining to the *Palatum osseum.*

RESULTS

In *F. magnificens,* the *Facies dorsalis regionis frontalis* exhibits an elongate, medial *Depressio frontalis,* the caudal end of which reaches the *Pars rostralis regionis parietalis.* The *Depressio frontalis* is more pronounced on the *Pars caudalis regionis frontalis,* where it divides the *Prominentia frontoparietalis* (*sensu* Posso & Donatelli, 2005). In *S. leucogaster,* the *Angulus craniofacialis* is extremely obtuse and both *Depressio frontalis* and *Prominentia frontoparietalis* are so attenuated that *Regiones frontalis et parietalis* have a planar to slightly convex surface (Figs. 1: A-C; 2: A-C). The *Cranium* is more dorsoventrally compressed in *S. leucogaster* than in *F. magnificens.* The average ratio between the cranium depth and width is 0.81 (range: 0.80-0.84) in the former and 0.75 (range: 0.69-0.78) in the latter.

The *Maxilla* in *F. magnificens* is dorsally compressed on its proximal one-third and gradually tapers from base to apex to a strongly down-curved *Hamulus rostri* (*sensu* Livezey & Zusi, 2006b). In *S. leucogaster,* the *Maxilla* is convex from side to side and tapers to a sharp, slightly decurved point (Figs. 1: A; 2: A). The *Maxilla* is long relative to the syncranium length in both species. The average ratio between the *Maxilla* and syncranium lengths is 0.7 (range: 0.67-0.72) in *F. magnificens* and 0.59 (range: 0.58-0.60) in *S. leucogaster.*

In *F. magnificens,* the *Margo tomialis rostri maxillae* (to the exclusion of the *Pars apicis*) is slightly curved in lateral view, whereas in *S. leucogaster* it is somewhat straight. In the two studied species, the *Facies ventralis rostri* is strongly ossified; *i.e.,* the *Processus palatini ossium premaxillarium* are medially fused with each other so that no *Fenestra ventromedialis* (*sensu* Livezey & Zusi, 2006b) is present (Figs. 1: D; 2: D).

In *F. magnificens,* the *Zona flexoria craniofacialis* appears as a thin and narrow transverse band across the *Proccessus frontales ossis premaxillaris et Os nasale* at their *junctura* with *Ossa frontalia.* In *S. leucogaster,* the compressed portions of *Proc. frontales ossis premaxillaris et Os nasale* consist of a very thin laminae bordered by *eminentiae ossea,* so that the *Zona flexoria craniofacialis* appears as a deep *sulcus* (Figs. 1: C; 2: C).

