



**UNIVERSIDADE DE BRASÍLIA**

**FACULDADE DE AGRONOMIA E MEDICINA VETERINÁRIA**

**PROGRAMA DE PÓS-GRADUAÇÃO EM SAÚDE ANIMAL**

**ANATOMIA COMPARADA, FORÇA DE MORDIDA E  
CORRELAÇÕES FUNCIONAIS DOS MÚSCULOS  
MASTIGATÓRIOS DE PSITACÍDEOS**

**ANA CAROLINA LOURENÇO FAILLACE**

**TESE DE DOUTORADO EM SAÚDE ANIMAL**

**BRASÍLIA/DF**

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**TESE DE DOUTORADO SUBMETIDA AO PROGRAMA DE PÓS-GRADUAÇÃO EM SAÚDE ANIMAL COMO PARTE DOS REQUISITOS NECESSÁRIOS À OBTENÇÃO DO GRAU DE DOUTOR EM SAÚDE ANIMAL.**

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*“O mundo não está em seus livros e mapas. Ele está lá fora”*

*- O Hobbit: Uma Jornada Inesperada.*

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## RESUMO

O grupo dos psitacídeos é composto em sua maioria por aves de plumagem colorida, altas habilidades cognitivas e um bico forte e curvo, sendo este a principal ferramenta utilizada pela ave para interagir com o seu ambiente. Dentre seus principais usos estão a coleta e processamento de itens alimentares, interações sociais, defesa, nidificação, escalada e mobilidade. Assim, o aparelho mastigatório é um sistema relevante para análises de correlações funcionais entre forma e ecologia. Muitas das espécies que integram este diverso grupo consomem castanhas e sementes, além de outras partes de plantas como frutos, flores e néctar. Por muito tempo especulou-se que a forte mordida dos psitacídeos estaria relacionada com o grande consumo de alimentos duros, porém poucos estudos tentam elucidar esta hipótese. Ainda, estas aves apresentam dois músculos mastigatórios únicos deste grupo – o m. etmomandibular e o m. pseudomasseter. Porém, o pseudomasseter apresenta diferentes graus de desenvolvimento dependendo da espécie e até da idade do indivíduo, podendo estar em sua forma bem desenvolvida, parcialmente desenvolvida e completamente ausente. Tal inconsistência também é especulado que seja por alguma relação à alimentação destas aves, mas novamente com escassos dados empíricos presentes na literatura. Por fim, uma das formas de se estimar a força de mordida de uma espécie utilizando dados anatômicos é pela análise da área transversal fisiológica (PCSA) dos músculos mastigatórios, e então calcular a força de mordida com modelos biomecânicos considerando o crânio como um sistema de alavancas. Entretanto, o crânio dos psitacídeos é altamente cinético, sendo que o modelo normalmente usado para aves disponível na literatura não leva este fator em consideração. Dessa forma, utilizando 27 espécies de diferentes pesos corporais e dietas, objetivou-se: a) descrever e comparar a anatomia dos músculos da mastigação das espécies, b) analisar a arquitetura muscular e correlacionar com a principal dieta de cada espécie, c) estimar a força de mordida através de modelos anatômicos de biomecânica, d) apresentar um novo modelo para estimar a força de mordida em psitacídeos. Confirmou-se que realmente há uma variação não só do m. pseudomasseter como na composição do arco suborbital nas espécies estudadas. Concluiu-se que: a) a massa muscular e o PCSA teve correlação positiva com o peso corporal, b) não houve correlação entre força de mordida e dieta, porém, foi encontrado um maior comprimento das fibras musculares dos músculos depressores de mandíbula e protractor do pterigóide e quadrado (que auxiliam na abertura de bico) em nectívoros e espécies que consomem muitos frutos, reforçando que estas espécies apresentam maior ângulo de abertura de boca, c) o modelo biomecânico apresentado que considera a maior cinética craniana dos psitacídeos estimou maiores valores de força de mordida do que o modelo convencional, porém não foi possível realizar sua validação devido a falta de dados *in vivo* de força de mordida para as espécies estudadas.

**Palavras-chave:** Anatomia funcional, aparelho mastigatório, dieta, psitacídeos.

## ABSTRACT

Psittaciformes (henceforth, parrots) is largely composed of birds with colorful plumage, high cognitive abilities, and a strong, curved beak, which serves as the primary tool these birds use to interact with their environment. Some of its main functions are collecting and processing food items, social interactions, defense, nesting, climbing, and mobility. As such, the masticatory apparatus is a relevant system for analyzing functional correlations between morphology and ecology. Many of the species within this diverse group consume nuts and seeds, as well as other plant parts such as fruits, flowers, and nectar. For a long time, it has been speculated that the strong bite force of parrots is related to their consumption of hard food items; however, few studies have attempted to elucidate this hypothesis. Furthermore, these birds exhibit two masticatory muscles unique to this group – the *m. ethmomandibularis* and the *m. pseudomasseter*. The *pseudomasseter*, however, shows varying development degrees depending on the species and even the age of the individual. It may be well developed, partially developed, or entirely absent. This inconsistency is also speculated to be linked to dietary habits, but again, empirical data in the literature are scarce. One way to estimate the bite force of a species using anatomical data is through analysis of the physiological cross-sectional area (PCSA) of the masticatory muscles, and subsequently calculating bite force using biomechanical models that consider the skull as a lever system. However, the skull of parrots is highly kinetic, and the available model in literature commonly used for birds does not take this factor into account. Thus, using 27 species with varying body weights and diets, the aims of this study were to: a) describe and compare the anatomy of the masticatory muscles across species, b) analyze muscle architecture and correlate it with the primary diet of each species, c) estimate bite force through anatomical biomechanical models, and d) present a new model to estimate bite force in parrots. It was confirmed that there is indeed variation not only in the *m. pseudomasseter* but also in the composition of the suborbital arch among the species studied. It was concluded that: a) muscle mass and PCSA show positive allometry with body mass, b) no correlation was found between bite force and diet; however, longer muscle fiber lengths were observed in mandible depressors and protractor muscles (which assist in beak opening) for nectivorous and high fruit-consuming species, supporting that these species exhibit greater gape, c) the biomechanical model presented, which accounts for the increased cranial kinesis in parrots, estimated higher bite force values than the conventional model, although validation was not possible due to the lack of *in vivo* bite force data for the studied species.

**Keywords:** Diet, functional anatomy, masticatory apparatus, psittaciformes.

## LISTA DE ABREVIACÕES

- AMEP – Músculo adutor da mandíbula, parte profunda; *m. adductor mandibulae externos, pars profunda*
- AMER – Músculo adutor da mandíbula, parte rostral; *m. adductor mandibulae externos, pars rostralis*
- AMEV – Músculo adutor da mandíbula, parte ventral; *m. adductor mandibulae externos, pars ventralis*
- AMEVPM – Músculos adutor da mandíbula, parte ventral e pseudomasseter; *mm. adductor mandibulae externos, pars ventralis et pseudomasseter*
- AMP – Músculo adutor da mandíbula posterior; *m. adductor mandibulae posterior*
- BF – Força de mordida
- EM – Músculo etmomandibular; *m. ethmomandibularis*
- FL – Comprimento do fascículo
- MF – Força muscular
- PCSA – Área transversal fisiológica
- PD – Músculo pterigoide dorsal; *m. pterigoideus dorsalis*
- PDL – Músculo pterigoide dorsal, parte lateral; *m. pterigoideus dorsalis, pars lateralis*
- PDM – Músculo pterigoide dorsal, parte medial; *m. pterigoideus dorsalis, pars medialis*
- PM – Músculo pseudomasseter; *m. pseudomasseter*
- PPQ – Músculo protractor do pterigoide e quadrado; *m. protractor pterygoideus et quadrati*
- PSS – Músculo pseudotemporal superficial; *m. pseudotemporalis superficialis*
- PV – Músculo pterigoide ventral; *m. pterigoideus ventralis*
- PVL – Músculo pterigoide ventral, parte lateral; *m. pterigoideus ventralis, pars lateralis*
- PVM – Músculo pterigoide ventral, parte medial; *m. pterigoideus ventralis, pars medialis*

# CAPÍTULO I

## 1. Introdução

Atualmente, há mais de 400 espécies de psitacídeos espalhadas por todos os continentes, com exceção da Antártica (Hbw and Birdlife International, 2022; Tobias et al., 2022). Este grupo é comumente caracterizado por seu bico grande e forte, plumagens coloridas e altas habilidades cognitivas (Carril; Degrange; Tambussi, 2015; O'Neill et al., 2021). Há ainda grande diversidade em tamanho corporal dentro deste grupo, com a espécie de menor peso sendo do gênero *Micropsitta*, com 12g, a maior espécie voadora é a Arara-azul (*Anadorhynchus hyacinthinusi*), com 1300g, e o Cácapo (*Strigops habroptilus*) sendo o maior psitacídeo não voador, com alguns indivíduos chegando a 3000g (Eason et al., 2006; Bird et al., 2020). Apesar dessas aves estarem presentes em diversos *habitats*, a maioria das espécies estão relacionadas com ambientes florestais (arborizado), onde encontram seus principais alimentos (Benavidez et al., 2018).

Psitacídeos são comumente descritos como tendo hábitos alimentares generalistas, ou seja, consomem diversos itens alimentares ao longo das estações (Matuzak; Bezy; Brightsmith, 2008; Renton et al., 2015; Voltura et al., 2024). A maioria das espécies têm frutas e sementes como seus principais alimentos, mas há exceções como os Lóris (Loriini), que consomem majoritariamente néctar e pólen e a Kea (*Nestor notabilis*), que consome vertebrados e até carcaças (Moermond; Denslow, 1985; Schwing, 2010; Lee et al., 2014). O Cácapo é o único exemplar de papagaio herbívoro, consumindo folhas, brotos e caules (Powlesland, 2006).

Alimentar-se é um comportamento fundamental para a manutenção da vida (Corbin; Lowenberger; Gray, 2015). Dessa forma, o aparelho mastigatório precisa ser adaptado para acessar os principais itens da dieta daquela espécie, tornando ele um ótimo elemento para estudos de adaptação e funcionalidade ecológica da interação indivíduo-ambiente (Hartstone-Rose et al., 2021). Entendimento anatômico da musculatura associada à mastigação, bem como de biomecânica e de força são fundamentais para se explorar possíveis correlações entre morfologia e ecologia (Deutsch et al., 2020).

A musculatura mastigatória dos psitacídeos possui algumas particularidades frente às outras aves, como a presença dos músculos pseudomasseter e etmomandibular, únicos deste grupo, a ausência do músculo pseudotemporal profundo e a presença de um ventre

externo da parte lateral do músculo pterigoide ventral, descrita em apenas dois gêneros de papagaios (Hofer, 1950; Burton, 1974; Tokita, 2004). O músculo pseudomasseter (PM) apresenta uma grande variação morfológica entre diferentes espécies de papagaios e entre indivíduos da mesma espécie, podendo ser desde um ventre muscular bem definido até poucas fibras musculares associados à fáscia (Hofer, 1953). Esta inconsistência continua sendo alvo de investigações, sendo proposto possíveis associações à dieta dos psitacídeos (Tokita, 2004; Carril; Degrange; Tambussi, 2015). Observa-se também variações em algumas regiões de inserção muscular como o próprio arco suborbital, local de origem do PM, podendo se apresentar desde um ligamento, totalmente ossificado ou com extensa ossificação e fusão com o processo zigomático (Berlioz, 1941; Smith, 1975). Dessa forma, este sistema muscular ainda carece de maiores investigações.

Os nove músculos dos psitacídeos associados com o movimento de bico podem ser categorizados funcionalmente em adutores de mandíbula, depressores de mandíbula, protrator de quadrado (causa elevação da maxila) e depressores de maxila (Hofer, 1950; Faillace et al., 2025). A mordida dos psitacíformes exige movimento tanto da mandíbula como da maxila, sendo este último agindo como uma bigorna para firmar o alimento no bico (Dickinson; Young; Granatosky, 2022). Apesar dos psitacídeos serem comumente associados com altas forças de mordida, são poucos os estudos que estimam ou que oferecem valores *in vivo* de mordida desses animais. Dessa forma, dados empíricos são relativamente escassos, e correlações de força de mordida com hábitos alimentares são limitadas (Carril; Degrange; Tambussi, 2015).

Existem várias técnicas para se calcular força de mordida – coletas *in vivo*, com uso de transdutores de força, através de técnicas anatômicas e modelos de biomecânica, utilizando cadáveres ou crânios, e com reconstruções através de modelos computacionais (Curtis et al., 2010; Lappin; Jones, 2014; Ginot et al., 2019). Cada técnica apresenta vantagens e desvantagens, porém a mais comumente acessível é a estimativa da força de mordida com modelos biomecânicos associados à dados da fisiologia muscular (a chamada área transversal fisiológica – PCSA). Esta metodologia foi utilizada em algumas espécies de psitacídeos (Carril; Degrange; Tambussi, 2015; Harrison et al., 2024), mas o modelo biomecânico utilizado nestes estudos não considerava a contribuição do movimento da maxila na mordida destas aves.

Este estudo objetivou descrever a topografia dos músculos mastigatórios de 27 espécies de psitacídeos, sendo 13 espécies de ocorrência no Brasil, um país com

importante *hotspot* de biodiversidade. Ainda, visou-se estimar a força de mordida destes indivíduos, investigar possíveis correlações entre a dieta específica e as características da arquitetura muscular com a força total gerada pela mordida destas espécies e apresentar um modelo anatômico que considera o movimento da maxila como componente relevante para estimar a força de mordida em psitacídeos.

## 2. Revisão de literatura

### 2.1. Ecologia dos psitacídeos

Os psitacídeos são classificados em cinco famílias principais: Strigopidae (endêmicos da Nova Zelândia), Cacatuidae (cacatuas e similares), Psittacidae (da África e sul da Australásia), Psittaculidea (sul e sudeste Asiático) e Psittichasidae (principalmente Nova Guiné e Madagascar) (Smith; Thom; Joseph, 2024). Apesar dessa divisão filogenética e geográfica, os psitacídeos, no geral, são extremamente adaptáveis ao seu ambiente e, aliado a uma dieta igualmente plástica, se acomodam rapidamente há novos habitats, tendo grande sucesso como espécies invasoras (Mori; Menchetti, 2021).

De forma geral, podemos classificar os psitacídeos como generalistas, ou seja, não apresentam restrições alimentares (Voltura et al., 2024). Poucas são as espécies relatadas que possuem predileção para itens específicos – o Maracanã-do-buriti (*Orthopsittaca manilatus*) percorre extensas áreas procurando pela fruta do Buriti (*Mauritia*; *Mauritiella*); o Cácapo é exclusivamente herbívoro e se alimenta de folhas (*Leptospermum*, *Lepidothamnus*) o *Micropsitta* é o único gênero de papagaio registrada a consumir fungos, provavelmente devido ao seu diminuto peso corporal (Eason et al., 2006; Powlesland, 2006; De Faria; Abreu; Bianchi, 2007).

A maioria dos psitacídeos neotropicais se alimentam principalmente de plantas nativas e suas partes, porém espécies urbanizadas ou próximas a plantações consomem frutos e sementes exóticas, além de grãos e cereais provenientes de colheitas (Benavidez et al., 2018; Marques et al., 2018; Voltura et al., 2024). Esta grande gama de itens alimentares permite que os psitacídeos adaptem sua dieta dependendo da estação do ano, ajustando o consumo de frutas em diferentes estágios de desenvolvimento (verdes ou maduras) e quantidade de sementes ou castanhas (Galetti, 1997; Matuzak; Bezy; Brightsmith, 2008). Por fim, em algumas regiões com solo pobre em nutrientes, como na

floresta amazônica, diversas espécies consomem barro presente em grandes paredões naturais para suplementar a carência de certos minerais (Lee et al., 2014).

O bico dos papagaios não é limitado apenas a aquisição de alimentos. Devido ao seu formato curvo distinto e a sua grande força de mordida, os psitacídeos são o único grupo de aves que utiliza o bico como um “terceiro membro” de apoio para se locomover (Young et al., 2023; Dickinson; Young; Granatosky, 2024). Essa função única do bico dos psitacídeos é presente em todas as famílias, e o excelente comportamento de escalada pode ser observado em quase todas as espécies de psitacídeos, o que é condizente com o comportamento de nidificar em troncos e forragear em árvores, consumindo frutos, cascas, sementes e flores.

## *2.2. Os músculos da mastigação*

Nos psitacídeos, devido ao alto grau de cinética craniana, a mastigação se dá principalmente pelo movimento de adução e abdução de mandíbula e maxila (Bock, 1964). Este grupo é considerado isognata, ou seja, morde principalmente com a ponta do bico, fazendo com que os grupos musculares de ambos os lados do crânio contribuam de forma proporcional à força de mordida (Carril; Degrange; Tambussi, 2015). Este grupo de aves apresenta, em média, 12 músculos associados com a movimentação de bico: os adutores externos de mandíbula (compostos por três partes distintas), o variável pseudomasseter, o etmomandibular (descrito apenas em psitacíformes), um pequeno adutor da mandíbula posterior, um único pseudotemporal (o profundo está ausente nestas aves), o protrator de pterigóide e quadrado e os maciços pterigóides (podem ser divididos em quatro partes) (Hofer, 1950) (Figura 1).