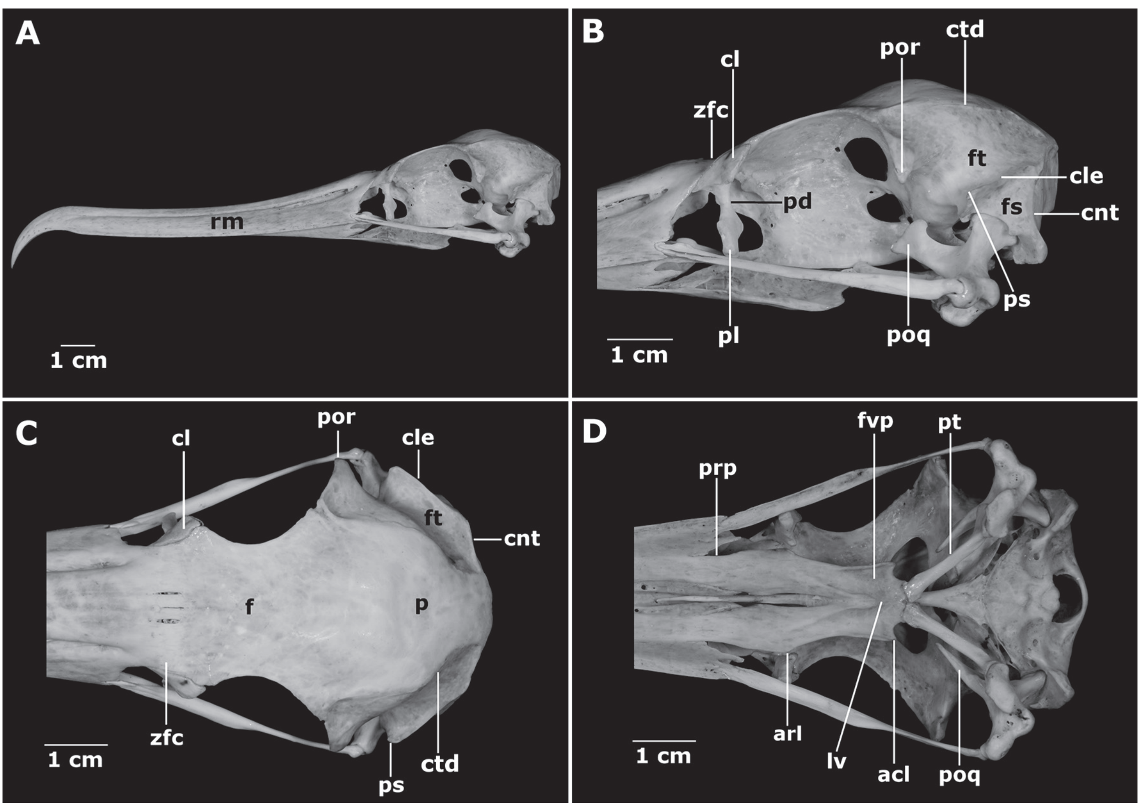

FIGURE 1: Lateral (**A, B**), dorsal (**C**) and ventral (**D**) views of the skull of Magnificent Frigatebird *Fregata magnificens. Ramus mandibulae* (**rm**), *Zona flexoria craniofacialis* (**zfc**), *Caput ossis lacrimalis* (**cl**), *Processus descendens ossis lacrimalis* (**pd**), *Pes ossis lacrimalis* (**pl**), *Processus postorbitalis* (**por**), *Processus orbitalis quadrati* (**poq**), *Crista temporalis dorsalis* (**ctd**), *Crista laminae externae cranii* (**cle**), *Crista nuchalis transversae* (**cnt**), *Processus squamosalis* (**ps**), *Fossa musculorum temporalium* (**ft**), *Fossa subtemporalis* (**fs**), *Regio frontalis* (**f**), *Regio parietalis* (**p**), *Processus rostralis ossis palatini* (**prp**), *Angulus rostrolateralis* (**arl**), *Fossa ventralis partis lateralis palatini* (**fvp**), *Lamellae ventralis* (**lv**), *Angulus caudolateralis* (**acl**), *Os pterygoideus* (**pt**).

The *Junctura* (*naso-*) *frontolacrimalis* is mostly lateral to the *Zona flexoria craniofacialis* in *F. magnificens* and ventrocaudal to it in *S. leucogaster.* In the latter species, the *Caput ossis lacrimalis* rostrally fits into a 'notch' on the *Margo caudalis processus maxillaris ossium nasalium* (Figs. 1: A, B; 2: A, B).

The *Fossa musculorum temporalium* (*sensu* Zusi & Livezey, 2000) is well delineated and deep in the two species. The *Cristae* (*lineae*) *temporales dorsales* in *F. magnificens* approach each other on the *Region parietalis,* but remain separated by an average 12.31 mm (range: 11.00-13.67) medial ridge, whereas in *S. leucogaster,* the crests unite to form a narrow *Crista* (*linea*) *nuchalis sagittalis.* In the two species, the *Margo caudalis fossae* is bounded in large part by a laminar ridge structure (*i.e., Crista laminae externae cranii, sensu* Livezey & Zusi, 2006b) running ventrolaterally and terminating in a short *Processus squamosalis* (*sensu* Posso & Donatelli, 2005). The ridge is more prominent in *S. leucogaster* so that the *fossa* is deeper in this species than in *F. magnificens* (Figs. 1: B, C; 2: B, C).

In both species, the *Pars maxillaris palatinae* consists of a dorsoventrally compressed *Processus rostralis palatini.* The length of the *Proc. rostralis* (measured rostrally from the *Zona flexoria palatina* to the *Margo rostralis partis choanalis*) exceeds that of the rest of the *Os palatinum,* especially in *S. leucogaster* (Figs. 1: D; 2: D).

In *F. magnificens,* the *Lamellae dorsalis partis choanalis palatinae* are moderately-high ridges that fuse together to form the *Crista dorsomedialis.* These lamellae are rudimentary in *S. leucogaster.* The *Lamellae ventrales partis choanalis* are medially-fused and form a low *Crista ventralis* in *F. magnificens* and a prominent *Carina ventromedialis* in *S. leucogaster* (Figs. 1: B, D; 2: B, D).