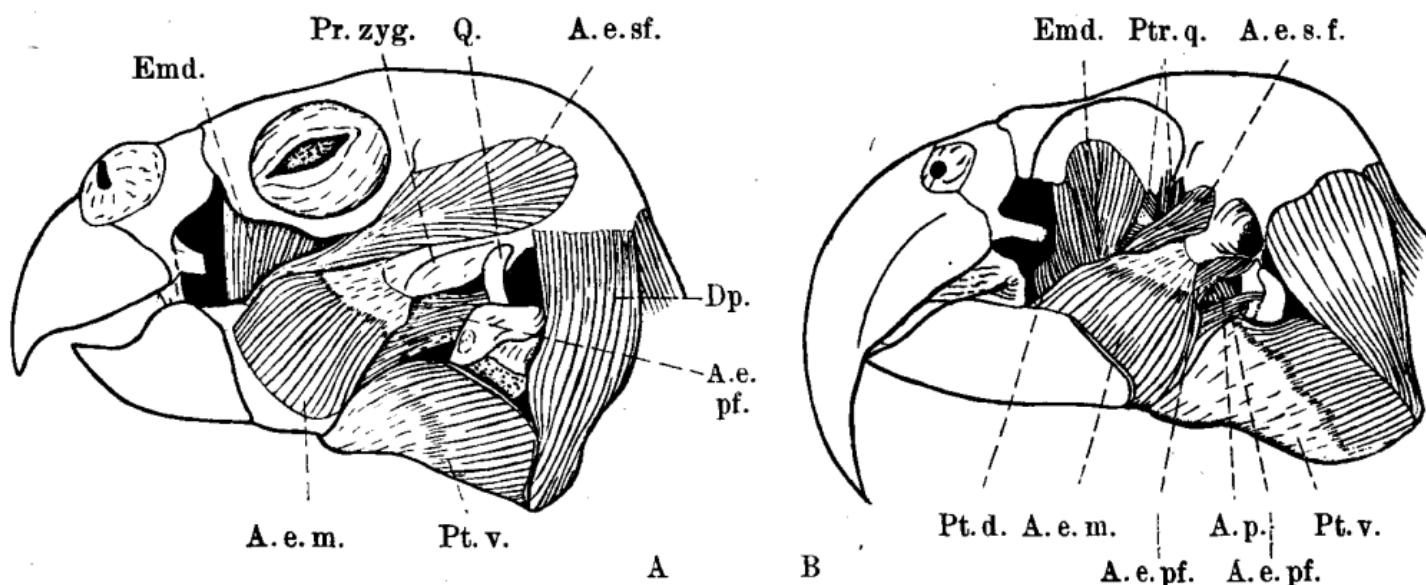


Figura 1 – Ilustração de Hofer (1950) do aparelho mastigatório de *Strigops habroptilus* (A) e *Nestor notabilis* (B). A.e.m. – adutor externo da mandíbula, parte ventral; A.e.pf. – adutor externo da mandíbula, parte profunda; A.e.sf. – adutor externo da mandíbula, parte rostral; A.p. – adutor da mandíbula posterior; Emd. Etmomandibular; Pt.v. – pterigóide ventral, parte lateral; Dp. – depressor da mandíbula, parte superficial; Ptr.q. – protrator do pterigóide e quadrado; Pr.zyg. – processo zigomático; Q. – quadrado.

Dessa forma, podemos categorizar estes músculos baseados no movimento gerado (Quadro 1).

QUADRO 1 - Grupos musculares da mastigação de psitacídeos e suas principais ações.

| Função principal                                       | Grupo muscular                                                                                                                                                                                                                                       |
|--------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Adução de mandíbula                                    | PM: <i>m. pseudomasseter</i><br>AME: <i>adductor mandibulae externus</i><br>AMP: <i>m. adductor mandibulae posterior</i><br>EM: <i>m. ethmomandibularis</i><br>PSS: <i>m. pseudotemporalis superficialis</i><br>PV: <i>m. pterigoideus ventralis</i> |
| Protração de quadrado e pterigoide (abdução de maxila) | PPQ: <i>m. protractor pterygoideus et quadrati</i>                                                                                                                                                                                                   |
| Depressor de maxila                                    | PV: <i>m. pterigoideus ventralis</i><br>PD: <i>m. pterigoideus dorsalis</i>                                                                                                                                                                          |

|                        |                                     |
|------------------------|-------------------------------------|
| Depressor de mandíbula | DMS: <i>m. depressor mandibulae</i> |
|------------------------|-------------------------------------|

Fonte: Faillace et al., 2025.

Muitos dos músculos adutores de mandíbula possuem outras funções, como por exemplo o AMP, que serve para estabilizar o osso quadrado, o PM em auxiliar no movimento lateral da mandíbula, enquanto os do grupo AME permitem um movimento de cisalhamento com a maxila (Hofer, 1950; Homberger, 2003). O complexo grupo dos pterigóides é o único que move a maxila ventralmente através da retração do osso palatino, porém o PV e uma parte do PD também geram, em menor grau, adução da mandíbula através de sua protração (Hofer, 1950; Bock, 1964; Bhattacharyya, 2013; Homberger, 2017).

### 2.3. Força de mordida e correlações funcionais

Os sarcômeros são as unidades funcionais dos músculos esqueléticos, e sua disposição sequencial formando fibras ao longo do ventre muscular permitem que o músculo contraia (encurtamento) e relaxe (estiramento). As fibras musculares, por sua vez, são agrupadas em fascículos, e dispostos de forma paralela ou penada (em ângulo) dependendo da função e especialização do músculo. Cada compartimentação possui seu próprio envoltório muscular composto de tecido conjuntivo: o endomísio reveste a fibra muscular, o perimísio recobre os fascículos e o epimísio reveste o ventre muscular em sua totalidade.

Para se estimar a força muscular, podemos utilizar a área transversal fisiológica (PCSA), uma estimativa de força baseada na relação entre a massa muscular (MM) sob o comprimento das fibras (FL), multiplicada pelo ângulo de penação ( $\theta$ ):

$$PCSA = \frac{MM}{FL \cdot \theta}$$

Os dois elementos fundamentais que ditam a força total que um músculo esquelético é capaz de gerar são o volume do músculo (associado a massa muscular) e o FL. Quanto maior o volume, maior a quantidade de sarcômeros e, conseqüentemente, de fascículos, permitindo mais força de contração. Fascículos dispostos em ângulo ao longo do ventre muscular serão mais curtos quando comparado com fascículos dispostos de forma paralela, mas em contrapartida, são mais numerosos (Figura 2). Dessa forma, músculos penados possuem maior força do que os com fibras dispostas em paralelo. Tanto a força máxima que um músculo pode exercer quando à velocidade de contração possuem limites

fisiológicos relacionado ao volume muscular e a quantidade e disposição de suas fibras. Dessa forma, temos um chamado *trade off*: músculos penados geram mais força, mas permitem uma amplitude e velocidade de movimento reduzido, enquanto os com fibras dispostas em paralelo geram menos força, mas conseguem uma amplitude maior e mais velocidade de encurtamento, gerando movimentos mais rápidos (Herrel; Van Wassenbergh; Aerts, 2012). Além disso, se um músculo esquelético for desproporcionalmente volumoso com o intuito de aumentar sua força máxima exercida, será danoso para o animal por consumir muita energia e nutrientes, além de ser mais pesado e correr o risco de causar lesões ósseas e articulares.

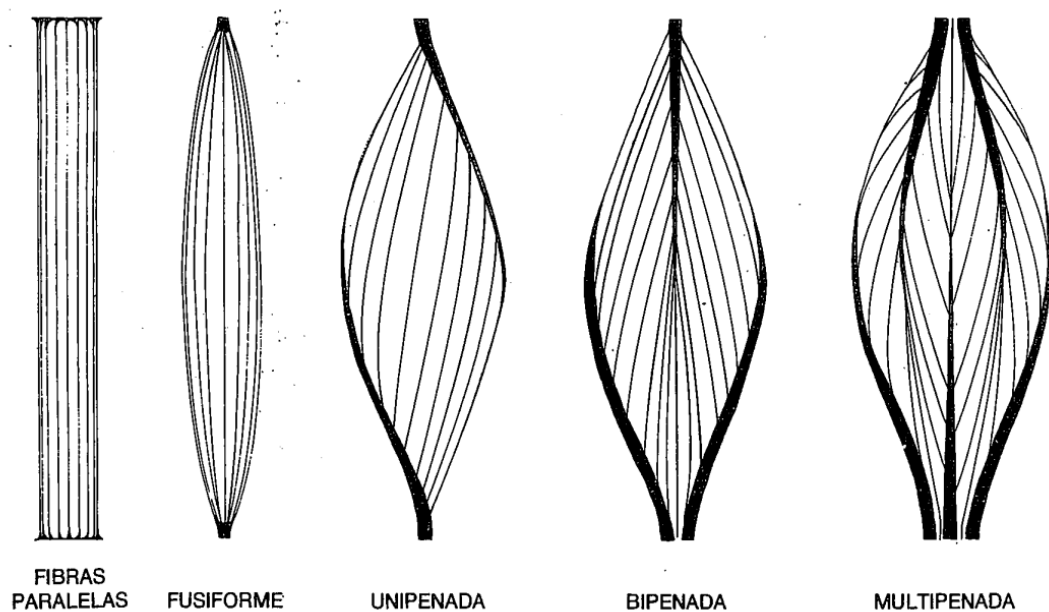


Figura 2 – Diferentes disposições de fibras nos ventres de músculos esqueléticos. Note a diferença de comprimento e quantidade entre os paralelos e fusiformes e os penados. Fonte: Getty; Sisson e Grossman (1986).

Estudos de força de mordida (BF) em aves já foram realizados para vários grupos, incluindo galoanseriformes e struthioniformes (Sakamoto; Ruta; Venditti, 2019; Carril et al., 2021), fringílideos, estrilídios e tentilhões de Darwin (Van Der Meij; Bout, 2004; Herrel et al., 2005), membros das famílias accipitridae e falconidae (Sustaita; Hertel, 2010), e psitacíformes (Carril; Degrange; Tambussi, 2015; Cost et al., 2020; Dickinson; Young; Granatosky, 2022; Harrison et al., 2024). Estes estudos foram feitos ou com coleta *in vivo* da BF das aves, ou através de estimativas anatômicas.

Em alguns grupos como fringílídeos e tentilhões (Fringillidae; Thraupidae) há forte correlação de BF com a dieta predominantemente de sementes destas espécies (Van Der Meij; Bout, 2004; Herrel et al., 2005). Tal correlação não ocorre com os psitacídeos por exemplo, que possuem alta BF e dietas ricas em alimentos duros (Bright et al., 2019), o que sugere que, pelo menos para as aves no geral, a dieta não é um bom preditor para BF (Felice et al., 2019; Navalón et al., 2019).

Outras características morfológicas podem ser exploradas para interações com BF, como massa muscular (MM) e massa corporal (BM). Nos fringílídeos e estrilídios, Van Der Meij e Bout (2004) encontraram uma alometria positiva (um aumento “desproporcional” entre uma variável e outra) entre a MM e BM destes grupos. Ao estudar 122 espécies de 14 ordens, Deeming; Harrison e Sutton (2022) encontraram alometria positiva da BF com BM em passeriformes, enquanto os não passeriformes exibiram isometria. Ainda, a MM dos passeriformes teve alometria positiva com BF, enquanto os não passeriformes mostraram um comportamento negativo entre estas variáveis. Um estudo comparando diversos grupos de aves identificou também um comportamento negativo entre MM e BM de anseriformes e struthioniformes, sendo positivo em passeriformes e psitacíformes, e isométrico em rapinantes diurnos (Harrison; Sutton; Deeming, 2022). Estas diferentes correlações reforçam a complexidade das interações ecológicas, comportamentais e filogenéticas na morfologia do aparelho mastigatório das aves.

#### 2.4. Cinética craniana e biomecânica da mastigação

A maioria das aves possuem um crânio procinético, ou seja, a maxila se movimenta relativa ao resto do crânio (Bout; Zweers, 2001). Diferente de alguns grupos de aves, os psitacídeos não possuem ligamentos (ex. ligamento pós orbital) que restringem ou associam estruturas de crânio, permitindo que a mandíbula e maxila realizem movimentos mecanicamente isoladas uma da outra (Bock, 1964). Psitacídeos, em particular, são capazes de abduzir a maxila em ângulos de aproximadamente 40°, tendo uma maior mobilidade frente a outros grupos de aves, que atingem de 5 a 15° em média (Young et al., 2023).

Apenas dois estudos de biomecânica de cinética craniana em aves utilizando modelos computacionais foram descritos para *Zonotrichia albicollis* (pardal de garganta branca) e *Columba livia* (pombo doméstico) e, apesar de terem boa sensibilidade para estimar os

movimentos reais das espécies respectivas, não estimam força de mordida (Van Gennip; Berkhoudt, 1992; Hoese; Westneat, 1996).

Ao estudar a força de mordida de rapinantes diurnos através de modelos anatômicos, Sustaita (2008) detalha as forças e alavancas do sistema mastigatório destas aves, mas acaba considerando apenas a mandíbula como elemento móvel, sendo a maxila estática. Posteriormente, Carril; Degrange e Tambussi (2015) empregam o mesmo modelo em psitacídeos, com as mesmas considerações cinéticas. Baseado na literatura levantada para esta pesquisa, nenhum estudo considera o movimento da maxila para estimativa anatômica de força de mordida nas aves.

### **Objetivos gerais**

Esta pesquisa objetivou descrever a anatomia topográfica dos músculos da mastigação das 27 espécies de psitacídeos, além de estimar a força total de mordida destes indivíduos através de modelos anatômicos de biomecânica, a fim de investigar correlações funcionais da morfologia muscular com fatores associados com dieta.

### **Objetivos específicos**

1. Comparar origem, inserção e forma dos diferentes músculos em cada espécie, a fim de identificar peculiaridades espécie-específicas;
2. Calcular valores musculares, como comprimento de fascículo, área transversal fisiológica e força muscular de cada músculo, além de estimar a força de mordida;
3. Testar dois novos modelos anatômicos de biomecânica para estimar força de mordida em psitacídeos e comparar com o modelo já descrito na literatura;
4. Correlacionar força de mordida e valores musculares com as características alimentares de cada espécie.

### Informações adicionais

1. O artigo apresentado no Capítulo II desta tese (Variation in parrot jaw musculature) foi publicado na forma *Open Access* na revista *The Anatomical Record* em 7 de abril, 2025 (<http://doi.org/10.1002/ar.25667>).
2. O artigo apresentado no Capítulo III desta tese (Bite force estimates and morphological correlations of jaw muscles in parrots) está formatado para posterior submissão à revista *The Anatomical Record*.

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## CAPÍTULO II

### Variation in parrot jaw musculature

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#### Abstract

Psittaciformes, the order which encompasses parrots and their relatives are highly diverse and well known for most of them having a strong and curved beak used for multiple behaviors. The muscles related to the masticatory apparatus should reflect this functional complexity, however, few studies have described the cranial myology across the order. Through original dissections, we describe and compare the masticatory musculoskeleton of 27 species – the most taxonomically diverse sample of psittaciformes to date. As in previous studies, we found osteological differences in the configuration of the suborbital arch, zygomatic process and temporal fossa, and while most muscles are relatively similar across the order, there are notable exceptions found in the morphology of the *m. pseudomasseter*, *m. adductor mandibulae externus, pars rostralis* and a *venter externus* portion of the *m. pterygoideus ventralis, pars lateralis* found in both of the *Platyercus* species that we dissected. Our findings reinforce the amazing anatomical diversity found within this group – data that can be incorporated into future studies of the biomechanics and diversification of this order. Further analysis should focus on a. filling in more of the remarkable number of species across the order, especially uncommon and functionally interesting taxa unavailable in the present study, b. examining dietary specialization to understand whether dietary adaptive signals are encoded within this anatomy and c. advancing to anatomical studies with other techniques such as DiceCT to visualize the relationship and biomechanics of these muscles in 3D space and be able to evaluate specimens relatively non-destructively, a priority for hard to dissect (e.g., small) taxa and (e.g., rare) specimens that collections wish to more fully preserve.

**Keywords:** Psittaciformes, masticatory myology, descriptive anatomy, comparative anatomy.

## 1. Introduction

Psittaciformes, the order that encompasses parrots, macaws, cockatoos, parakeets (simplified hereafter as “parrots”), are among the most diverse extant birds containing approximately 400 species worldwide (HBW and BirdLife International, 2022) grouped into four main families: Strigopoidae, Cacatuidae, Psittacidae and Psittaculidae (Gill et al., 2024). Generally recognized by their strong curved beak, parrots are mostly granivorous though their diets also often include nectar, fruit, and nuts, with some species consuming fungi, small vertebrates and carrion (Navalón et al., 2019). Many have a highly plastic diet and vary their food depending on environment and season (Benavidez et al., 2018).

Beyond its adaptation for diverse feeding abilities, the bird beak serves a wide range of non-masticatory behaviors such as preening, nest building, agonistic and antagonistic social interaction and defense (Corbin et al., 2015; Bright et al., 2019; Navalón et al., 2019; Dickinson et al., 2022). It is also in a form of tripedal locomotion has been the subject of recent work (Reader et al., 2022; Dickinson et al., 2024). The muscles that move the jaw apparatus should reflect this functional complexity. Although previous studies have provided anatomical information for some members of the Order, albeit with some limitations (Hofer, 1950, 1953; Dubale and Rawal, 1965; Carril et al., 2015; Homberger, 2017), building further on these historical samples and providing new visualizations of the anatomy of this group of birds will allow us to better understand their biomechanics.

To this end, we aim to describe the masticatory muscles of the broadest interspecific sample to date (including more than a dozen species that have not been previously described) of Psittaciformes, with focus on the surprisingly diverse masticatory morphologies present in the different lineages. Beyond the diverse interspecific sample, broadly spanning the Psittaciformes families found outside of New Zealand, our sample also includes a special subfocus on a range of neotropical species present in Brazil – hotspot for parrot diversity (Vergara-Tabares et al., 2020).

### 1.1 *The masticatory apparatus of Psittaciformes*

The cranial architecture of parrots is more complex than that of other neognaths due to their highly mobile nasofrontal hinge which allows for increased movement of the upper beak, their completely ossified suborbital arch found in some genera, as well as two novel masticatory muscles – the ethmomandibularis and pseudomasseter (Hofer, 1950, 1953; Smith, 1975; Tokita, 2003; Carril et al., 2015). These anatomical characteristics may relate to the exceptional diversity of Psittaciformes beak behavioral abilities and could potentially play a key role in phylogenetic, ecological, and behavioral studies of this order.

This is in large part because these features vary among the taxa within the Order. For example, in an examination of the masticatory muscles of nine species (mostly lacking

neotropical species), Hofer (1950) and both (Berlioz, 1941) and Smith (1975) found the pseudomasseter (PM) and the suborbital arch respectively to be of variable development. Others reported similar findings in other species, with PM being absent in *Ara*, *Diopsittaca*, *Aratinga*, *Orthopsittaca* and *Psittacus*, and present albeit underdeveloped in *Myopsitta* and *Agapornis* (Zusi, 1993; Porto, 2004; Tokita et al., 2007; Carril et al., 2015; Cost et al., 2022).

Similar differences have been reported for the suborbital arch (Smith, 1975; Zusi, 1993), an important attachment site for PM, which can be either a completely ossified ring or a short orbital process with a ligament. Other authors (Tokita, 2004; Carril et al., 2015) investigated a possible embryological relation to a complete suborbital arch and a well-developed PM, but concluded that they act independently and that the ancestral condition was an ossified ring and the presence of PM, with the derived conditions (incomplete ring and absent PM) arising independently many times throughout parrot evolution. Homberger (2003) provides some functional correlation between these structures, mainly related to force constraints of the skull.

The goal of this study is to provide a comprehensive description of the complex masticatory myology of parrots, offering new insights for previously undescribed species, and a detailed comparative, topographical and myological description of the jaw muscles, based on their origin and insertions, in broad samples of parrots.

## **2. Materials and Methods**

Our sample includes 27 species from the three largest of the four families within the Order, Cacatuidae, Psittaculidae and Psittacidae (Table 1). Unfortunately, we were not able to include any of the four Strigopoidae species as all of the member of this basal most Psittaciformes branch endemic to New Zealand are rare, endangered and not readily available for dissection. Our sample includes species commonly found as pets, endangered species (HBW and BirdLife International, 2022), and geographically dispersed species.

Most of the specimens were fresh, kept frozen until use, and others were fluid preserved specimens, formalin fixed and then stored in 70% ethanol (Table 1). All specimens were adults in good musculoskeletal condition. All fresh specimens were from either the Wild Animals Screening Center (CETAS-DF; Federal District, Brazil), donated from private veterinary clinics (VET - located in the city of Brasília, Federal District, Brazil), or provided by Hartstone-Rose Lab (AHR) at North Carolina State University (North Carolina, USA), obtained as byproducts of the pet trade or from sanctuaries. The wet specimens were from both The Smithsonian National Museum of Natural History (NMNH; Washington, USA), or the Ornithology Division of North Carolina Museum of Natural Science (NCMNS), North Carolina, USA. Because all deceased animals were sourced from either a museum, private practice, or research collection, this work was deemed exempt from ethical regulation by the governing bodies in both of the places where data were collected: the Animal Ethics Committee according to Brazilian (item

6.1.10/RN n° 30/2016 of DBCA) and North Carolina State University's Institutional Animal Care and Use Committee.

All anatomical nomenclature follows the Nomina Anatomica Avium (Baumel et al., 1993) and other cited literature. All figure diagrams were constructed using the free software Inkscape.

Table 1. List of specimens used in this research.

| Family        | Species                           | Identification number | Source | Preparation method |
|---------------|-----------------------------------|-----------------------|--------|--------------------|
| Cacatuidea    | <i>Cacatua moluccensis</i>        | 401010                | AHR    | Frozen             |
|               | <i>Nymphicus hollandicus</i>      | -                     | VET    | Frozen             |
| Psittaculidea | <i>Agapornis fischeri</i>         | TR 91/24              | CETAS  | Frozen             |
|               | <i>Platycercus elegans</i>        | 401012                | AHR    | Frozen             |
|               | <i>Platicercus eximius</i>        | 401013                | AHR    | Frozen             |
|               | <i>Melopsittacus undulatus</i>    | -                     | CETAS  | Frozen             |
|               | <i>Lorius garrulus</i>            | 505820                | NMNH   | Fluid              |
|               | <i>Neophema splendida</i>         | 401016                | AHR    | Frozen             |
|               | <i>Eclectus roratus</i>           | 542228                | NMNH   | Fluid              |
|               | <i>Vini australis</i>             | 319750                | NMNH   | Fluid              |
|               | <i>Trichoglossus haematodus</i>   | 616027                | NMNH   | Fluid              |
|               | <i>Psittacula cyanocephala</i>    | 401014                | AHR    | Frozen             |
| Psittacidea   | <i>Polytelis anthopeplus</i>      | 401017                | AHR    | Frozen             |
|               | <i>Ara ararauna</i>               | TR 1889               | CETAS  | Frozen             |
|               | <i>Ara rubrogenys</i>             | 401009                | AHR    | Frozen             |
|               | <i>Amazona aestiva</i>            | TR 195, TR 1359/2023  | CETAS  | Frozen             |
|               | <i>Alipiopsitta xanthops</i>      | -                     | CETAS  | Frozen             |
|               | <i>Aratinga solstitialis</i>      | 401015                | AHR    | Frozen             |
|               | <i>Aratinga auricapilus</i>       | -                     | CETAS  | Frozen             |
|               | <i>Brotogeris chiriri</i>         | TR 373                | CETAS  | Frozen             |
|               | <i>Diopsittaca nobilis</i>        | TR 43/23              | CETAS  | Frozen             |
|               | <i>Guaruba guarouba</i>           | -                     | CETAS  | Frozen             |
|               | <i>Psittacara leucophthalma</i>   | TR 524                | CETAS  | Frozen             |
|               | <i>Pionus menstruus</i>           | -                     | CETAS  | Frozen             |
|               | <i>Orthopsittaca manilatus</i>    | TR 59                 | CETAS  | Frozen             |
|               | <i>Phyrrhura molinae</i>          | 401011                | AHR    | Frozen             |
|               | <i>Rhynchopsitta pachyrhyncha</i> | 16198                 | NCMNS  | Fluid              |

## 2.1. Dissection

For each specimen, the skin was removed and the masticatory musculature exposed on one side. Then, each individual muscle was identified and photographed, with its origin and insertion recorded (Figs. 1, 2, 3). Each muscle was successively removed from the head to expose each successively deeper layer of musculature. To allow further access to deeper muscles, the jugal bone was cut at its quadratojugal joint and reflected rostrally. In species with an ossified suborbital arch, the structure was also clipped to allow visualization and removal of the internal adductor muscles.

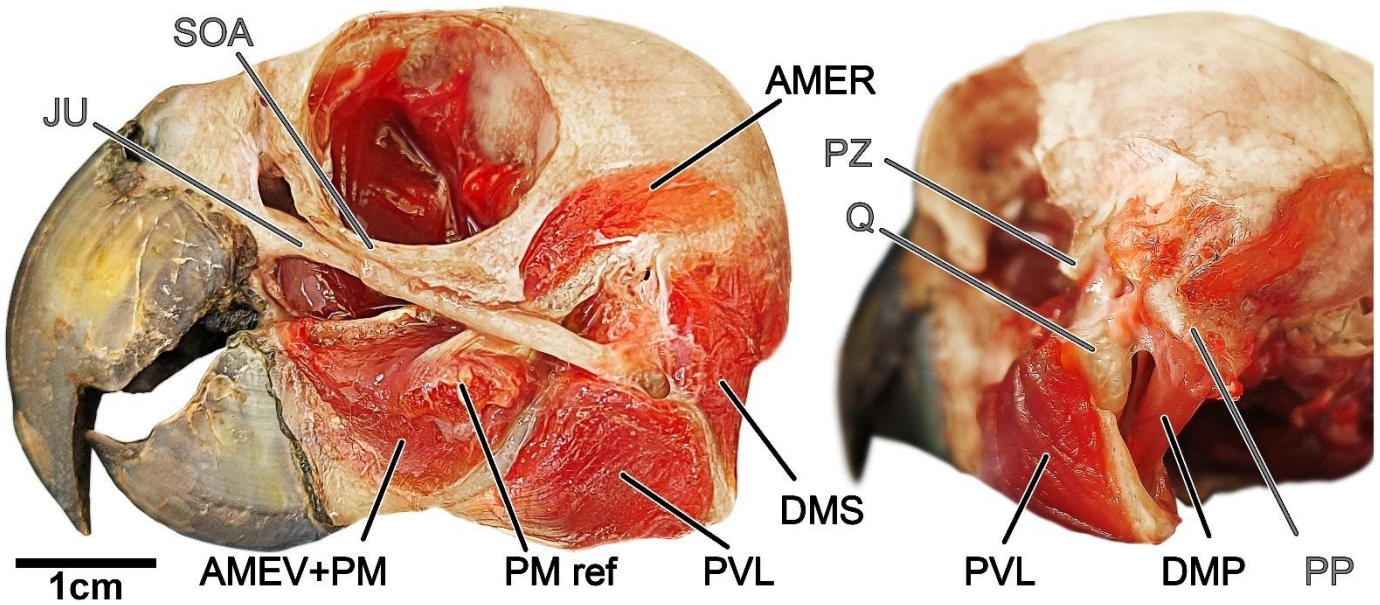


Figure 1. Dissection of *Amazona aestiva* in lateral (left) and caudolateral (right) view, demonstrating the general topography of the masticatory muscles found in psittacines. In B, the suborbital arch, jugal bone and zygomatic process were removed to visualize the deep musculature. JU: jugal bone; SOA: suborbital arch with a bony process extending caudoventrally; PZ: zygomatic process; Q: quadrate; PP: paraoccipital process. AMEV+PM: *mm. pseudomasseter et adductor mandibulae externus, pars ventralis*; PMref: *m. pseudomasseter* partially isolated from its attachment site and ventrally reflected; PVL: *m. pterigoideus ventralis, pars lateralis*; DMS: *m. depressor mandibulae, pars superficialis*; AMER: *m. adductor mandibulae externus, pars rostralis*; DMP: *m. depressor mandibulae, pars profunda*. Scale bar is 1 cm.

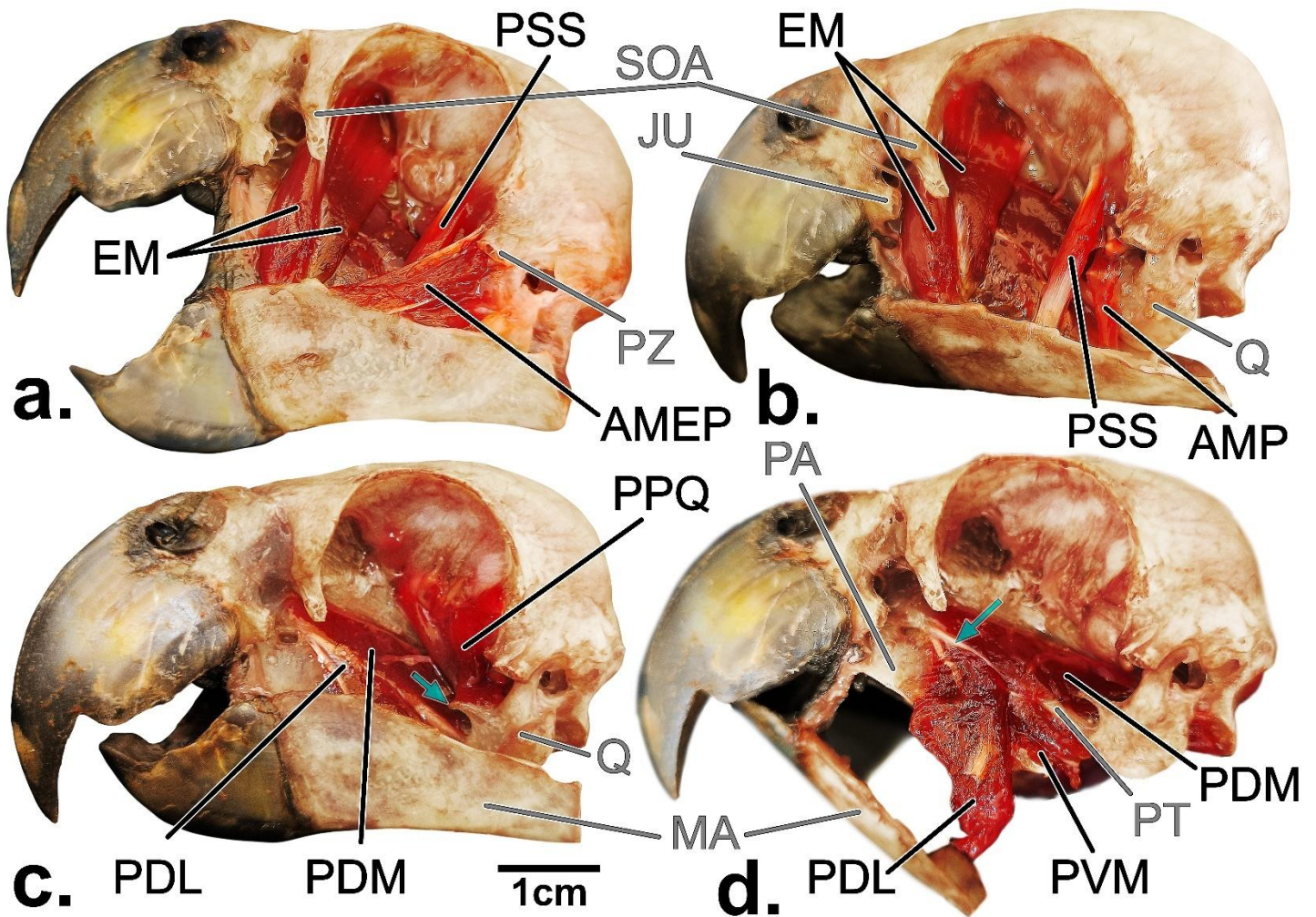


Figure 2. Lateral view of dissected *Amazona aestiva* demonstrating the general topography of the masticatory muscles found in psittacines. In a - d the suborbital arch, jugal bone and zygomatic process were removed to visualize the deep musculature. In D, the mandible was ventrally reflected to show the palatine bone and pterygoid muscle complex. JU: jugal bone; SOA: suborbital arch; PZ: zygomatic process; Q: quadrate; MA: mandible PA: palatine; PT: pterygoid. EM: *m. ethmomandibularis*; AMEP: *m. adductor mandibulae externus, pars profunda*, notice its three different parts; PSS: *m. pseudotemporalis superficialis*; AMP: *m. adductor mandibulae posterior*; PDL: *m. pterigoideus dorsalis, pars lateralis*; PDM: *m. pterigoideus dorsalis, pars medialis*; PPQ: *m. protractor pterigoideus et quadrati*; PVM: *m. pterigoideus ventralis, pars medialis*. The arrowhead in C demonstrates the orbital process of the quadrate bone, where PPQ and AMP attach. The arrowhead in d is pointing at the aponeurosis that separates PDL from PDM. Scale bar is 1 cm.

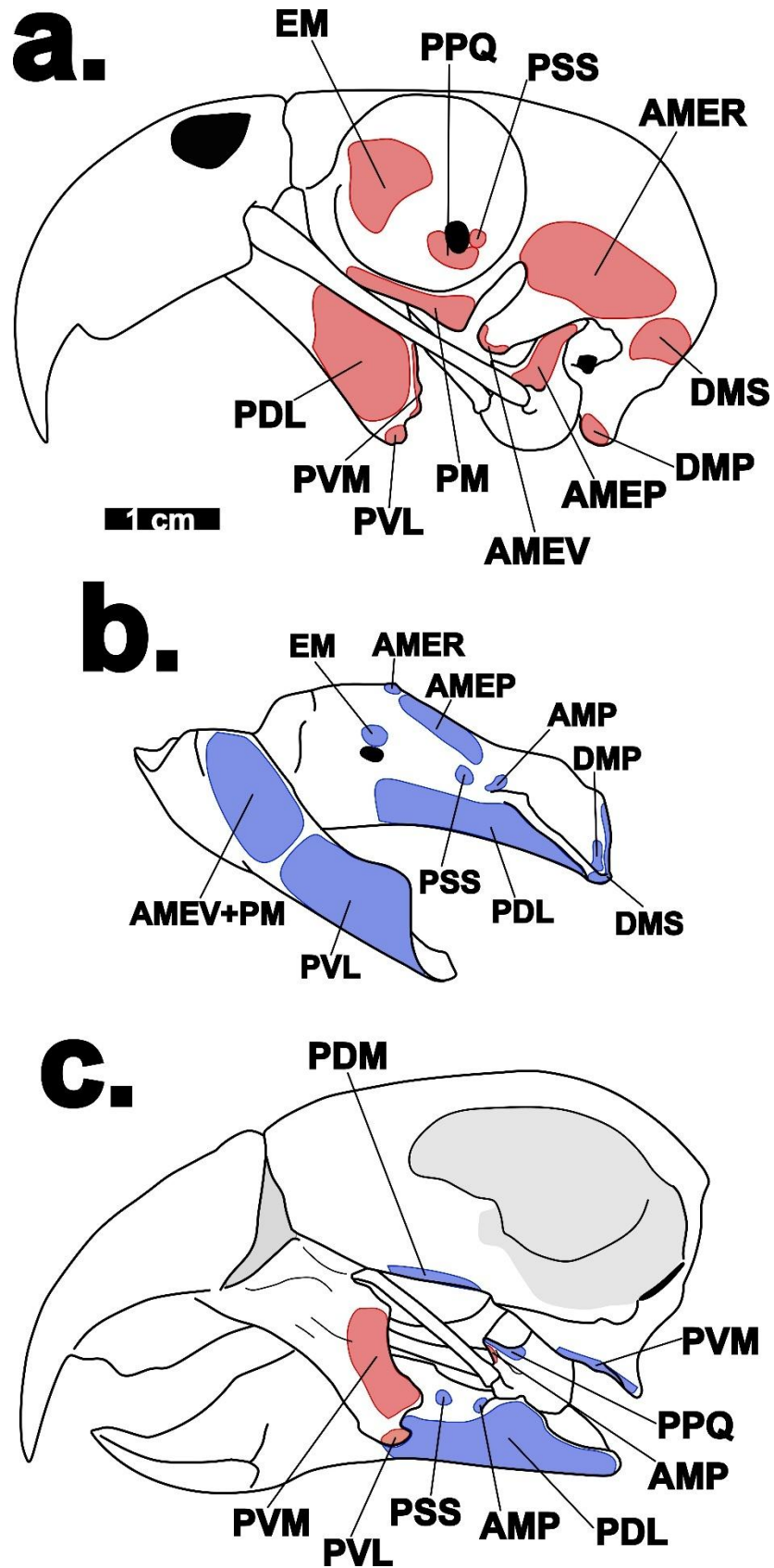


Figure 3. Origins (red) and insertions (blue) of the masticatory muscles in *Amazona aestiva*. a is lateral view of the skull without the mandible; b is an oblique dorsocaudal view of the mandible; c is a medial view of a skull and mandible cut along the midline.

PM: *m. pseudomasseter*; AMEV: *m. adductor mandibulae externus, pars ventralis*; AMER: *m. adductor mandibulae externus, pars rostralis*; AMEP: *m. adductor mandibulae externus, pars profunda*; EM: *m. ethmomandibularis*; PSS: *m. pseudotemporalis superficialis*; PPQ: *m. protractor pterygoideus et quadrati*; AMP: *m. adductor mandibulae posterior*; PVL: *m. pterigoideus ventralis, pars lateralis*; PVM: *m. pterigoideus ventralis, pars medialis*; PDL: *m. pterigoideus dorsalis, pars lateralis*; PDM: *m. pterigoideus dorsalis, pars medialis*; DMS: *m. depressor mandibulae, pars superficialis*; DMP: *m. depressor mandibulae, pars profunda*. Grey areas in c represent cavities. Scale bar is 1 cm.

The blue-fronted parrot (*Amazona aestiva*) was used as a representative species in our study due to a. its possessing the complete set of relatively easily visualized jaw muscles, b. its average size (adult average weight of 400 grams; (Bird et al., 2020), and c. its availability; multiple specimens were available to us at the dissection laboratory where this research was conducted allowing confirmation of its fundamental anatomy.