The *Fossa ventralis partis lateralis palatinae* is rostrocaudally short and moderately deep in *F. magnificens,* whereas it is longer and deeper in *S. leucogaster.* Both *Crista obliqua et Angulus rostrolateralis partis lateralis palatinae* are present only in *F. magnificens.* The *Angulus caudolateralis partis lateralis palatinae* is present in the two species (Figs. 1: D; 2: D).

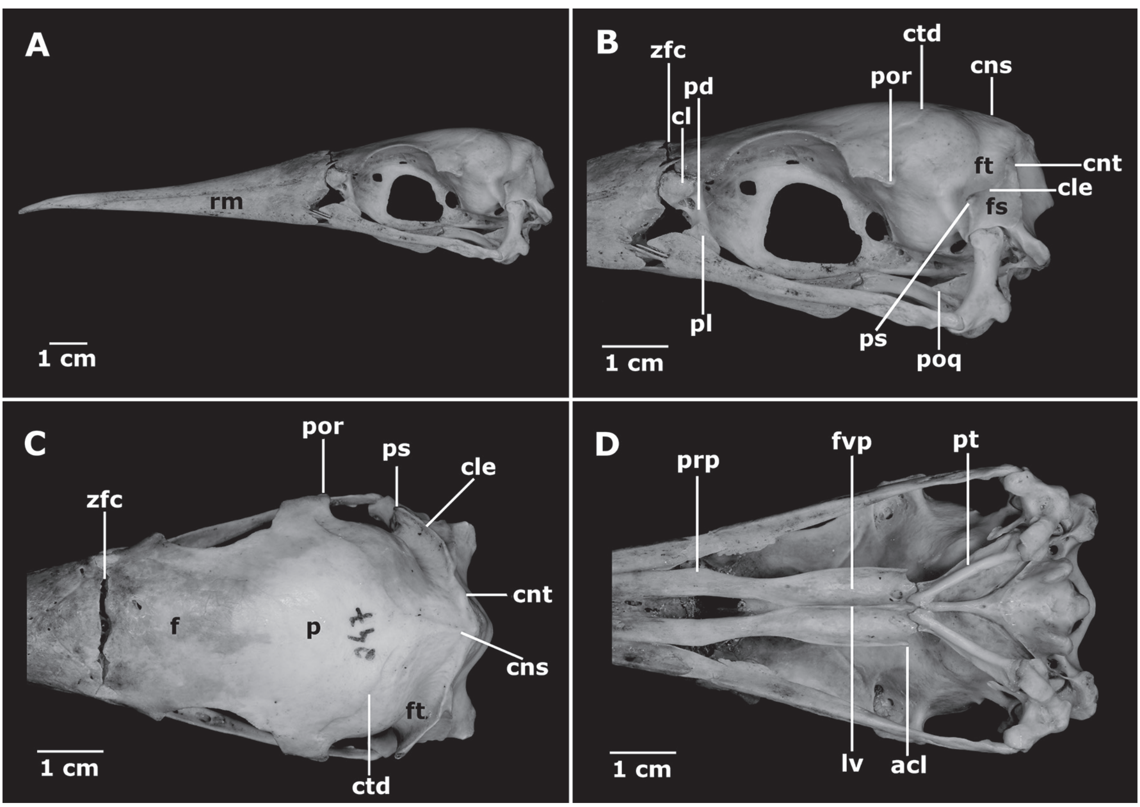

FIGURE 2: Lateral (**A, B**), dorsal (**C**) and ventral (**D**) views of the skull of Brown Booby *Sula leucogaster. Ramus mandibulae* (**rm**), *Zona flexoria craniofacialis* (**zfc**), *Caput ossis lacrimalis* (**cl**), *Processus descendens ossis lacrimalis* (**pd**), *Pes ossis lacrimalis* (**pl**), *Processus postorbitalis* (**por**), *Crista temporalis dorsalis* (**ctd**), *Crista nuchalis sagittalis* (**cns**), *Crista nuchalis transversae* (**cnt**), *Crista laminae externae cranii* (**cle**), *Processus squamosalis* (**ps**), *Processus orbitalis quadrati* (**poq**), *Fossa musculorum temporalium* (**ft**), *Fossa subtemporalis* (**fs**), *Regio frontalis* (**f**), *Regio parietalis* (**p**), *Processus rostralis ossis palatini* (**prp**), *Fossa ventralis partis lateralis palatini* (**fvp**), *Lamellae ventralis* (**lv**), *Angulus caudolateralis* (**acl**), *Os pterygoideus* (**pt**).