## 2.2 Myological description

Muscles were categorized into four different functional groups based on their origin and insertion: mandibular adductors, protractors of quadrate and pterygoid bones, maxillary depressors, and mandibular depressors. We provide some muscle synonyms used in selected literature in Table 2.

Table 2 – Synonym of the psittaciform jaw muscles and their main functions used in this study and selected literature, from oldest to newest.

| Muscle Name | Synonym                                                                                                                                                                                                                                | Main Function                                                                                                                                                                                  |
|-------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| PM          | Pseudomasseter <sup>a,b,c,d</sup>                                                                                                                                                                                                      | Mandibular adductor <sup>a,c,d</sup><br>Mandibular adductor, lateral movement of mandible <sup>b</sup>                                                                                         |
| AMEV        | Adductor mandibulae externus medialis <sup>a</sup><br>Adductor mandibulae externus ventralis <sup>b</sup><br>Adductor mandibulae externus pars ventralis <sup>c</sup><br>Adductor mandibulae externus superficialis <sup>d</sup>       | Mandibular adductor <sup>a</sup><br>Mandibular adductor, lateral movement of mandible <sup>b</sup><br>Elevates mandible <sup>c,d</sup>                                                         |
| AMER        | Adductor mandibulae externus superficialis <sup>a</sup><br>M. adductor mandibulae rostralis temporalis <sup>b</sup><br>Adductor mandibulae externus pars rostralis <sup>c</sup><br>Adductor mandibulae externus profundus <sup>d</sup> | Mandibular adductor <sup>a</sup><br>Mandibular adductor, lateral movement of mandible; Raises and retract mandible, support quadrate rotation <sup>b</sup><br>Elevates mandible <sup>c,d</sup> |
| AMEP        | Adductor mandibulae externus profundus; rostradorsal part and caudoventral part <sup>a</sup>                                                                                                                                           | Mandibular adductor <sup>a</sup>                                                                                                                                                               |

|     |                                                                                                                                                                                                                                        |                                                                                                                                                                                                                                                            |
|-----|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|     | Adductor mandibulae externus caudalis <sup>b</sup><br>Adductor mandibulae externus pars profundus <sup>c</sup><br>Adductor mandibulae externus medialis <sup>d</sup>                                                                   | Mandibular adductor, lateral movement of mandible <sup>b</sup><br><br>Elevates mandible <sup>c,d</sup>                                                                                                                                                     |
| AMP | Pseudotemporalis profundus* <sup>b</sup><br>Adductor mandibulae ossi quadrati <sup>c</sup><br>Adductor mandibulae posterior <sup>d</sup>                                                                                               | Stabilizes quadrate from rotation <sup>b</sup><br>Elevates mandible <sup>c,d</sup>                                                                                                                                                                         |
| EM  | Ethmomandibularis <sup>a,b,c,d</sup>                                                                                                                                                                                                   | Elevates mandible <sup>a,b,c,d</sup>                                                                                                                                                                                                                       |
| PSS | Pseudotemporal superficial <sup>a,b,c,d</sup>                                                                                                                                                                                          | Raises mandible <sup>a,b,c,d</sup>                                                                                                                                                                                                                         |
| PPQ | Protractor quadrati <sup>a,b</sup><br>Protractor pterygoideus et quadrati <sup>c,d</sup>                                                                                                                                               | Raises maxilla via protraction of quadrate bone <sup>a,b,c,d</sup>                                                                                                                                                                                         |
| PV  | Pterygoideus ventralis <sup>a</sup><br><br>Pterygoideus lateralis ventralis <sup>b</sup><br><br>Pterygoideus ventralis pars medialis, pars lateralis <sup>c</sup><br>Pterygoideus ventralis pars palatina et pterygoideus <sup>d</sup> | Moves mandible rostrally; close mandible and maxilla <sup>a</sup><br>Retracts palato-ptyergoid bone complex and moves mandible dorsally and rostrally; medial movement of mandible <sup>b</sup><br><br>Elevates mandible and lowers maxilla <sup>c,d</sup> |
| PD  | Pterygoid dorsalis <sup>a,d</sup><br>Retractor palatini et pterygoidei; Pterygoideus medialis <sup>b</sup><br>Pterygoideus dorsalis pars medialis, pars lateralis <sup>c</sup>                                                         | Moves mandible rostrally; close mandible and maxilla <sup>a</sup><br>Depresses maxilla and retracts palato-ptyergoid bone complex <sup>b</sup><br><br>Elevates mandible and lowers maxilla <sup>c,d</sup>                                                  |
| DM  | Depressor mandibulae <sup>a,b,c,d</sup>                                                                                                                                                                                                | Depresses mandible <sup>a,c,d</sup><br>Depresses mandible and support quadrate protraction <sup>b</sup>                                                                                                                                                    |

Following Carril et al. (2015) and Tokita et al. (2007), the *m. pseudomasseter* was classified as well-developed, underdeveloped or absent (Fig. 4). A well-developed muscle had a strong, defined belly that covered the jugal bone laterally and had a solid attachment to the suborbital arch (SOA). An underdeveloped muscle was identified as having few fibers that formed a slender structure that originated from the ventral part of the external

adductor of the mandible angled towards the SOA where it attached via a strong fibrous aponeurosis, covering the jugal laterally. These fibers usually went halfway through this connective tissue, not attaching directly to the arch. It was considered absent when no fibers or fibrous tissue originating from the external adductor could be identified.

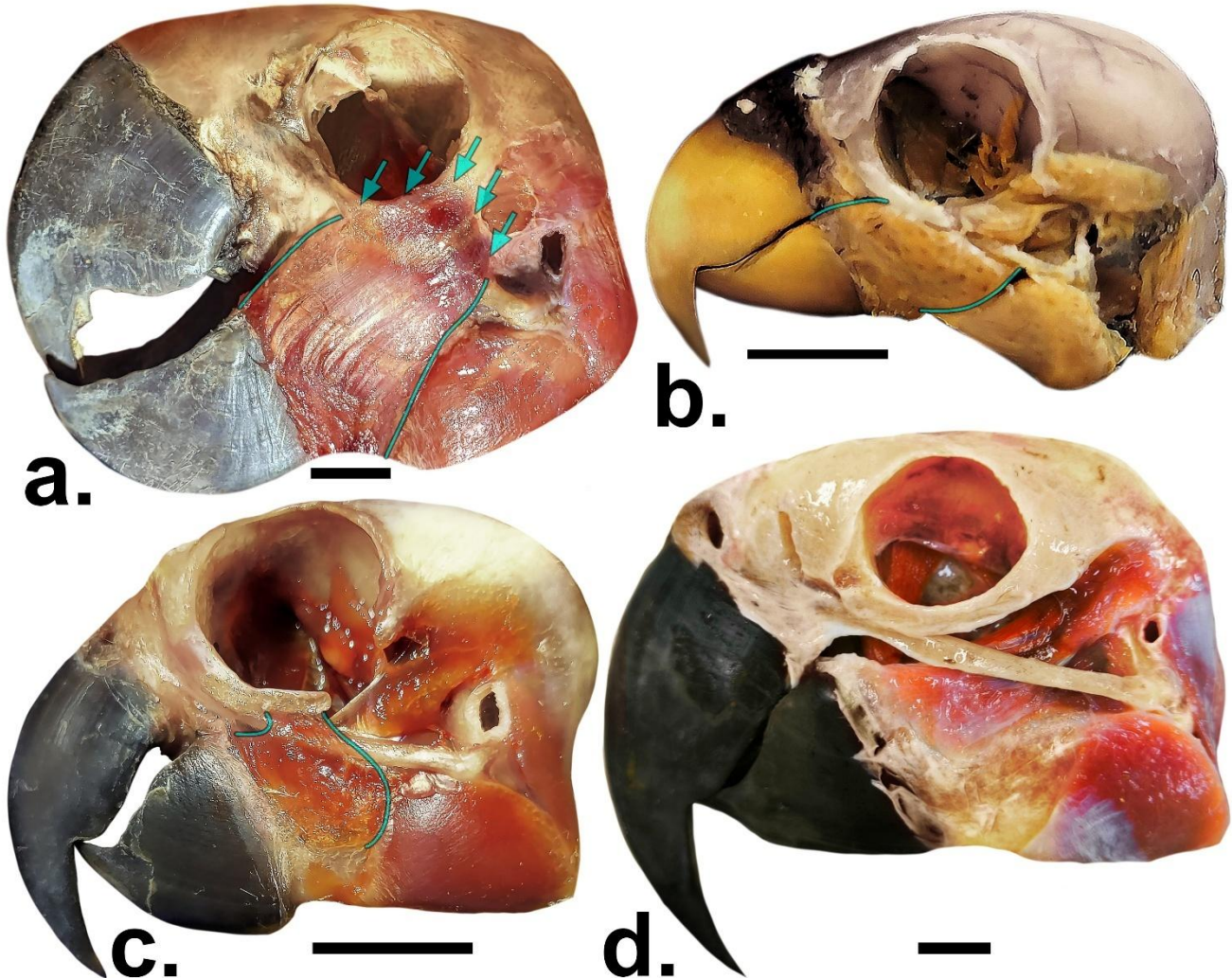


Figure 4. Lateral photos depicting three different developmental levels of *m. pseudomasseter* (outlined in teal) in different species. The PM is well-developed in *Cacatua moluccensis* (a) and *Trichoglossus haematodus* (b), underdeveloped in *Aratinga solstitialis* (c), and absent in *Ara ararauna* (d). The arrowheads in A point to the substantial insertion of *m. pseudomasseter* along the fused suborbital arch and zygomatic process. Scale bar is 1 cm.

### 2.3 Differences in masticatory muscle attachments

Following Smith (1975) and Zusi (1993) the SOA was classified as complete when it included a complete ossified ring on the ventral border of the orbit, or incomplete if it had a short bony projection of the lacrimal bone that extends caudally and limits the first half of the ventral border of the orbit, leaving the caudoventral part bordered by the suborbital

ligament (Fig. 5). Usually, the postorbital process was small when the arch was incomplete.

Following Schodde et al. (2013) the temporal fossa (a depression on the lateral aspect of the skull directly related to the rostral part of the external adductor of the mandible), was classified as deep, with a well-developed crista temporalis bordering the structure, or shallow and weakly muscled (Fig. 5).

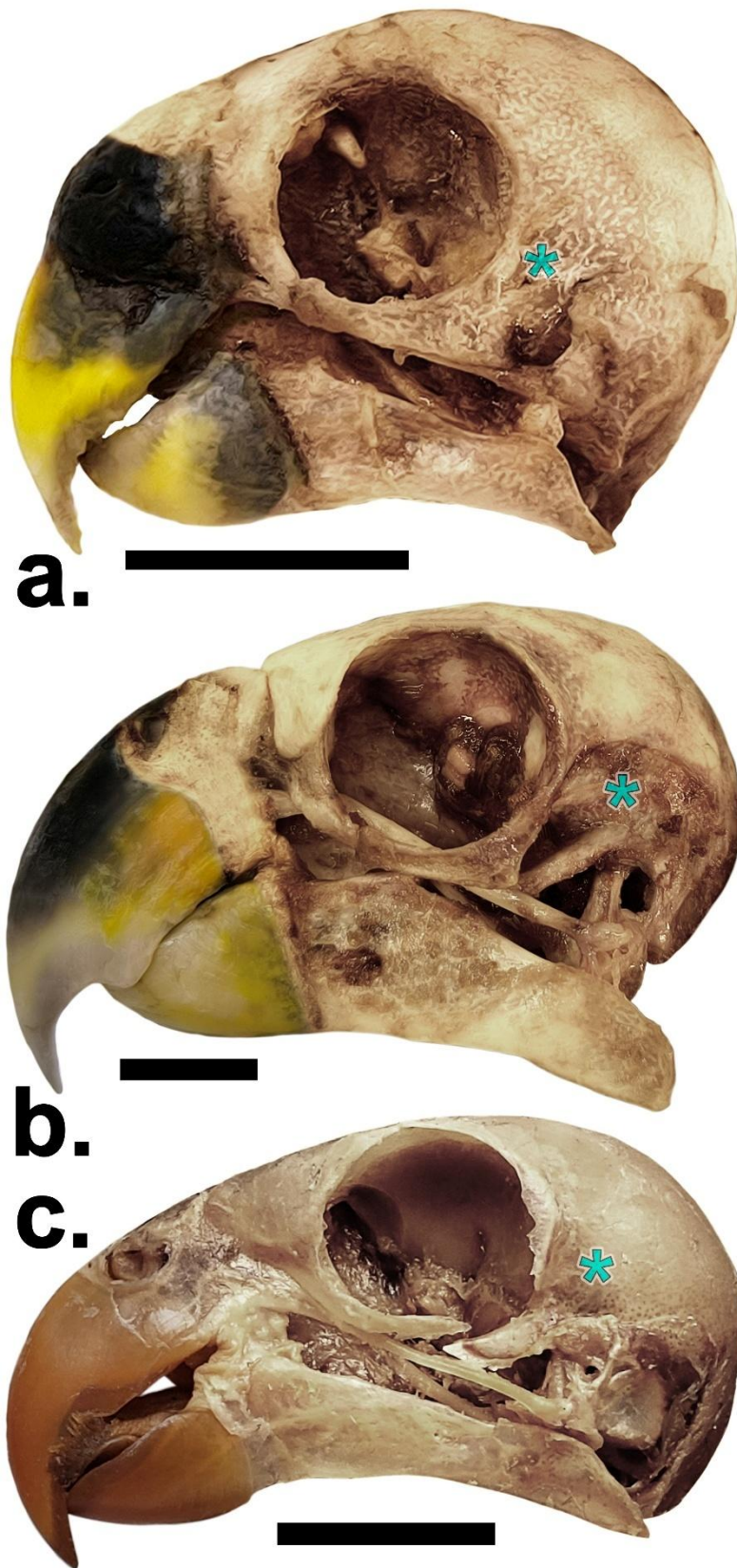


Figure 5. Lateral photos of three dissected different species depicting osteological variations in the suborbital arch and temporal fossa (\*). A: *Melopsittacus undulatus*; B:

*Alipiopsitta xanthops*; C: *Vini australis*. Notice a complete suborbital arch fused with the zygomatic process in A, a complete ossified suborbital arch B, and incomplete in C. Scale bar is 1 cm.

### 3. Results

The general topology was preserved across the genera, with some notable exceptions that will be further discussed. Thus, a general description for each muscle is presented based on the blue-fronted parrot, *Amazona aestiva* as a representative species based on its average size (adult specimens weigh on average 400 grams) and because it possesses the complete set of masticatory muscles (Porto, 2004). Descriptions of major differences found between species are highlighted after this general description.

#### 3.1 Mandibular adductors

##### *M. pseudomasseter* (PM) (Fig. 1; 3a, b)

The *m. pseudomasseter* is the most superficial external adductor of the mandible and is a well-developed muscle that attaches from the lateral mid-third of the mandibular ramus alongside the rostral half of *m. adductor mandibulae externus, pars ventralis* (AMEV), with which it shares fibers. It extends dorsally, covering the lateral aspect of the jugal bone and strongly attaches to the ventrolateral surface to the suborbital arch (SOA), where it originates. The ossified SOA has a distinct bony process on its caudal margin extending ventrocaudally (Figure 1a, 7b), also serving as an attachment to this muscle.

##### *M. adductor mandibulae externus, pars ventralis* (AMEV) (Fig. 1; 3a, b)

The *m. adductor mandibulae externus, pars ventralis* has a tendinous origin at the tip of the zygomatic process and inserts on the lateral aspect of the mid-third of the mandible. On its attachment site on the mandible, it is partially fused with *m. pseudomasseter*. This muscle is ventrocaudal to *m. adductor mandibulae externus, pars rostralis* (AMER) and lateral to *m. adductor mandibulae externus, pars profunda* (AMEP).

##### *M. adductor mandibulae externus, pars rostralis* (AMER) (Fig. 1; 3a, b)

The *m. adductor mandibulae externus, pars rostralis* muscle originates in the well-defined temporal fossa and covers most of its surface. It extends ventromedially to the zygomatic process, creating a caudal boundary to the orbit. Some of the muscle belly covers the dorsal and lateral aspect of zygomatic process. It inserts on the coronoid process of the mandible via a strong tendon. This muscle is dorsocranial to *mm. pseudomasseter et adductor mandibulae externus, pars ventralis*.

##### *M. adductor mandibulae externus, pars profunda* (AMEP) (Fig. 2a; 3a, b)

The *m. adductor mandibulae externus, pars profunda*, the deepest part of the external mandibular adductor, has three notable parts: a slender dorsal belly, a middle belly that is

also the largest and a short ventral belly. The extensive origin of this muscle starts on the medial side of the zygomatic process and extends along the body of the quadrate, the rostral aspect of the quadratojugal cotyle and the orbital process of the quadrate. Its broad insertion is caudal to AMER and on the dorsal border and medial aspect of the mandible. The dorsal belly originates on the medial aspect of the zygomatic process (sharing some fibers with AMEV) and attaches caudomedial to the coronoid process of the mandible, just rostral of the attachment of the middle belly. The latter has a fleshy origin along the otic process of the quadrate. Finally, the ventral belly originates rostrally along the quadratojugal cotyle of the quadrate, inserting medially in the mandible just rostral to *m. adductor mandibulae posterior* (AMP).

*M. ethmomandibularis* (EM) (Fig. 2a, b; 3a, b)

The *m. ethmomandibularis* is a large, triangular shaped muscle with an ample origin rostrrodorsal to the interorbital septum (mesethmoid) and in the ectethmoid, with a single tendon inserting on the medial aspect of the mandible, dorsal to the single mandibular fenestrae. Since it originates in two different bones, it has visibly different bundles of parallel muscle fibers, but they do not visibly form separate bellies.

*M. pseudotemporalis superficialis* (PSS) (Fig. 2a, b; 3)

The *m. pseudotemporalis superficialis* is a thin and long muscle that originates caudal to the optic foramen and *m. protractor pterygoideus et quadrati* (PPQ) and inserts medial on the mandible.

*M. adductor mandibulae posterior* (AMP) (Fig. 2b; 3b, c)

The *m. adductor mandibulae posterior* is a small, rectangular shaped muscle originates on the lateral aspect of the orbital process of the quadrate and inserts medial to the mandible, rostral to the quadratomandibular joint. This muscle also acts as a stabilizer for the quadratomandibular joint.

### *3.2 Protractor of quadrate and pterygoid bone*

*M. protractor pterygoideus et quadrati* (PPQ) (Fig. 2c; 3a, c)

The *m. protractor pterygoideus et quadrati* is a parallel fiber muscle has a relatively large origin ventral and caudal to the ophthalmic nerve foramen in the orbit, with its insertion on the dorsal and medial aspect of the small orbital process of the quadrate. Similar to EM, this muscle may seem superficially to have two separate bellies, but they hardly ever completely separate.