In *F. magnificens,* the *Processus orbitalis ossis quadrati* is long and extends dorso-medially parallel to the *Pars caudalis orbitae;* it is somewhat rectangular in shape, with a flattened spatulate, bifid *terminus.* In *S. leucogaster,* the *Proc. orbitalis* is a thin, triangular plate with apex directed rostrally (Figs. 1: B; 2: B).

The *Pars symphisialis mandibulae* is short, representing less than 0.1 in proportion to the whole *Ramus mandibulae,* and lateromedially compressed in both studied species. In *F. magnificens* the *Apex* (*terminus*) *rostri* is slightly curved downward relative to the *Margo tomialis mandibulae,* whereas it is straight and tapers to a sharp point in *S. leucogaster* (Fig. 3: A, B).

The *Facies medialis* (*lingualis*) *et ventralis partis intermediae rami mandibulae* are often formed by the *Os spleniale* in many bird taxa (Baumel & Witmer, 1993). However, in the studied species, this bone also seems to contribute to the *Facies dorsalis mandibulae.* Accordingly, the *Pars intermedia mandibulae* appears wide in dorsal view, forming a *Sulcus* (aut *Planum*) *paratomialis* (*sensu* Livezey & Zusi, 2006b), especially in *S. leucogaster* (Fig. 3: A, B).

There are two short *Proccessus pseudocoronoidei manidibulae* (*sensu* Donatelli, 1996), one dorsolaterally located and one dorsally, in *F. magnificens.* In *S. leucogaster,* the single *Proc. pseudocoronoideus* is a bipartite, robust *tuberostitas* on the *Margo dorsalis rami mandibulae.* The small *Tuberculum pseudotemporales* is positioned caudal to the *Fossa aditus canalis neurovascularis* in *F. magnificens* and dorsal to it in *S. leucogaster* (Fig. 3: A, B).

The *Cotylae lateralis et medialis fossae articularis quadratica* are deep and separated by a 'flange-like' *Crista intercotylare* on the *Margo medialis cotylae medialis.* This crest is higher in *F. magnificens* than in *S. leucogaster.* In the two species, the *Fossa caudalis processus medialis mandibulae* is shallow and the *Processus lateralis et retroarticularis mandibulae* have a tubercular shape (Fig. 3: A, B).

DISCUSSION

The two studied species feed on epipelagic flying fish (Exocoetidae) and flying squids (Ommastrephidae) (Diamond & Schreiber, 2002; Schreiber & Norton, 2002), or opportunistically on demersal fish from fisheries discards (Calixto-Albarrán & Osorno, 2000; Branco *et al.,* 2005, 2007). Nevertheless, their feeding strategies are markedly different (Schreiber & Clapp, 1987).

Like its congeners, *F. magnificens* cannot dive or land on water as most seabirds do, because their plumage is not waterproof. Instead, it seizes prey with its bill on, or near to, the surface while in flight, or force other seabirds to disgorge, or give up, their prey so they can steal it (Schreiber & Clapp, 1987; Diamond & Schreiber, 2002). The long, hook-tipped bill in frigatebirds is believed to be adapted for snatching prey from near the water surface (Nelson, 1976; Schreiber & Clapp, 1987; Schreiber & Burguer, 2001). Schreiber & Burguer (2001) even stated that frigatebirds often use their hooked bills to pin fish between both jaws until they can flip around and swallow them.

Boobies may also size prey in the air, but they mainly do so by plunge diving and underwater pursuit (Nelson, 1978; Schreiber & Clapp, 1987). Besides having a long *Rostrum* that tapers to a point, *S. leucogaster* also has a dorsoventrally flattened cranium. These features together may help reduce water resistance when the bird plunge-dives, or swims underwater for fish. A flat-streamlined skull has been correlated with active underwater pursuit of fish in cormorants, for example (Owre, 1967; Burger, 1978).

In the two studied species, the *Facies ventralis rostri maxillae* is ossified and both the *Margines tomiales maxillae et mandibulae* run straight long most of their lengths; furthermore, the *Pars intermedia mandibulae* is mediolaterally wide. In New Caledonian Crow *Corvus moneduloides* (Corvidae), the straight *Tomia* and wide *Ramus mandibullae* are among the structural characters that provide precise yet strong grip for holding tools in the bill (Matsui *et al.,* 2016). Thus the *Rostrum* in both *F. magnificens* and *S. leucogaster* seems adapted for holding prey firmly while it is being swallowed.