### *3.3 Maxillary depressors*

*M. pterygoideus ventralis, pars medialis et pars lateralis* (PVM; PVL) (Fig. 1; 2d; 3)

The *m. pterygoideus ventralis* is a complex muscle that is divided into a lateral and medial part. The *pars lateralis* has a fleshy insertion on the lateral aspect of the caudal third of the mandibular ramus, wraps ventrally around the ventral edge of the mandibular

ramus and originates with a strong tendon on the caudolateral angle (*angulus caudolateralis*) of palatine bone. The *pars medialis* originates caudodorsal to the origin of *pars lateralis*, along the caudal margin of the palatine. It extends along the medial aspect of the palatine and inserts on the ventral side of the paraoccipital process.

*M. pterygoideus dorsalis, pars medialis et pars lateralis* (PDM; PDL) (Fig. 1; 2c, d; 3)

The *m. pterygoideus dorsalis* is just as complex as the ventral pterygoid and can also be separated into lateral and medial parts. Here, *pars medialis* occupies the dorsal aspect of the palatine bone and extends dorsal to the pterygoid bone, inserting along the basioccipital bone. The *pars lateralis* originates along the lateral aspect of the palatine, inserting medially in the mandible, rostral and ventral to the medial cotyle of the mandible.

### 3.4 Mandibular depressor

*M. depressor mandibulae, pars superficialis et pars profunda* (DMS, DMP) (Fig. 1, 3a, b)

The *m. depressor mandibulae pars superficialis* has a large origin along the nuchal crest (*crista nuchalis transversalis*) and the paraoccipital process, with a strong insertion on the caudal margin of the mandibular ramus, caudal to the quadratomandibular joint. The *pars profunda* is a small cylindrical muscle with its origin on the paraoccipital process and insertion on the medial cotyle of the mandible.

### 3.5 Main comparative aspects

*M. pseudomasseter* (Fig. 4)

The *m. pseudomasseter* was classified as well-developed, underdeveloped, or absent, following comments by Hofer (1950) and personal observation.

It is well-developed in *Cacatua moluccensis*, *Nymphicus hollandicus*, *Amazona aestiva*, *Lorius garrulus*, *Trichoglossus haematodus*, *Melopsittacus undulatus*, *Pionus menstruus* and *Alipiopsitta xanthops*. Particularly in the cockatoo, this muscle is massive, being one of the largest external adductors of the mandible. Its insertion extends from the ventrolateral aspect of the SOA to the zygomatic process (that is partially fused with the suborbital arch) and is connected to the jugal arch via connective tissue.

It is underdeveloped in *Aratinga solstitialis*, *A. auricapillus*, *Eclectus roratus*, *Rhynchopsitta pachyrhyncha*, *Neophema splendida*, *Platycercus elegans*, *P. eximius*, *Phyrura molinae*, *Polytelis anthopeplus*, *Psittacula cyanocephala*, *Vini australis*, *Orthopsittaca manilatus*, *Agapornis fischeri*, *B. chiriri*, and *Guaruba guarouba*.

It is absent in *Ara ararauna*, *A. rubrogenys*, *Diopsittaca nobilis*, and *Psittacara leucophthalmus*.

*M. adductor mandibulae externus, pars rostralis* (Fig. 6)

The *m. adductor mandibulae externus pars rostralis* in *C. moluccensis* and in *Nymphicus hollandicus* extends from the temporal fossa (TF) through a tunnel formed by the fusion of the caudal part of the suborbital arch (i.e., postorbital process) and the tip of the zygomatic process. In *N. hollandicus*, possibly due to its size and the fusion of the zygomatic process, AMER and AMEP share multiple fibers and are harder to differentiate.

A similar bony conformation of the SOA to the cockatoo and cockatiel exists in *M. undulatus*, but the fusion is with the whole zygomatic process which forms almost a complete wall separating the orbital cavity from the temporal fossa, apart from a minuscule foramen (~1mm in diameter) that allows for scarce AMER fibers to pass through. In this species, most of AMER is restricted to the caudal aspect of the orbit.

In *Neophema splendida* and *Polytelis anthopeplus*, due to a shallow TF, the AMER is mostly restricted to the caudal part of the orbit. In *Platycercus elegans*, *P. eximius*, and *Vini australis*, AMER originates in the caudal part of the orbit and laterally covers the zygomatic process up to its insertion on the coronoid process of the mandible. In *Vini australis*, the zygomatic process appears relatively longer than in other species with similar size.

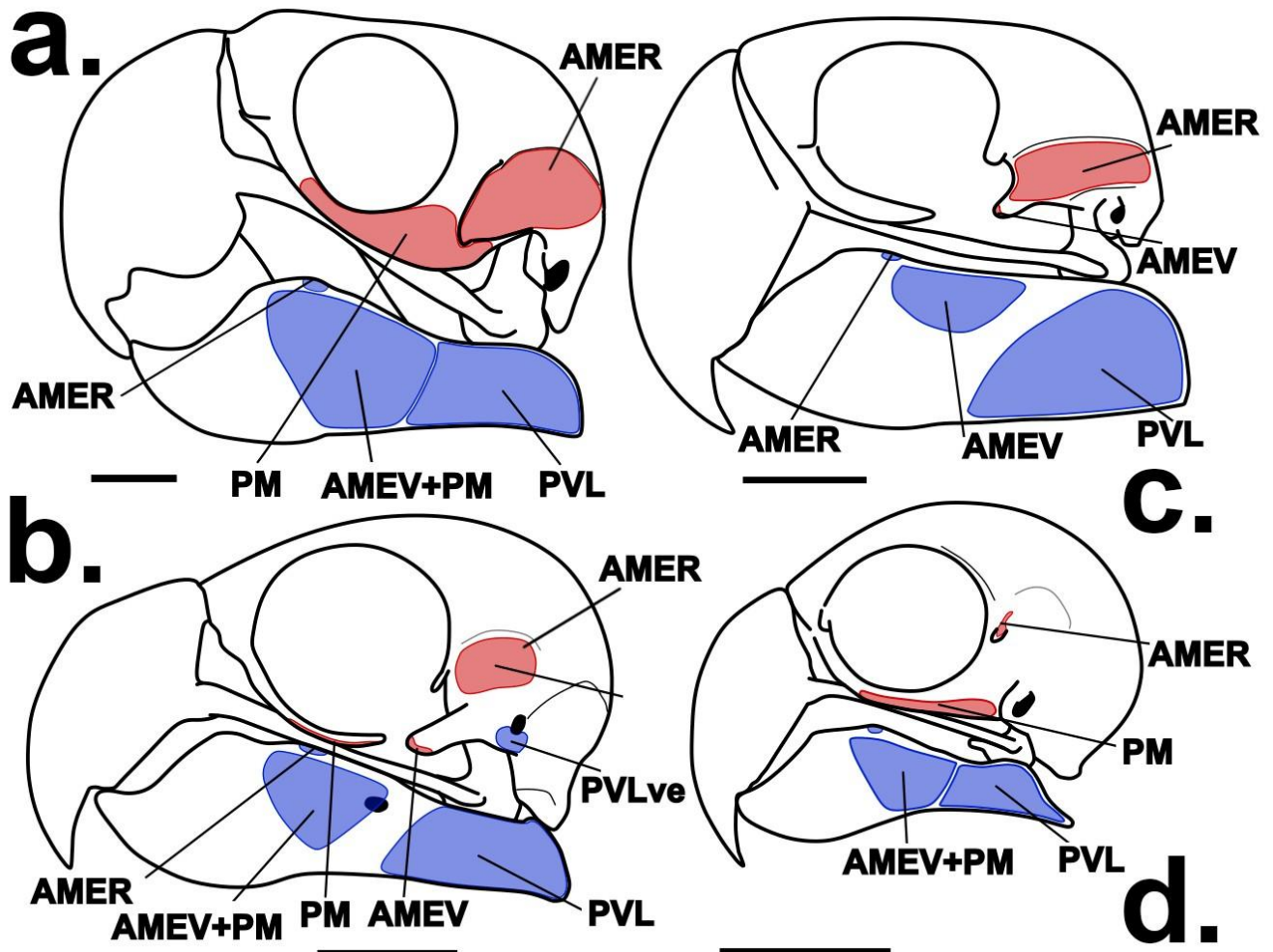


Figure 6. Diagram showing variations in origins (red) and insertions (blue) of some masticatory muscles in different species of psittaciniforms, lateral view. A: *Cacatua moluccensis*; B: *Platycercus eximius*; C: *Melopsittacus undulatus*; D: *Diopsittaca nobilis*. PM: *m. pseudomasseter*; AMEV: *m. adductor mandibulae externus, pars ventralis*; AMER: *m. adductor mandibulae externus, pars rostralis*; PVL: *m. pterigoideus ventralis, pars lateralis*; PVLve: venter externus of *m. pterigoideus ventralis, pars lateralis*. Scale bar is 1 cm.

#### *M. ethmomandibularis*

The distal part of *m. ethmomandibularis* in *P. leucophthalma* and *D. nobilis* was partially fused with *m. pterigoideus dorsalis*, but it still kept its strong tendinous insertion on the medial aspect of the mandible.

#### *M. pterigoideus ventralis, pars lateralis* (Fig. 7)

Part of *m. pterigoideus ventralis pars lateralis* on *Platycercus elegans* and *P. eximius*, extends over the dorsal border of the mandible, lateral to the quadratojugal joint. It inserts ventrally to a wall-like bony projection of exoccipital bone that caudally bounds

the external acoustic meatus. This extension is called *venter externus* and was only observed in this genus.

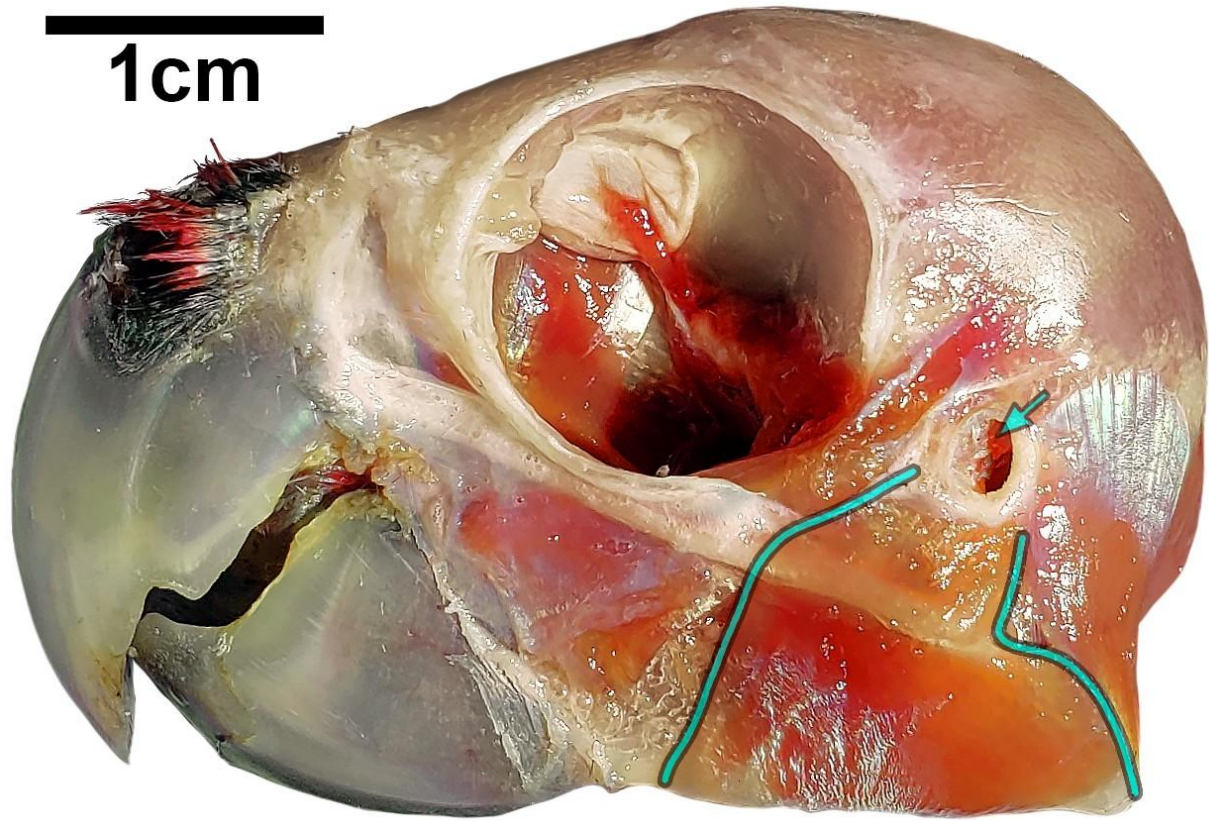


Figure 7. Lateral view of dissected *Platycercus elegans* showing *m. pterygoideus ventralis pars lateralis* with its *venter externus*, both outlined in teal. Note the insertion of *venter externus* ventral to the external acoustic meatus (arrow). Scale bar is 1 cm.

#### Suborbital arch (Fig. 5)

The suborbital arch (SOA) is complete in *Ara*, *Diopsittaca*, *Amazona*, *Cacatua*, *Melopsittacus*, *Alipiopsitta*, *Pinous*, *Nymphicus*, *Aratinga*, *Rhynchopsitta* and *Guarouba*. In *Amazona*, *Alipiopsitta* and *Pionus* there is a defined, roughly square-shaped bony process (Figs 1a, 5b) that serves as an attachment to PM. In the cockatoo and cockatiel, this bony process of the SOA is massive and fuses to the rostral part of the zygomatic process, forming a large tunnel through which AMER passes (Fig. 6a, b). In *Melopsittacus*, the arch is fused to the body of the zygomatic process and the bony process from the caudal aspect of the SOA extends further ventral, partially covering the jugal bone laterally.

Interestingly, in one specimen of *Amazona aestiva* dissected, the bony process from the SOA was enlarged and partially fused with the zygomatic process on one side and on the opposite side, the bony process was enlarged but did not make contact with the zygomatic process. This feature created a small tunnel through which AMER passed in a similar way to *Cacatua* and *Melopsittacus*.

All other species studied had an incomplete arch with a suborbital ligament that covered the caudal half of the ventral aspect of the arch, with the bony process of the lacrimal bone still serving as an attachment site to underdeveloped PM.

#### Temporal fossa (Fig. 5)

The temporal fossa was shallow in *Platycercus elegans*, *P. eximius*, *N. splendida*, *Polytelis anthopeplus*, *V. australis* and *M. undulatus*. All presented very few muscle fibers from AMER extending to this structure. In *Brotogeris*, *Orthopsittaca* and *Psittacara*, the fossa was shallow, but a thin AMER occupied the fossa.

## **4. Discussion**

As has been documented previously (Hofer, 1950, 1953; Carril et al., 2015), although there is a general psittaciformes masticatory musculoskeletal apparatus, there are subtle, but important, variations in configurations between lineages. Out of the 13 masticatory muscles of parrots, two (*m. adductor mandibulae externus, pars rostralis* and *mm. pseudomasseter et adductor mandibulae externus pars ventralis*) are most variable among the different species, with one (“*venter externus*” of *m. pterygoideus ventralis, pars lateralis*) being present in only one genus studied. That is, most of the masticatory muscles were generally consistent in configuration across the parrot species analyzed in this research, though there are considerable variations in some specific structures and notable slight variation in origin and insertion in some muscle groups – especially due to differences in skull (e.g., shorter, more rounded) and bill shape among the species studied.

### *4.1 Similarities within the psittaciformes masticatory musculoskeletal apparatus*

The majority of the masticatory muscles are jaw adductors, but due to the highly mobile nature of the avian skull, particularly in the psittaciformes, many muscles are associated with multiple biomechanical functions. The masticatory muscles of the avian head can be functionally organized into mandible adductors, maxillary depressors, mandibular depressors and protractors of the quadrate and pterygoid bones (Homberger, 2017). The *m. depressor mandibularis* is the only muscle that actively causes the opening of the jaw via depression of the mandible. The external adductor of the mandible complex, along with *m. pseudotemporalis superficialis*, *m. ethmomandibularis* and *m. adductor mandibulae posterior*, causes jaw adduction. The latter also acts as a stabilizer for the quadratomandibular joint. Both the external adductors complex and pterygoid complex also supports the retraction of the palato-ptyergoid system, thereby depressing the maxilla (Homberger, 2017). *M. protractor pterygoideus et quadrati* (PPQ) is an important protractor of the pterygoid bone, causing maxillary abduction and consequent opening of the bill.

Because of their general anatomy, even though parrots have broad geographical range, habitat and foraging behavior, all possess a prokinetic skull. Their beak is a highly versatile tool that is used not only for feeding, but also for various behaviors such as

digging (Corbin et al., 2015), consuming clay in nutrient lacking environment (Lee et al., 2010), nest building in trees (Ramírez-Herranz et al., 2024), climbing (Bhullar et al., 2016; Young et al., 2022) and social interactions. The skull of psittaciformes is generally highly prokinetic when compared to other neognaths, and even relative to its sister clade, the passerines (Zusi, 1993). This is due to, among some novelties further discussed here, a synovial craniofacial joint that allows the beak to be used as an all-purpose tool (Young et al., 2023). These osteological and arthrological adaptations are accompanied by an equally adapted set of muscles to generate motion. The elaborate parrot beak movement has been interpreted as conferring functional advantages that allow them to perform diverse behaviors of ecological relevance (Bout and Zweers, 2001) and, as a result, this configuration was preserved across the group.

One remarkable example of this functional abilities conferred by the Psittaciformes beak is that, along with the Puerto Rican spindalis (*Spindalis portoricensis*), they are the only group recorded to use their beak for climbing and walking (Dickinson et al., 2024). Additionally, the great dexterity of the beak allows them to consume seeds and other hard items by placing them at the tip of the bill and then initiating a crack by mandibular adduction while the upper beak stabilizes the food item and acts as an anvil, minimizing lateral movement of the mandible (Hrabar and Perrin, 2002; Homberger, 2003). This is different from other granivorous passerines (e.g., finches) that place the seed close to the joint on one side of the beak prior to adduction (Mielke and Van Wassenbergh, 2022). The parrot's mobile skull may decrease the force required to open the jaw, increasing bite force potential (Bout and Zweers, 2001). Furthermore, along with their ability to handle food and other materials with their feet, parrots use their beaks to access food items ranging from nectar and lichen to fruit and hard seeds and even carrion in extreme cases (Navalón et al., 2019).

Recent analysis on tripedal locomotion in parrots has demonstrated that the beak is an important component of this novel mode of locomotion (Reader et al., 2022; Dickinson et al., 2024). Thus, it is possible that the parrots' strong bite force and kinetic skull may not relate most directly to feeding ecology but, rather, to the use of the beak for locomotion or others of its diverse functions.

#### 4.2 Variation within the psittaciformes masticatory musculoskeletal apparatus

The *m. pseudomasseter* (PM) is unique to psittaciformes (Hofer, 1950, 1953; Tokita and Nakayama, 2014; Carril et al., 2015). This muscle cannot be considered homologous since the embryological origin of PM is related to *m. adductor mandibular externus* (Tokita, 2004; Carril et al., 2016). Due to its high variability throughout psittaciformes, this muscle was first classified merely as a binary: either developed or absent altogether (Hofer, 1950; Zusi, 1993). However, upon further investigation, it is clear that there are diverse fiber arrangements originating from *m. adductor mandibulae externus pars ventralis* (AMEV) which insert on the suborbital arch (SOA) via an aponeurotic sheet, covering the jugal arch laterally (Figure 4), reinforcing the need for more elaborate categorization. Tokita et al. (2007) and Carril et al. (2015) propose a third

‘underdeveloped PM, where it is composed of mostly aponeurosis with minimal fiber development and a strong attachment to the SOA. Out of the 24 genera we studied, eight had a well-developed PM, 13 had an underdeveloped and three were absent.

Functionally, the PM in psittaciformes is a mandibular adductor and, since it has a more rostral attachment than its origin muscle AMEV, it could add more mechanical biting force (Tokita, 2004; Carril et al., 2015). A tradeoff between force and velocity occurs in jaw movement, where the further out a muscle’s line of action is from the jaw joint fulcrum, the stronger the bite movement can be, but it also must stretch further for mandibular abduction (Deutsch et al., 2020; Hartstone-Rose et al., 2021). Due to its lateral position, it may also allow for transverse movement of the mandible (Homberger, 2003).

Similarly to described in some mammals (Hartstone-Rose et al., 2021) and birds (Soons et al., 2015), dietary correlation to masticatory myology in parrots has been hypothesized. Empirical analysis of the skull of parrots through geometric morphometric suggest that diet had little influence over other nondietary factors on the evolution of the skull and beak of this group (Bright et al., 2019). The species that had the most developed PM were *Cacatua* and *Nymphicus* (Cacatuidae), with the cockatoo consuming fruits, nuts, and insects and the cockatiel being a more restricted seed eater (Rumanta et al., 2019). Other species such as *Melopsittacus* (Psittaculidae) and *Amazona*, *Pionus* and *Alipiopsita* (all members of Psittacidae) also presented a well defined PM, where only *Melopsittacus* has a preference for granivory (Voltura et al., 2024). Another curious find is that *Trichoglossus* and *Lorius*, which consume mainly nectar and fruit (McDonald, 2003), also have a well-developed PM. In contrast, *Ara* possesses a massive bill and consume hard seeds and coconut (Lee et al., 2014), but has no PM. Investigations concerning bite force estimations and diet in parrots are needed to further assess adaptive significance of this muscle.

Bite force has been found to directly relate to the masticatory muscle mass in parrots, and has been show to scale positively with body size of (Harrison et al., 2024), though this relationship does not seem to be constrained by dietary factors, but rather follows allometric and phylogenetic patters (Bright et al., 2019). Thus, the fact that the large, hard object feeding *Ara* lacks a PM argues for further investigation to assess biomechanical significance of both the suborbital arch and this muscle.

Beyond this myological variation, the SOA itself is also variable among psittaciformes. Embryologically, the SOA starts as a caudal projection of the lacrimal bone that attaches to the postorbital process via a suborbital ligament (Tokita, 2004). In species that retain a complete SOA as adults, this ligament ossifies. The fusion of the SOA with the zygomatic process seems to be more present in members of Cacatuidae and in *Melopsittacus*, although some level of variation in this conformation has been described in *Cacatua* (Elzanowski and Mayr, 2018). All species with this SOA formation have a well-developed PM. This osteological configuration is not limited to parrots, and is also related to the attachment of *m. adductor mandibularis externus* in other species including some Galliformes and Picidae (Elzanowski and Mayr, 2018). Due to the possible

embryological relationship between both of these structures, it is hypothesized that this notable conformation is to allow for a better attachment of the PM (Tokita, 2004; Tokita et al., 2007; Carril et al., 2016), since it is an important attachment for this muscle (Zusi, 1993). However, some taxa such as *Ara* and *Strigops* have the arch but lack the PM (Hofer, 1953). It has also been proposed that an ossified SOA and well-developed PM are the ancestral characters in parrots, with the ossified SOA possibly helping to constrain stress forces caused by the jaw muscles, meaning that the absence of either or both features would be the derived condition (Tokita, 2004; Carril et al., 2015; Dickinson et al., 2022).

The other muscle inherent to parrots is *m. ethmomandibularis* (EM). Functionally, it acts as a powerful jaw adductor and, due to its rostral attachment on the interorbital septum, it also performs rostral translation of the mandible. Furthermore, it has the highest mechanical advantage of the internal jaw adductors (Homberger, 2017). This muscle was consistent in morphology among all 27 species included in our study. However, Carril et al. (2015) described this muscle as having two bellies in *Myiopsitta monachus*, and, contrary to our findings, Porto (2004) described the same characteristic in *Ara* and *Anodorhynchus*. Although our sample did not include *Myiopsitta* and *Anodorhynchus*, neither of the two *Ara* species we studied had separate EM bellies. We agree with the description done by (Hofer, 1950) that because of its ample origin on the interorbital septum and ectethmoid bone, and its rostral and deep position within the skull, it has different fiber arrangements for each region that inserts, giving the appearance of multiple bellies, but no superficial distinction of the belly could be made in any species studied. This difference in fiber orientation may help in increasing the force when closing the beak. Porto (2004) is unclear on his definition of muscle belly and separate origins.

The belly extending from *m. pterygoideus ventralis, pars lateralis* (PVL) and inserting on the ventral border of the external acoustic meatus is called *venter externus* (Hofer, 1950). This muscle was not found in *Neophema splendida*, the other Platycercinae dissected in this study, but a similar albeit more extensive belly (also attaches in the SOA) was found in *Cyanoramphus novaezelandiae* (Hofer, 1950; Burton, 1974). However, the name “*venter externus*” has been used in other avian species such as *Treron phoenicoptera*, *Ducula (aenea) nicobarica*, *Ducula badia* (Columbidae), *Dinopium javanense*, *Melanerpes cruentatus* and *Dendropicos (Mesopicus) griseocephalus* (Picidae) (Bhattacharyya, 1994; Donatelli, 2012) to describe the part of PVL that slings over the mandible and inserts in its lateral aspect. Although this sling is present in all parrots, we interpret it as merely an extension of the same *pars lateralis* present in other avians, thus, being different than the *venter externus* used by Hofer (1950). Unfortunately, the Nomina Anatomica Avium (1993) does not consider nor reference this nomenclature and thus further work should be done to disambiguate the meaning of this term.

Functionally, the *m. pterygoideus ventralis* retracts the palato-ptyergoid bone complex, depressing the upper beak (Homberger, 2017). Although its adaptive significance is unclear, it has slightly more angled fibers from PVL, attaching ventral to the external acoustic meatus, which can allow it to act as a mandibular adductor (Hofer,

1950) and may allow a slight caudal pull on the mandible and restriction of medio-lateral motion of the quadratomandibular joint.

#### 4.3 Limitations and Future Directions

Although we found both remarkable consistency and subtle variation within our parrot sample, there are important extensions of this work that should be encouraged. Particularly, future research should a. fill in more of the remarkable number of species across the order, especially the basal New Zealand parrots enabling further refinement of our understanding of the ancestral state of this anatomy across the order, b. examine other dietary specialists to more fully understand whether any dietary adaptive signals are encoded within this anatomy and c. contribute to the advances in anatomical studies with other techniques such as DiceCT to generate comprehensive muscle models allowing us to examine the biomechanics of these complex musculoskeletal relationships in three-dimensional space.

Even though we had access to a great number of genera, including some endangered species such as *Guaruba guarouba*, *Aratinga solstitialis* and *Cacatua moluccensis*, for a truly complete understanding of the morphospace of the order, it would be important to include the basal Strigopidae, the African parrots of Psittacinae and better representation of Cacatuidae. The two extant genera of New Zealand parrots have substantially derived anatomy that has resulted from their extensive isolation from the continent, including specialized diets and the loss of flight in *Strigops* (Schwing, 2010; Froggatt and Gill, 2016). The polyphyletic African parrots are usually represented only by *Psittacus*, even though they are comprised of ten other species (Schweizer et al., 2010; HBW and BirdLife International, 2022), being underrepresented in most analysis. Finally, *Cacatua* is a relevant branch of Psittaciformes, with its members restricted to Australasia and presenting particular musculoskeletal characteristics. Including these samples may potentially allow for a more comprehensive understanding of the ancestral state of the Psittaciformes.

Although the current study focuses on the qualitative description of this complicated anatomy, the next step to this research is to include quantification of these muscles (mass, fascicle length and physiological cross-sectional area), preferably across a large range of body sizes, to better access the relationships between dietary ecology and functional anatomy of the masticatory apparatus. This information is relevant to investigate if any of the discussed specializations might allow the detection of diet-related musculoskeletal correlates that have eluded ours and previous research.

The use of advanced imaging techniques has some benefits as opposed to physical dissection – factors such as specimen size and rarity are easily bypassed. It also allows for more precise data generated, the possibility to estimate muscle strength (Cost et al., 2022) and better presentation via high quality digital images readily available (To et al., 2021).

## 5. Conclusion

Although most of the jaw muscles of psittaciformes were consistent across the 27 species included in our sample, several musculoskeletal elements differed in specific taxa. The muscles that were most variable were related to the external adductor of the mandible group, namely the *m. pseudomasseter* and both *pars rostralis* and *pars ventralis* of *m. adductor mandibulae externus*. The osteological features that serve as an attachment site for these muscles, namely the suborbital arch, zygomatic process and temporal fossa, also had some degree of variation.

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### CAPÍTULO III

## **Bite force estimates and morphological correlations of jaw muscles in parrots**

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### **Abstract**

Psittaciformes are one of the most diverse groups of avians, usually recognized by their strong beak and hard seeds cracking abilities. Their beak serves as the primary mode of interaction with their environment and as such, the jaw musculature has the potential of being used to infer dietary and other ecological behaviors. Parrots also have the unique *m. pseudomasseter*, a mandibular adductor with varying levels of development among the different species. However, correlations between diet and bite force are limited in recent literature. We aimed to investigate scaling patterns of muscle architectural data and bite force estimates via anatomical models, as well as presenting two novel, potential biomechanical models for this group. Muscles were processed via acid digestion and biomechanical models were based on lever-arms systems. We concluded that parrots do indeed have proportionately high bite force, and that muscle mass, physiological cross-sectional area (PCSA) and bite force scaled positively against body mass, but fascicle length did not. When compared to underdeveloped and absent states, the well-developed *m. pseudomasseter* was related to increased muscle force and PCSA of the mandibular adductors, but not for bite force. There was no correlation between dietary mechanical properties with bite force, but we found longer fascicles in muscles related to maximum gape (mandibular depressors and protractor of quadrate and pterygoid) in nectivorous and mainly soft food consuming birds. Finally, the new anatomical models estimated higher bite force than the regular model, but validation was not possible due to lack of published *in vivo* data.

**Keywords:** Psittaciformes, masticatory myology, comparative anatomy, dietary correlates.

## 1. Introduction

The order Psittaciformes encompassing parrots, macaws and cockatoos (henceforth ‘parrots’) is among the most diverse groups of extant birds, with over 400 species worldwide (HBW and BirdLife International, 2022) that can be grouped into five main families: Strigopoidae, Cacatuidae, Psittacidae, Psittichasidae and Psittaculidae (Gill et al., 2024; Smith et al., 2024). The group spans more than two orders of body size range from the 12g *Micropsitta spp.* to the 2000g *Strigops habroptilus* – the only flightless member of the order (Powlesland, 2006; Bird et al., 2020).

Largely curious birds, parrots enjoy exploring their environments using their generally broad beaks and thick tongues to dexterously manipulate items, including food (Homberger, 2017). The beak serves as the primary mode of interaction with their environment and is not limited to food consumption: it is used for a wide range of behaviors such as preening, seed husking, nest building, social interaction, defense and even locomotion (Corbin et al., 2015). As such, the jaw musculature of parrots is complex, potentially reflecting adaptive characters that can be used to infer dietary and other ecological behaviors (Hartstone-Rose et al., 2021; Faillace et al., 2025).

Skeletal muscles are comprised of muscle fibers organized in units of fascicular bunches which are capable of contraction (shortening) and relaxation (stretching) and, when associated with movable joints, resulting in movement. In analyzing bite force, it is possible to calculate force estimates using analyses of the organization and length of fascicles in individual jaw muscles: Because fascicles are capable of stretching a percentage of their overall length and can theoretically contract in the same amount of time regardless of their length, longer fibers are related to both greater gape and faster movement (Herrel et al., 2012).

Similarly, force is related to the number of fibers a muscle contains such that a greater number of shorter fibers can be packed into a muscle of a given size, resulting in a higher bite force (Herrel et al., 2012; Hartstone-Rose et al., 2019). Thus, by measuring fascicle length (FL; a gape proxy) and muscle mass, it is possible to calculate each jaw muscle’s physiological cross-sectional area (PCSA; a force proxy), and, consequently, estimate total bite force (BF) by combining these with a force constant (e.g., 30 N; (Carril et al., 2015)) and measures of leverage for each muscle and specific bite points (Deutsch et al., 2020; Hartstone-Rose et al., 2021).

Scaling patterns of muscle architectural data also helps to explain muscle function. For example, while some vertebrate groups such as bats and musteloids have a positive relation between diet hardness and PCSA, felids, canids and primates have no clear relationship among these variables (Dickinson and Hartstone-Rose, 2023). The South American Band-winged nightjar (*Systellura longirostris*) has a high angled gape and fast beak-closing speed, with its mandibular adductor muscles having larger PCSA and FL (meaning higher muscle force and faster bite) when compared to other zoophagous birds (Demmel Ferreira et al., 2019). The jaw muscles of multiple birds of prey are also reported

to be functionally specialized to prey capture and killing as well as other ecological behavior (Sustaita, 2008; Pestoni et al., 2018; Wang et al., 2024).

Muscle mass and BF scaling patterns differ among avians, with these factors exhibiting positive allometry in parrots and some passerines, isometry in estrildids, finches and raptors and even negative allometry in some orders like Anseriformes, suggesting this relationship is influenced by phylogeny and muscle functional group (van der Meij and Bout, 2004; Deeming et al., 2022; Harrison et al., 2022). Other vertebrates also present varying correlation among these variables, with lizard and tuatara BF scaling with body size (Isip et al., 2022). In the Order Carnivora and in the bird-eating bat, skull morphology is related to high BF, but there is high divergencies with diet and BF within mammals (Shi et al., 2020; Hartstone-Rose et al., 2021).

Biomechanical models are capable of testing the relationship between morphology and ecological and behavioral factors (Westneat, 2003; Sustaita, 2008; Ginot and Blanke, 2024). Biomechanical models used to analyze these factors in birds are adapted mainly from those developed on the less mobile mammalian jaw, and as a result, they generally do not completely account for the highly prokinetic nature of the avian skull (Sustaita, 2008; Carril et al., 2015; Harrison et al., 2024). Because the jaw muscles of parrots have many functions and usually act on more than one joint, a more biologically sound model should take these various functions and factors into consideration (Hofer, 1950; Bock, 1966). To this end, we aim to investigate the relationships between muscle architectural correlates and bite force with ecological and behavioral factors across a broad sample of psittaciformes as well as to analyze three different potential biomechanical models of bite force estimation in this lineage.

### 1.1 The masticatory apparatus of parrots

The cranial architecture of parrots is characterized by a highly mobile nasofrontal hinge (NFH) which allows for increased movement of the upper beak (Bock, 1964; Zusi, 1993). Many genera possess an ossified suborbital arch that contributes to maxillary force transmission related to their high bite force (Homberger 2003, Smith 1975). Some groups take this character to the extreme, where in *Cacatua* and *Melopsittacus*, for example, the suborbital arch is partially fused with the zygomatic process, forming a bony tunnel transversed by the external adductor of the mandible (Smith, 1975).

While this group is highly phenotypically heterogenous, most of the jaw muscles are relatively consistent, though with notable size-related and topographic variation (Faillace et al., 2025). Parrots present two novel mandibular adductor muscles, namely *m. ethmomandibularis* (EM) and *m. pseudomasseter* (PM), with some species having a well-developed PM, most exhibiting an underdeveloped PM and few species without this muscle at all (Hofer, 1950; Tokita, 2003; Carril et al., 2015). While EM functions as a jaw adductor, PM can help in the sideways movement of the mandible (Homberger, 2003). Only two genera have the “*venter externus*”, an extension of *m. pterygoideus ventralis* that attaches ventral to the external acoustic meatus, functioning adducting the mandible and causing slight retraction of the jaw, possibly helping in beak opening (Hofer, 1950;

Faillace et al., 2025). Whilst there is no real consensus in the functional grouping of parrots' jaw muscles, many authors have presented similar functionality to most of the masticatory muscles in birds (Hofer, 1950; Bock, 1966; Baumel et al., 1993; Bhattacharyya, 2013). In this study, we follow the functional categorization presented in our previous work (Faillace et al., 2025).

### 1.2 Dietary ecology of Psittaciformes

Most parrots are considered generalist feeders, mainly consuming vegetation such as fruit, seeds, nuts, leaves and flowers. Among the few exceptions are the nectivorous lorries and lorikeets (Loriini) that mostly consume nectar and pollen, the Pygmy parrot (*Micropsitta*) that consumes fungi and lichen, and the Kea (*Nestor notabilis*) which has been documented to consume carrion (McDonald, 2003; Schwing, 2010; Navalón et al., 2019). Most species can be considered opportunistic generalists, consuming any food available in the habitat depending on the season and geographical range or switching dietary composition in response to fluctuating food availability (Moermond and Denslow, 1985; Benavidez et al., 2018; Voltura et al., 2024). Parrots with specialized diets tend to consume items available year-round or are likely to be highly mobile, traveling long distances to locate their preferred food (Renton et al., 2015). The red-bellied macaw (*Orthopsittaca manilatus*), for example, consumes mostly buriti fruit (*Mauritia flexuosa*), a type of palm tree found in wet areas and the Brazilian Cerrado, often traveling great distances to locate it (Silva and Melo, 2015).