The bill (*Rostrum*) is rostrocaudally elongated in both *F. magnificens* and *S. eucogaster,* such that it is on average 70% of the whole skull length in the former and 60% in the latter. Longer bills allow rapid movements of the bill tip, thus facilitating the seizing of fast-moving prey (Ashmole, 1968). The possession of longer bills in the two studied species also means that their *Musculi mandibulae* are more posteriorly positioned in relation to the *Apex rostri.* Such a posterior position of the *Mm. mandibulae* results in low mechanical advantage for the mandible opening-closing lever, indicating adaptations for fast, rather than strong, bite (Zusi, 1962; Burger, 1978). In cormorants, which also have the *Mm. mandibulae* more posteriorly placed relative to the bill tip, the long, fast-moving mandibles have been considered to be advantageous for 'mandibulating' prey (Owre, 1967; Burger, 1978). In contrast, birds with proportionally shorter bills, such as Collared

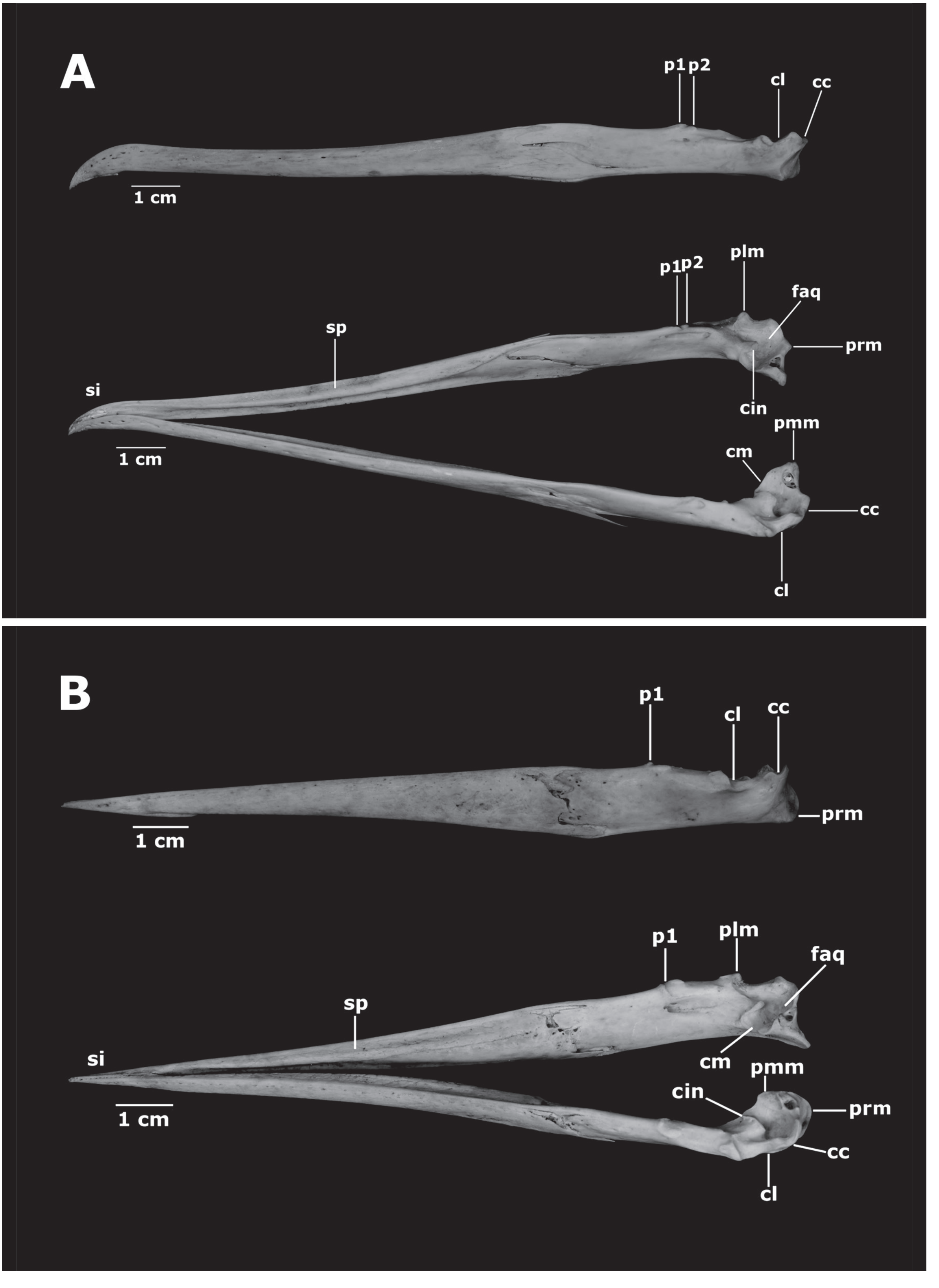

FIGURE 3: Lateral and dorsolateral views of the mandible (*Mandibula*) of Magnificent Frigatebird *Fregata magnificens* (**A**) and Brown Booby *Sula leucogaster* (**B**). *Pars symphisialis* (*rostrum mandibulae*) (**si**), *Sulcus paratomialis mandibulae* (**sp**), *Processus pseudocoronoidei mandibulae* (**p1, p2**), *Cotyla lateralis fossae articularis quadratica* (**cl**), *Cotyla caudalis fossae articularis quadratica* (**cc**), *Processus retroarticularis partis caudalis mandibulae* (**prm**), *Processus lateralis partis caudalis mandibulae* (**plm**), *Fossa articularis quadratica* (**faq**), *Cotyla medialis fossae articularis quadratica* (**cm**), *Crista intercotylare* (**cin**), *Processus medialis partis caudalis mandibulae* (**pmm**).

Forest-Falcon *Micrastur semitorquatus* (Falconidae) and Rufous-browed Peppershrike *Cyclarhis gujanensis* (Vireonidae), have a strong bite for tearing flesh (Silva, *et al.* 2012; Previatto & Posso, 2015a, b).