A vast number of Psittaciformes are either described as granivore, frugivore, or spanning both categories (Lopes et al., 2016; Voltura et al., 2024). It has been proposed that since smaller species can only consume small obdurate items or take small bites out of soft larger items, they would tend more toward frugivory and even nectivory, while larger species that can access both large and small food items would tend to granivory to supply for greater energetic needs (Matuzak et al., 2008). Since there is high variation in body mass among parrots, their dietary needs should be reflected in the variation of their dietary breadth and composition (Benavidez et al., 2018) and the adaptations of their masticatory apparatuses as a result.

### 1.3 Bite force and jaw biomechanics of parrots

Although renowned for their high BF, very few studies at present have empirically measured bite force data of Psittaciformes. Published *in vivo* data collected via force transducers is limited to *Agapornis rosicollis*, some species of *Ara* (*Ara macao*, *Ara ararauna*, *Ara militaris*, *Ara chloropterus*, *Ara severus*, *Ara glaucogularis*), *Anodorhynchus hyacinthinus*, *Trichoglossus haematodus* and *Eupsittula* (*Aratinga*) *cunicularis* (Dickinson et al., 2022; Harrison et al., 2024). Cost et al. (2022) estimated BF for *Psittacus erithacus* via 3D muscles resultants rendered in micro-computed tomography. Estimations using anatomical data have been calculated for at least 19 species using varying methodology, making it difficult to compare these estimates between studies (Carril et al., 2015; Harrison et al., 2024).

Because the upper and lower jaw move independently and are articulated with multiple other mobile cranial bones, there are six main joints in the parrots' skull that relate to beak abduction and adduction: the quadratomandibular joint (QMJ), the synovial nasofrontal hinge (*zona flexoria craniofacialis*) (NFH), the quadrato-squamoso-otic joint, the maxillopalatine joint, the pterygopalatine joint and the quadratopterygoid joint (Bock, 1966; Homberger, 2003). All movable joints can be activated simultaneously by multiple muscles or muscle groups. Mandibular adduction is the main active component during biting in parrots, while the upper beak stabilizes the food item, minimizing lateral movement of the mandible and also contributing to bite force (Hrabar and Perrin, 2002; Homberger, 2003; Dickinson et al., 2022). Since the main fulcrum for maxillary depression is the NFH, we have included this joint in biomechanical analysis for bite force estimates in this group.

#### *1.4 Aims and hypotheses*

Our research focused on two main aspects, comprised by different hypotheses:

##### *1.4.1 Do muscle architectural variables correlate with diet and function?*

H1 – Anatomically estimated total adductor muscle force in species with a well-developed *m. pseudomasseter* (PM) should be higher than those with underdeveloped or absent PM.

H2 – Anatomically estimated bite force (BF) of species with a well-developed PM should be higher than ones with underdeveloped or absent PM.

H3 – Nectivorous feeders and species that consume a high proportion of fruit and nectar will have longer fascicles in beak abductive muscles when compared to taxa with more obdurate diets.

H4 – Species with more obturate diets will have higher anatomically estimated BF than taxa with softer diets.

H5 – Both jaw muscle mass and anatomically estimated BF will scale with body mass.

##### *1.4.2 Which bite force model is more appropriate to estimate bite force in Psittaciformes?*

H6 – All models should have statistically different total BF estimates.

H7 - The models that consider both mandibular adduction and maxillary depression in total BF will have higher force estimates than the single level model.

## 2. Materials and Methods

### 2.1 Sample

As in our recent paper describing the gross myological configuration of these taxa (Faillace et al., 2025), our sample for this investigation consists of 27 species from the families Cacatuidae, Psittaculidae and Psittacidae (Table 1), ranging from common pet species to threatened species (HBW and BirdLife International, 2022) and spanning most of the body size range of the group (Bird et al., 2020) from *Melopsittacus undulatus* at 29g to *Ara ararauna* at 1040g.

Table 1 – Sample size, body mass, dietary mechanical properties, source and preparation method of parrot specimens used.

| Family        | Species                         | Body mass (g)<br>* | Dietary mechanical properties<br>** | Identification number | Source | Preparation method |
|---------------|---------------------------------|--------------------|-------------------------------------|-----------------------|--------|--------------------|
| Cacatuidea    | <i>Cacatua moluccensis</i>      | 845                | H                                   | 401010                | AHR    | Frozen             |
|               | <i>Nymphicus hollandicus</i>    | 94,61              | H                                   | -                     | VET    | Frozen             |
| Psittaculidea | <i>Agapornis fischeri</i>       | 48,3               | H                                   | TR 91/24              | CETAS  | Frozen             |
|               | <i>Platycercus elegans</i>      | 123,86             | H                                   | 401012                | AHR    | Frozen             |
|               | <i>Platycercus eximius</i>      | 104                | H                                   | 401013                | AHR    | Frozen             |
|               | <i>Melopsittacus undulatus</i>  | 29                 | H                                   | -                     | CETAS  | Frozen             |
|               | <i>Lorius garrulus</i>          | 143                | S                                   | 505820                | NMNH   | Fluid              |
|               | <i>Neophema splendida</i>       | 38,6               | H                                   | 401016                | AHR    | Frozen             |
|               | <i>Eclectus roratus</i>         | 480,76             | M                                   | 542228                | NMNH   | Fluid              |
|               | <i>Vini australis</i>           | 49,5               | S                                   | 319750                | NMNH   | Fluid              |
|               | <i>Trichoglossus haematodus</i> | 113,25             | S                                   | 616027                | NMNH   | Fluid              |
|               | <i>Psittacula cyanocephala</i>  | 65,99              | M                                   | 401014                | AHR    | Frozen             |
|               | <i>Polytelis anthopeplus</i>    | 170                | H                                   | 401017                | AHR    | Frozen             |
| Psittacidea   | <i>Ara ararauna</i>             | 1040               | H                                   | TR 1889               | CETAS  | Frozen             |
|               | <i>Ara rubrogenys</i>           | 550                | H                                   | 401009                | AHR    | Frozen             |
|               | <i>Amazona aestiva</i>          | 451                | M                                   | TR 195, TR 1359/2023  | CETAS  | Frozen             |
|               | <i>Alipiopsitta xanthops</i>    | 327,37             | H                                   | -                     | CETAS  | Frozen             |
|               | <i>Aratinga solstitialis</i>    | 119,62             | S                                   | 401015                | AHR    | Frozen             |
|               | <i>Aratinga auricapilus</i>     | 130                | M                                   | -                     | CETAS  | Frozen             |
|               | <i>Brotogeris chiriri</i>       | 61,6               | S                                   | TR 373                | CETAS  | Frozen             |
|               | <i>Diopsittaca nobilis</i>      | 150,91             | H                                   | TR 43/23              | CETAS  | Frozen             |
|               | <i>Guaruba guarouba</i>         | 194                | H                                   | -                     | CETAS  | Frozen             |
|               | <i>Psittacara leucophthalma</i> | 158                | H                                   | TR 524                | CETAS  | Frozen             |
|               | <i>Pionus menstruus</i>         | 251                | M                                   | -                     | CETAS  | Frozen             |

|                                       |        |   |        |       |        |
|---------------------------------------|--------|---|--------|-------|--------|
| <i>Orthopsittaca manilatus</i>        | 372    | H | TR 59  | CETAS | Frozen |
| <i>Phyrrhura molinae</i>              | 77,09  | M | 401011 | AHR   | Frozen |
| <i>Rhynchopsitta<br/>pachyrhyncha</i> | 324,77 | H | 16198  | NCMNS | Fluid  |

(\*) average body mass following Wilman et al. (2014) and Bird et al. (2020)

(\*\*) based on the mechanical properties of the most common food items consumed in the wild. H – hard; S – Soft; M – Mixed. See “Dietary categorization” below.

The majority of specimens were fresh and kept frozen until use, with only a few preserved specimens being formalin fixed and stored in 70% ethanol (Table 1). Only adult individuals in good musculoskeletal condition were included in our study. Fresh specimens were ethically obtained from the Wild Animals Screening Center (CETAS-DF; Federal District, Brazil), donated from private veterinary clinics (VET - located in the city of Brasília, Federal District, Brazil) or deceased, domestically bred animals obtained through the taxidermy industry by the Hartstone-Rose Lab (AHR) at North Carolina State University (North Carolina, USA). Wet specimens were from the Smithsonian National Museum of Natural History (NMNH; Washington, USA), and the Ornithology Division of North Carolina Museum of Natural Science (NCMNS; North Carolina, USA). This work was deemed exempt from ethical regulation by the respective governing bodies: the Animal Ethics Committee according to Brazilian law (item 6.1.10/RN n° 30/2016 of DBCA) and North Carolina State University’s Institutional Animal Care and Use Committee.

## 2.2 Physiological cross-sectional area

All anatomical designations are based on our previous research on the gross myological descriptions of the masticatory anatomy of parrots (Faillace et al., 2025). The nomenclature used followed the *Nomina Anatomica Avium* (Baumel et al., 1993) and, in particular cases, other cited literature. Jaw muscles were categorized based on their main function in bill kinesis (Table 2) following published literature (Hofer, 1950; Bock, 1966; Baumel et al., 1993; Homberger, 2003; Bhattacharyya, 2013).

Table 2 – Psittaciformes jaw muscles' function.

| Main function                                 | Muscles names                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
|-----------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Mandibular adductors                          | <p>AMEV+PM: <i>mm. pseudomasseter et adductor mandibulae externus, pars ventralis</i></p> <p>AMER: <i>m. adductor mandibulae externus, pars rostralis</i></p> <p>AMEP: <i>m. adductor mandibulae externus, pars profunda</i></p> <p>AMP: <i>m. adductor mandibulae posterior</i></p> <p>EM: <i>m. ethmomandibularis</i></p> <p>PSS: <i>m. pseudotemporalis superficialis</i></p> <p>*PVL: <i>m. pterigoideus ventralis, pars lateralis</i></p> <p>*PVM: <i>m. pterigoideus ventralis, pars medialis</i></p> <p>*PDL: <i>m. pterigoideus dorsalis, pars lateralis</i></p> |
| Maxillary abductor (via quadrate protraction) | PPQ: <i>m. protractor pterigoideus et quadrati</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Maxillary depressors                          | <p>PVL: <i>m. pterigoideus ventralis, pars lateralis</i></p> <p>PVM: <i>m. pterigoideus ventralis, pars medialis</i></p> <p>PDL: <i>m. pterigoideus dorsalis, pars lateralis</i></p> <p>PDM: <i>m. pterigoideus dorsalis, pars medialis</i></p>                                                                                                                                                                                                                                                                                                                          |
| Mandibular depressors                         | <p>DMS: <i>m. depressor mandibulae, pars superficialis</i></p> <p>DMP: <i>m. depressor mandibulae, pars profunda</i></p>                                                                                                                                                                                                                                                                                                                                                                                                                                                 |

\* Homberger (2003) does not consider these muscles to be mandibular adductors, but other authors digress (Hofer, 1950; Bhattacharyya, 2013; Carril et al., 2015).

The jaw musculature was sharp dissected following standard protocol. All muscles were individualized and excised sequentially, with the exception of the pseudomasseter (when present) and the ventral part of the external adductor of the mandible that were removed *en bloc* due to high fusion between fibers at their attachments. After removal, all muscles were weighed using a digital scale (0,001g). Due to the complexity and variation of muscle fiber orientation, pennation angles were collected only in some birds, but were not used for calculations (Hartstone-Rose et al., 2019; Martin et al., 2020). Following Hartstone-Rose et al. (2021), individual muscles were placed in 30% nitric acid solution at room temperature to dissolve connective tissue to allow for the separation of individual fascicles. This took between six and 48 hours depending on specimen size and whether they were excised from fresh or fixed specimens. After digestion, muscles were transferred to 50% glycerol solution to neutralize the acid and prevent further digestion and then individual fascicles were separated, photographed and measured via ImageJ (Abràmoff et al., 2004). Depending on muscles size, between 10 and 30 fascicles were measured for each muscle (Martin, 2020).

FL were combined with their respective muscle masses to calculate the PCSA for each individual muscle with the following formula (Hartstone-Rose et al., 2021):

$$q = \frac{m}{lp}$$

where  $q$  is PCSA (cm<sup>2</sup>),  $m$  is muscle mass (g),  $l$  is average FL (cm) and  $p$  is a constant that describes muscle density (g/cm<sup>3</sup>). The muscle density used for fresh specimens was 1.0564 g/cm<sup>3</sup> (Carril et al., 2015), and 1.0022 g/cm<sup>3</sup> for fixed samples (Leonard et al., 2022a). While the museum specimens were often decades old, we used the short-term fixation correction factor presented by Leonard et al. (2022a) instead of the factor suggested for long-term fixed samples (Leonard et al., 2022b) for two main reasons: a) it resulted in muscle masses that were way over the average for the species with similar body mass suggesting this factor may not be appropriate for our sample, and b) the cited research used masticatory muscles in their short-term methodology, while their long-term research used limb musculature.

### 2.3 Biomechanical models

All models considered the bird skull as a system of lever-arms, with either one or two points of movement (fulcrum) – the QMJ alone or with the NFH – with the latter approach accounting for the BF contributions of both mandibular and maxillary movement. BF was estimated with the beak closed (i.e., 0° gape) at the most rostral point of the lower beak (with keratin sheath) since parrots are considered isognathous. Mechanical advantage for each individual muscle was estimated via lateral photographs of the skull using ImageJ (Abràmoff et al., 2004) where the origin and insertion centroids of single muscles were defined following dissection photos; the line of action (LOA) was created by connecting the centroids of each muscle attachments; in-levers were measured as the perpendicular distance between the fulcrum and each muscle's LOA; out-levers were calculated as the linear distance between the fulcrum and the tip of the bill.

Each muscle's output force ( $F_{out}$ ), or muscle force, was estimated following the adapted formula by Hildebrand et al. (2001):

$$F_{out} = F_{in} \times \frac{m}{M}$$

Where  $F_{in}$  is calculated by multiplying PCSA with the muscle tension constant of 30g/cm<sup>3</sup> (Medler, 2002; Soons et al., 2015);  $m$  is the muscle in-lever (cm) and  $M$  its out-lever (cm). Finally, BF was estimated as the sum of all  $F_{out}$  of the muscles that actively contributed to beak closure (i.e., mandibular adductors and maxillary depressors), multiplied by two, assuming muscles groups from both sides of the jaw were activated simultaneously. Three different bite force anatomical models were tested considering each of the jaw muscles' function (Table 2) and on which of the two fulcrums (only QMJ or both QMJ and NFH) the muscle groups act upon the most (Figure 1).

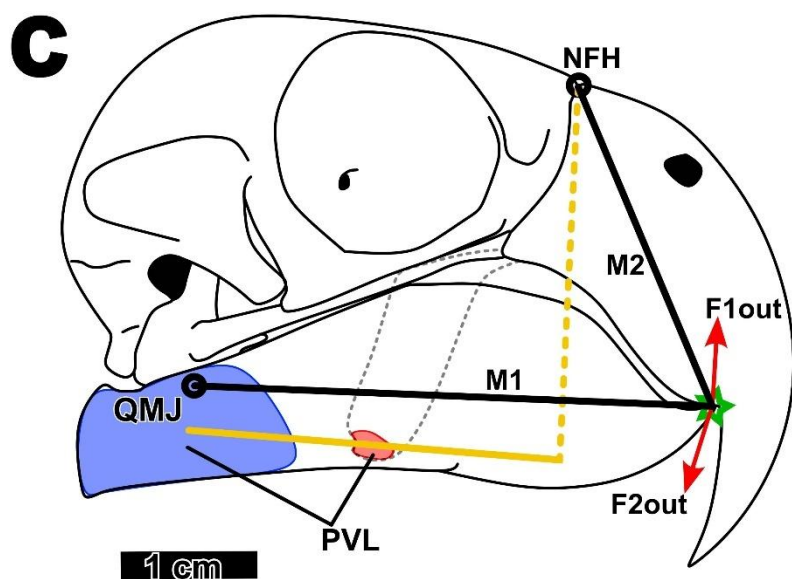
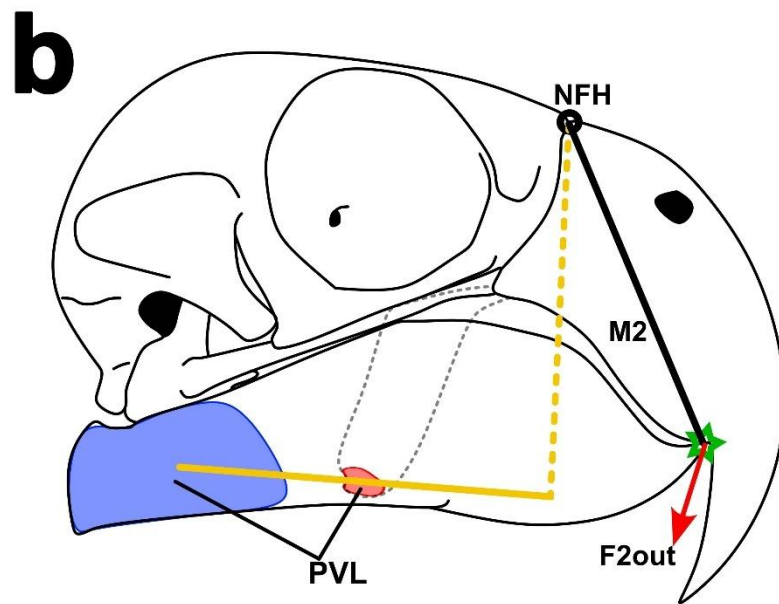
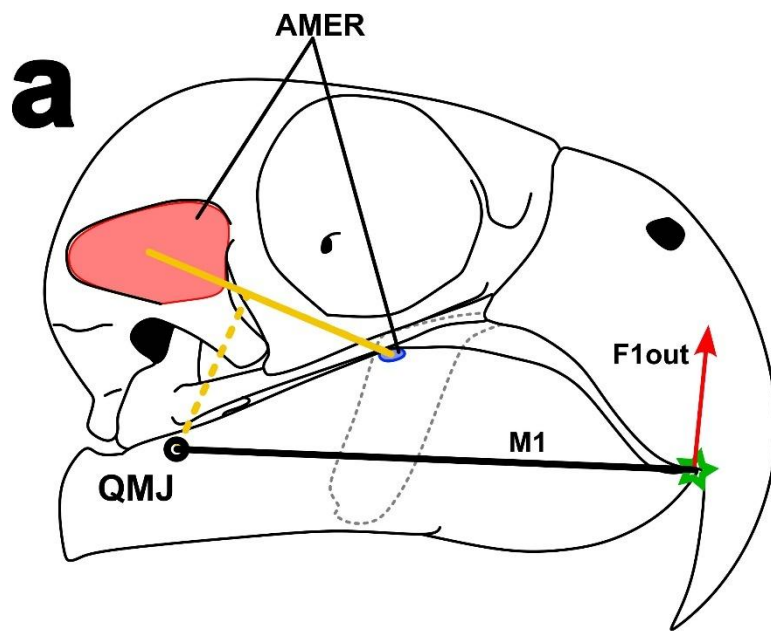


Figure 1 – Diagram a skull of an *Amazona aestiva* demonstrating muscle lever system using one mandible adductor (AMER) and one maxillary depressor (PVL) as examples. a: considering the quadratomandibular joint (QMJ) as the main fulcrum for the system; b: considering the nasofrontal hinge (NFH) as the main fulcrum for the system; c: considering both NFH and QMJ as main fulcrums for maxillary depressors. M1 – out-lever from QMJ to the bite point (green star); M2: out-lever from NFH to the bite point; Yellow dotted line: muscle's in-lever; Yellow line: muscle's line of action (LOA);  $F_{1out}$ : Output force of the mandible;  $F_{2out}$ : Output force of the maxilla. Notice the difference in force output represented by red arrow size.