Longer bills, unless they have stronger muscles, are proportionally weaker; therefore, less efficient for 'mandibulating' a struggling prey fish (Ashmole, 1968). In birds, depression of the *Mandibula* is mainly performed by the *M. depressor mandibulae,* whereas elevation is primarily accomplished by the *Mm. adductor mandibulae externus* (*Partes rostralis et ventralis*), *pterygoideus et pseudotemporalis profundus;* the last two named simultaneously assist in retracting the *Maxilla* (Vanden Berge & Zweers, 1993). The relative development of these muscle complexes has been often correlated with the area available for their attachment (Bock, 1964; Owre, 1967; Burger, 1978; Donatelli, 1996; Silva *et al.,* 2012; Previatto & Posso, 2015a).

In the studied species, the *Regio temporalis* and the *Palatum osseum* respectively provide broad surface areas for *Mm. adductor mandibulae externum* (*partes rostralis et ventralis*) *et pterygoideus.* The more extensive *Fossa musculorum temporalium* and the higher *Crista laminae externae* in *S. leucogaster,* proportionally, provide more area for attachment of the *M. adductor mandibulae externus* (*partes rostralis et ventralis;* Vanden Berge & Zweers, 1993). The *Procc. pseudocoronoidei mandibulae,* which serves as the insertion for the *Pars rostralis Mm. adductor mandibulae externus* (Vanden Berge & Zweers, 1993), is more robust in *S. leucogaster* than in *F. magnificens.* More surface area is also proportionally available for the *M. pterygoideus* in *S. leucogaster* than in *F. magnificens.* This muscle originates mainly on the *Lamella ventralis partis choanalis palatinae* and on *Fossa ventralis et Anguli rostrolateralis et caudolateralis partis lateralis palatinae* (Vanden Berge & Zweers, 1993; Livezey & Zusi, 2006a). Furthermore, in Sulidae, among other taxa, the *M. pterygoideus* spreads rostrad onto the *Proc. rostralis palatini* and the *Os maxillare* (Burton, 1984; Livezey & Zusi, 2006a). It also should be noted that in *F. magnificens,* the *Proc. orbitalis quadrati* is longer and thicker, and so is the *M. pseudotemporalis profundus* (Vanden Berge & Zweers, 1993). The differences notwithstanding, we infer that the *Mm. adductores mandibulae* in both *F. magnificens* and *S. leucogaster* are well developed, and propose that, despite the low mechanical advantage, their *Mandibulae* are still probably capable of a relatively powerful bite.

The *M. depressor mandibulae* also play a role in elevating the *Maxilla.* It originates on the *Fossa subtemporalis* and inserts into *Fossa caudalis et Proc. retroarticularis mandibularum* (Zusi, 1967; Vanden Berge & Zweers, 1993). The relative development of this muscle is correlated with the size and shape of the *Proc. retroarticularis;* however, elongation of the process alone does not necessarily imply that the *Mandibula* is depressed more powerfully (Bock, 1964). Rather, an enlarged *M. depressor mandibulae* will assist in elevating the *Maxilla* (Bock, 1964; Zusi, 1967). The *Proc. retroarticularis* is almost absent and the *Fossa subtemporalis* is shallow in both *F. magnificens* and *S. leucogaster;* therefore, we suggest that in these birds, elevation of the *Maxilla* mandible is mostly accomplished by *Mm. protractor pterigoidei et quadrati* and *M. pterygoideus* (Zusi, 1967).

In *F. magnificens,* the *Zona flexoria craniofacialis* is only slightly distinguishable in dorsal view, whereas in *S. leucogaster,* it has a 'hinge-like' structure, which is morphologically similar to those of cormorants (Shufeldt, 1902; Owre, 1967; Burger, 1978). The differences on the conformation of the *Zona flexoria craniofacialis* between the two studied species suggest the extent of elevation and retraction of the *Maxilla* is greater in *S. leucogaster* than in *F. magnificens.* The amplitude of protraction of the *Maxilla* in cormorants has been estimated to be relatively large, varying from 36 to 47 degrees (Burger, 1978); no similar information is available on frigatebirds. Cormorants and boobies generally size fish sideways in their jaws and then turn to swallow. The wide bill gaping allows cormorants, and probably boobies as well, to catch and swallow large prey whole (Burger, 1978; Schreiber & Burguer, 2001).

As already mentioned, the *M. pterygoideus* is also involved in the retraction of the *Maxilla* (Bock, 1964; Zusi, 1967). Burger (1978) estimated that a third of the 'biting force' (*i.e.,* adduction of the *Mandibula* and retraction of the *Maxilla*) in cormorants is exerted by this muscle alone. He also noted that a large *M. pterygoideus* is a reflection of how important cranial kinesis is for cormorants. Zusi (1967) pointed out that the widespread functions of cranial kinesis in birds are the maintenance of the primary axis of orientation of the bill and shock absorbing, the former because many birds rely on rapid grasping of tiny food items or of fast-moving prey and the latter because of the light structure of *Mandibula et Maxilla* and the *Palatum osseum.* In the studied species, two further mechanisms may contribute, in combination with cranial kinesis, to protect the *Mandibula* and *Maxilla* from disarticulation and damage; namely, the locking arrangement of the *Articulatio quadratomandibularis* (Bock, 1960, 1964) and the notch for the *Os lacrimale* on the *Margo caudalis processus premaxillaries ossium* *nasalium* (Cracraft, 1968), the latter present only in *S. leucogaster.*

The first mechanism of protection involves the incorporation of the 'flange-like' structure on the *Margo medialis cotylae medialis fossae articularis quadratica* that grips the *Condylus medialis ossis quadrati.* This 'locking device' provides, to some extent, protection against disarticulation of the mandible when it is depressed or elevated (Bock, 1960, 1964). This arrangement of the *Artic. quadratomandibularis* seems particularly important in species wherein rapid jaw movements are essential to prey capture.

The second mechanism serves as a stop to prevent the possible excessive retraction of the *Maxilla.* Bock (1964) considered that depression of the *Maxilla* beyond its normal position seems not possible because the *Mandibula* itself acts as a retractor stop (Bock, 1964; Zusi, 1967). Nevertheless, when birds forage, for example, their jaw apparatus is susceptible to a variety of forces other than that from the *Pars retractor musculi pterygoidei,* and such forces may cause abnormal retraction of the *Maxilla.* Thus, Cracraft (1968) hypothesized that the action of 'outside forces' has resulted in the evolution of other retractor stops to prevent breakage of *Zona flexoria craniofacialis* and disruption of the *Articulationes pterygo-palatina et quadratomandibularis.*

The retractor stop notch for the *Caput ossis lacrimalis* seems particularly important for *S. leucogaster,* which feeds singly or in flocks by plunging from heights of 10 to 15 m to depths of 1.5 to 2 m (Nelson, 1978; Clapp *et al.,* 1982). Boobies are at risk of accidentally colliding with, or being struck by, conspecifics when diving and swimming underwater for fish and squid. Machovsky Capuska *et al.* (2011) found evidence of collisions between conspecifics in plunge-diving Cape *Morus capensis* and Australasian Gannets *M. serrator* and between them and marine mammals and predatory fishes, but not of damaged bills. This suggests the relevance of retractor stop mechanisms in protecting the jaw apparatus against sudden external forces.

In summary, from our analysis of the osteology of the jaw apparatus in *F. magnificens* and *S. leucogaster,* we assumed that these birds are capable of rapid yet strong jaw movements. This is a particularly relevant conclusion, given that both species capture active, fast moving prey (*e.g.,* Clapp *et al.,* 1982; Schreiber & Clapp, 1987). We based our suggestions about dimensions and strength of muscles on the skeletal surface available for their attachment. Nevertheless, the feeding action of the jaws is also affected by the points and angles of insertion and origins of muscles, as well as the type of muscle fibres (Bock, 1964; Burger, 1978; Donatelli *et al.,* 2014; Previatto & Posso, 2015b). Thus, a more detailed hypothesis for the jaw movements and strength in *F. magnificens* and *S. leucogaster* and their relation with feeding habits should necessarily incorporate data on the jaw (*i.e.,* all parts of the *M. adductor mandibulae externus* and *Mm. pseudotemporalis, pterygoideus et depressor mandibulae*) and anterior neck musculatures (Owre, 1967; Burger, 1978).

RESUMO

Neste trabalho, descrevemos o crânio do tesourão, Fregata magnificens *(Fregatidae), e do atobá-pardo,* Sula leucogaster *(Sulidae), com ênfase nas estruturas associadas com os movimentos de abdução e adução da* Maxilla *e* Mandibula. *Tesourões e atobás são aves marinhas tropicais; que, de forma geral, consomem peixes-voadores e lulas. Os tesourões capturam suas presas em pleno voo, logo acima ou abaixo da superfície da água. Dessa forma, em* F. magnificens, *o* Apex maxillae *em formato de anzol pode ser considerado como uma adaptação para recolher presas próximas da superfície. Os atobás mergulham verticalmente, ou nadam sob a superfície para capturar suas presas. Em* S. leucogaster, *o crânio achatado dorso-ventralmente e o bico em formato cônico muito provavelmente contribuem para a redução da resistência da água quando a ave mergulha e/ou persegue suas presas. Em ambas as espécies, o Rostrum é longo se comparado ao comprimento do sincrânio (em média, 70% do comprimento total do sincrânio em* F. magnificens *e 60% e* S. leucogaster*); portanto, os* Musculi mandibulae *estão posicionados mais posteriormente em relação ao Apex rostri. Isso resulta em uma baixa vantagem mecânica do mecanismo de alavanca que promove a abertura e fechamento do bico; assim, provavelmente a velocidade do movimento é favorecida. Nas duas espécies, a* Fossa musculorum temporalium *e o* Palatum osseum *compreendem uma área ampla para a origem do* Musculus adductor mandibulae externus *(todas as partes) e do* M. pterygoideus. *O* Processus orbitalis quadrati *é mais longo e robusto em* F. magnificens *do que em* S. leucogaster; *e, sendo assim, o* Musculus pseudotemporalis profundus *provavelmente é mais desenvolvido naquela espécie. Sugerimos que os* Mm. adductores mandibulae *são bem desenvolvidos nas duas espécies; e, com isso, a* Maxilla *e a* Mandibula *também são capazes de uma adução forte. Em tesourões e atobás, há um mecanismos que contribue para a proteção da* Mandibula *e da* Maxilla *contra desarticulação e danos: a presença da* Crista intercotylare *na* Margo medialis cotylae media-

lis fossae articularis quadratica, *que fixa o* Condylus medialis ossis quadrati. *Em* S. leucogaster, *o entalhe na* Margo caudalis processus maxillaries ossium nasalium, *onde o* Caput ossis lacrimalis *se encaixa protege a* Maxilla *e a* Mandibula *contra a ação de forças externas quando a ave mergulha ou persegue suas presas. Hipóteses mais detalhadas sobre movimentos, força e rapidez das mandíbulas em* F. magnificens *e* S. leucogaster *e a relação dessas características com os hábitos alimentares desses animais devem, necessariamente, incluir dados sobre a musculatura mandibular e da região anterior do pescoço.*

Palavras-Chave: Anatomia funcional; Aparato mandibular; Aves marinhas; Musculatura da mandíbula; Sincrânio.

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