In the standard model BF-MA (Figure 1a), the mandible was modeled in isolation, with the QMJ being the only fulcrum and out-lever of the system. This is the standard biomechanical model for bite force estimation for birds (Soons et al., 2010; Sustaita and Hertel, 2010; Carril et al., 2015; Harrison et al., 2024).

The maxilla model BF-MX (Figure 1a,b) considered both the mandible and maxilla as moving parts. When the mandible was modeled in isolation, mandible adductors acted only upon the QMJ, with the exception of the pterygoid complex. When the maxilla was isolated, the pterygoid complex acted upon the NFH.

In the all-functional force model BF-ALL (Figure 1a,c), the pterygoid complex was further separated into four individual muscles - PVL, PVM, PDL and PDM – where PVL, PVM and PDL acted on both the QMJ and NFH, while PDM only acted on NFH. We considered PVM to also act on the mandible because of its intimate connection to PVL observed during dissection. For the three muscles that acted on both joints, their final muscle output forces ( $F_{out}$ ) calculated at each fulcrum were halved, assuming an equal amount of force transmitted at each joint, prior to total BF calculation.

## 2.4 Dietary categorization

Studies on feeding ecology in a number of parrots were used to derive general and specific data on food consumption and categories (Joseph, 1992; Stewart and Shephard, 1996; Galetti, 1997; Gilardi and Munn, 1998; McDonald, 2003; Reynolds, 2003; de Faria et al., 2007; Franklin et al., 2008; Boussekey et al., 2010; de Araujo and Marcondes-Machado, 2011; Laranjeiras, 2011; Lee et al., 2014; Wilman et al., 2014; Silva and Melo, 2015; Lopes et al., 2016; Galbraith, 2018; Marques et al., 2018; Rumanta et al., 2019; Ragusa-Netto, 2022; Tobias et al., 2022; Vilarta et al., 2024; Voltura et al., 2024). Diet was described based on the mechanical properties (MP) of food items most often consumed, which in turn directly influences the overall work needed to access that item. The four most consumed food items (when available) were identified and categorized into soft (S), hard (H) and a mix of soft and hard items (M) with nuts and seeds being the hardest to consume, followed by bark, leaves, then fruit and finally flowers and nectar being the least obdurate (Table 1). Arthropods were considered hard items for species that were reported to feed on insects.

## 2.5 Data analysis

Incomplete architectural data for a small set of muscles (lost due to sample preservation of some specimens) were either reconstructed following Hartstone-Rose et al. (2012) or, when fully missing, imputed using the “mice” package in R (R Development Core Team, 2024).

All statistical analyses were conducted in R. Preceding analyses, all data were linearized (cubic roots were taken for volumetric variables and square roots for area variables) and log-transformed to adjust the expectation for isometric slopes to 1 for all regressions. We calculated the weighted average of fascicle lengths following Hartstone-Rose et al. (2012) to adjust for size. We considered data to be statistically allometric if the 95% confidence interval of the slope was greater than 1. Architectural variables (muscle mass, fascicle length, PCSA, muscle force) and estimated bite force (BF) for each biomechanical model (total of three BF) were regressed against body mass (BM) using reduced major axis regression (RMA) to examine for allometry.

RMA residuals were then compared to dietary mechanical property (MP) and muscle functional group (FG – mandibular and maxillary only) to check for correlations between muscle numerical variables and categorical data. For this, analysis of variance (ANOVA) was used to check for model-variable interactions and Tukey-Kramer HSD test were used ( $\alpha = 0.05$ ) to determine statistical significance between each categorical group.

To test the relationship of the different developing levels of PM in muscle force and BF, PM was separated into three categories, following Faillace et al. (2025): present, when the muscle is well-developed; underdeveloped, when it's thin and fascia-like; absent, no muscle present. Each category was then analyzed using ANOVA.

## 3. Results

### 3.1. Muscle architectural variables

Architectural muscle data for each specimen are shown in Supplement Table 1 and 2. Estimated bite force for all models and species are presented in Table 3.

Table 3 – Estimated bite force (BF) for three biomechanical models.

| Species                      | Estimated bite force (N/cm <sup>2</sup> ) |        |        |
|------------------------------|-------------------------------------------|--------|--------|
|                              | BF-MA                                     | BF-MX  | BF-ALL |
| <i>Agapornis fischeri</i>    | 14,32                                     | 42,82  | 34,50  |
| <i>Alipiopsitta xanthops</i> | 68,66                                     | 148,88 | 122,95 |
| <i>Amazona aestiva</i>       | 57,19                                     | 171,59 | 126,19 |
| <i>Ara ararauna</i>          | 70,76                                     | 233,69 | 213,28 |

|                                   |        |        |        |
|-----------------------------------|--------|--------|--------|
| <i>Ara rubrogenys</i>             | 76,87  | 278,79 | 215,25 |
| <i>Aratinga auricapilus</i>       | 23,46  | 87,81  | 62,05  |
| <i>Aratinga solstitialis</i>      | 14,81  | 49,28  | 30,65  |
| <i>Brotogeris chiriri</i>         | 10,53  | 38,11  | 28,89  |
| <i>Cacatua moluccensis</i>        | 134,37 | 432,58 | 284,65 |
| <i>Diopsittaca nobilis</i>        | 29,73  | 103,72 | 79,83  |
| <i>Eclectus roratus</i>           | 72,40  | 216,69 | 153,00 |
| <i>Guaruba guarouba</i>           | 34,82  | 164,09 | 135,31 |
| <i>Lorius garrulus</i>            | 30,44  | 114,72 | 91,31  |
| <i>Melopsittacus undulatus</i>    | 7,28   | 18,11  | 14,56  |
| <i>Neophema splendida</i>         | 4,65   | 12,01  | 8,96   |
| <i>Nymphicus hollandicus</i>      | 12,27  | 31,63  | 21,40  |
| <i>Orthopsittaca manilatus</i>    | 38,45  | 96,61  | 62,37  |
| <i>Phyrrhura molinae</i>          | 42,23  | 141,14 | 85,28  |
| <i>Pionus menstruus</i>           | 12,15  | 58,61  | 37,63  |
| <i>Platycercus elegans</i>        | 14,50  | 61,07  | 51,23  |
| <i>Platycercus eximius</i>        | 11,79  | 35,08  | 29,12  |
| <i>Polytelis anthopeplus</i>      | 28,35  | 123,33 | 85,62  |
| <i>Psittacara leucophthalma</i>   | 15,23  | 37,25  | 27,95  |
| <i>Psittacula cyanocephala</i>    | 8,91   | 28,40  | 25,91  |
| <i>Rhynchopsitta pachyrhyncha</i> | 14,70  | 52,32  | 32,78  |
| <i>Trichoglossus haematodus</i>   | 29,76  | 74,78  | 39,57  |
| <i>Vini australis</i>             | 9,45   | 30,46  | 16,05  |

Estimated bite force (BF) in all three biomechanical models scaled with positive allometry to both body mass (BM) and muscle mass (MM) (Table 4). Weighted fascicle length (FL) showed no relation to estimated BF on any models.

Table 4 – Reduced major axis regression of estimated bite force (BF) for each biomechanical model versus total sum of muscle mass (MM), average fascicle length (FL) and total sum of body mass (BM).

| <b>y - variable</b>       | <b>Treatment</b>                       | <b>Intercept</b> | <b>Slope</b> | <b>Slope 95% CI</b> | <b>R<sup>2</sup></b> |
|---------------------------|----------------------------------------|------------------|--------------|---------------------|----------------------|
| Log<br>ALL <sup>1/2</sup> | Log BM <sup>1/3</sup>                  | -0,1831          | 1,4334       | (1,1733 - 1,7510)   | 0,7606               |
|                           | Log total Mandibular MM <sup>1/3</sup> | 1,0282           | 1,268        | (1,0905 - 1,4744)   | 0,865                |
|                           | Log total Mandibular MM <sup>1/3</sup> | 0,9388           | 1,2312       | (1,0647 - 1,4744)   | 0,8747               |
|                           | Log average Mandibular FL              | 1,2202           | 1,2937       | (0,9992 - 1,6748)   | 0,5981               |
|                           | Log average Maxillary FL               | 0,9589           | 0,569        | (0,3813 - 1,6748)   | 0,0047               |
| Log BF-MA <sup>1/2</sup>  | Log BM <sup>1/3</sup>                  | -0,5193          | 1,3578       | (1,1229 - 1,6418)   | 0,7847               |
|                           | Log total Mandibular MM <sup>1/3</sup> | 0,8361           | 1,2012       | (1,0805 - 1,4744)   | 0,9337               |
|                           | Log total Mandibular MM <sup>1/3</sup> | 0,7514           | 1,1663       | (1,0076 - 1,4744)   | 0,873                |
|                           | Log average Mandibular FL              | 1,0180           | 1,2255       | (0,9344 - 1,6748)   | 0,5557               |
|                           | Log average Maxillary FL               | 0,7705           | 0,539        | (0,3615 - 1,6748)   | 0,0094               |
| Log BF-MX <sup>1/2</sup>  | Log BM <sup>1/3</sup>                  | -0,0957          | 1,4101       | (1,1620 - 1,7112)   | 0,7765               |
|                           | Log total Mandibular MM <sup>1/3</sup> | 1,0960           | 1,2474       | (1,096 - 1,4744)    | 0,9007               |
|                           | Log total Mandibular MM <sup>1/3</sup> | 1,0080           | 1,2112       | (1,0738 - 1,4744)   | 0,9141               |
|                           | Log average Mandibular FL              | 1,2848           | 1,2727       | (0,9857 - 1,6748)   | 0,6068               |
|                           | Log average Maxillary FL               | 1,0278           | 0,5597       | (0,3754 - 1,6748)   | 0,0089               |

When exploring the effects of the functional grouping presented in Table 2 on BM, both the protractor of quadrates and pterygoid and the mandible depressors MM scaled with positive allometry (Figure 2). The average FL showed no interaction with BM. Finally, PCSA scaled with positive allometry to BM, supporting Hypothesis 5.

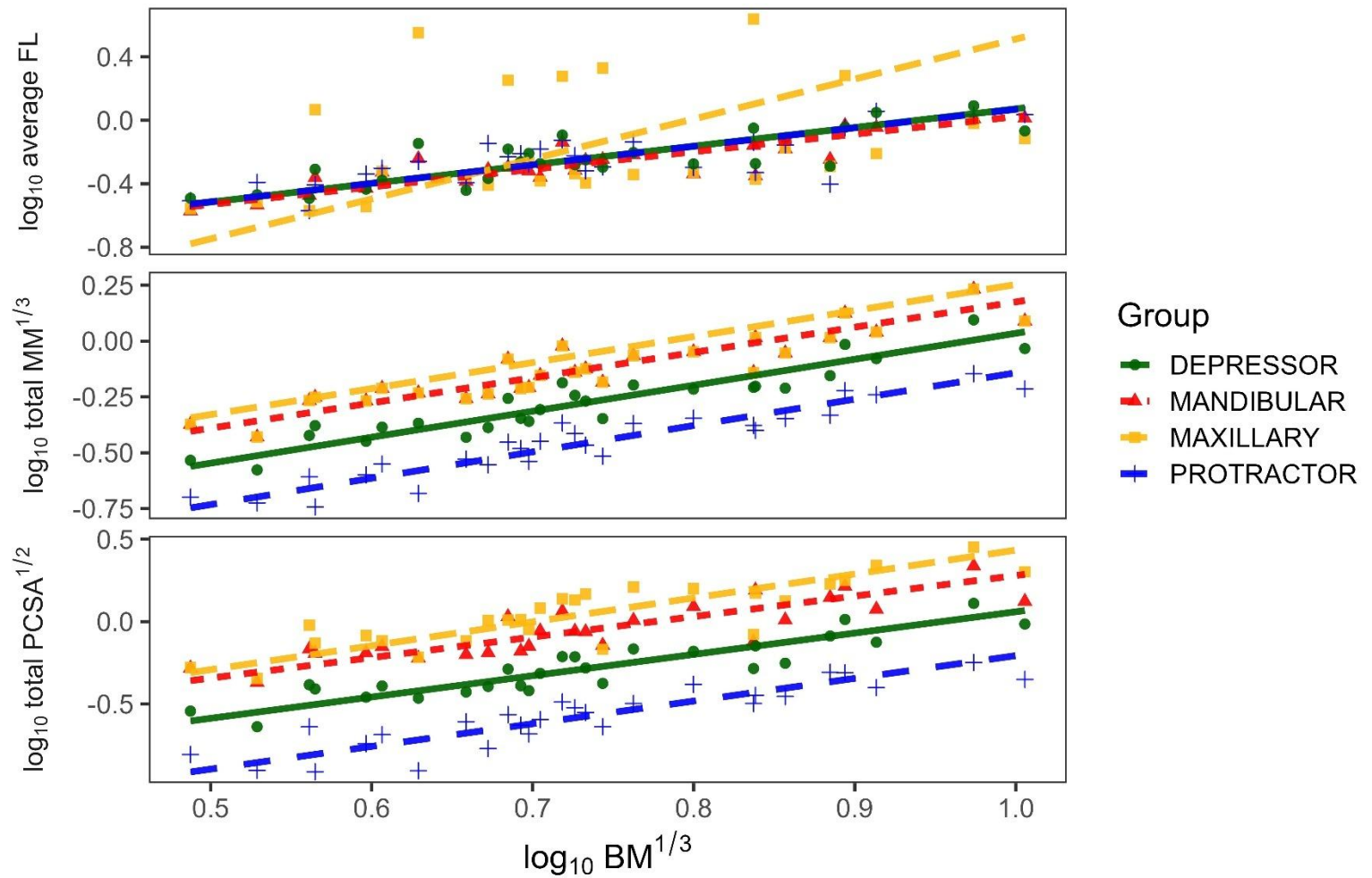


Figure 2 – Graphical representation of reduced major axis regression of total muscle mass (MM), average fascicle length (FL) and total physiological cross-sectional area (PCSA) of jaw muscles functional groups against body mass (BM).

Analysis of variance (ANOVA) for MM against the jaw muscles' functional groups showed statistical significance ( $p < 0.05$ ), where Tukey-Kramer HSD test showed that the maxillary depressors differed from all other groups, suggesting it had greatest muscle mass (Table 5). This trend was observed across the sample, with maxillary depressors (i.e. the pterygoid complex) being the most massive masticatory muscle followed by mandibular adductors (Figure 2).

Table 5 – Analysis of variance and Tukey-Kramer test for total of muscle mass (MM) and average fascicle length (FL) for functional groups.

| y-variable                  | ANOVA             |    |              |         |
|-----------------------------|-------------------|----|--------------|---------|
|                             | Treatment         | DF | DF Residuals | p value |
| Log total MM <sup>1/3</sup> | Functional Groups | 3  | 104          | 0,0001  |
| Log average FL              |                   | 3  | 104          | 0,0016  |

| y-variable                  | Tukey-Kramer Test   |         |                     |                  |
|-----------------------------|---------------------|---------|---------------------|------------------|
|                             | Group               | Diff    | Diff IC             | p value adjusted |
| Log total MM <sup>1/3</sup> | Mand Add-Dep Mand   | 0,1491  | (0,0375 -0,2607)    | 0,0039           |
|                             | Max Dep-Dep Mand    | 0,2179  | (0,1063 -0,3296)    | 0,0000           |
|                             | Protractos-Dep Mand | -0,1815 | (-0,2931 --0,0699)  | 0,0003           |
|                             | Max Dep-Mand Dep    | 0,0688  | (-0,0428 -0,1805)   | 0,3777           |
|                             | Protractos-Mand Dep | -0,3306 | (-0,4422 --0,2190)  | 0,0000           |
|                             | Protractos-Max Dep  | -0,3994 | (-0,5111 - -0,2878) | 0,0000           |
| Log average FL              | Mand Add-Dep Mand   | 0,0052  | (-0,1728 -0,1831)   | 0,9998           |
|                             | Max Dep-Dep Mand    | 0,2390  | (0,0610 -0,4168)    | 0,0037           |
|                             | Protractos-Dep Mand | 0,1110  | (-0,0665 -0,2893)   | 0,3639           |
|                             | Max Dep-Mand Dep    | 0,2340  | (0,0558 -0,4116)    | 0,0047           |
|                             | Protractos-Mand Dep | 0,1060  | (-0,0717 -0,2842)   | 0,4066           |
|                             | Protractos-Max Dep  | -0,3054 | (-0,3054 -0,0504)   | 0,2469           |

ANOVA and Tukey-Kramer HSD test for average FL against muscle functional groups showed that the maxillary depressors had longer fascicles than mandibular adductors and depressors of the mandible (Table 5).

Residuals for muscle force (MF) and PCSA of the mandibular adductors against BM, along with residuals from total BF on all models against BM, were analyzed using ANOVA to test for interaction between the development level of *m. pseudomasseter* (i.e. present, underdeveloped and absent) (Figure 3; Table 6). There was statistical significance for both MF and PCSA. Tukey-Kramer HSD test for MF showed that the category “present” was the greatest in value, with “underdeveloped” being smaller than it, but statistically similar to “absent”. For PCSA, on the other hand, “underdeveloped” was both the smallest value and statistically different from “present” and “absent”. Finally, total BF showed no interaction, suggesting that only MF and PCSA are influenced by the development levels of *m. pseudomasseter*, supporting Hypothesis 1 and rejecting Hypothesis 2.

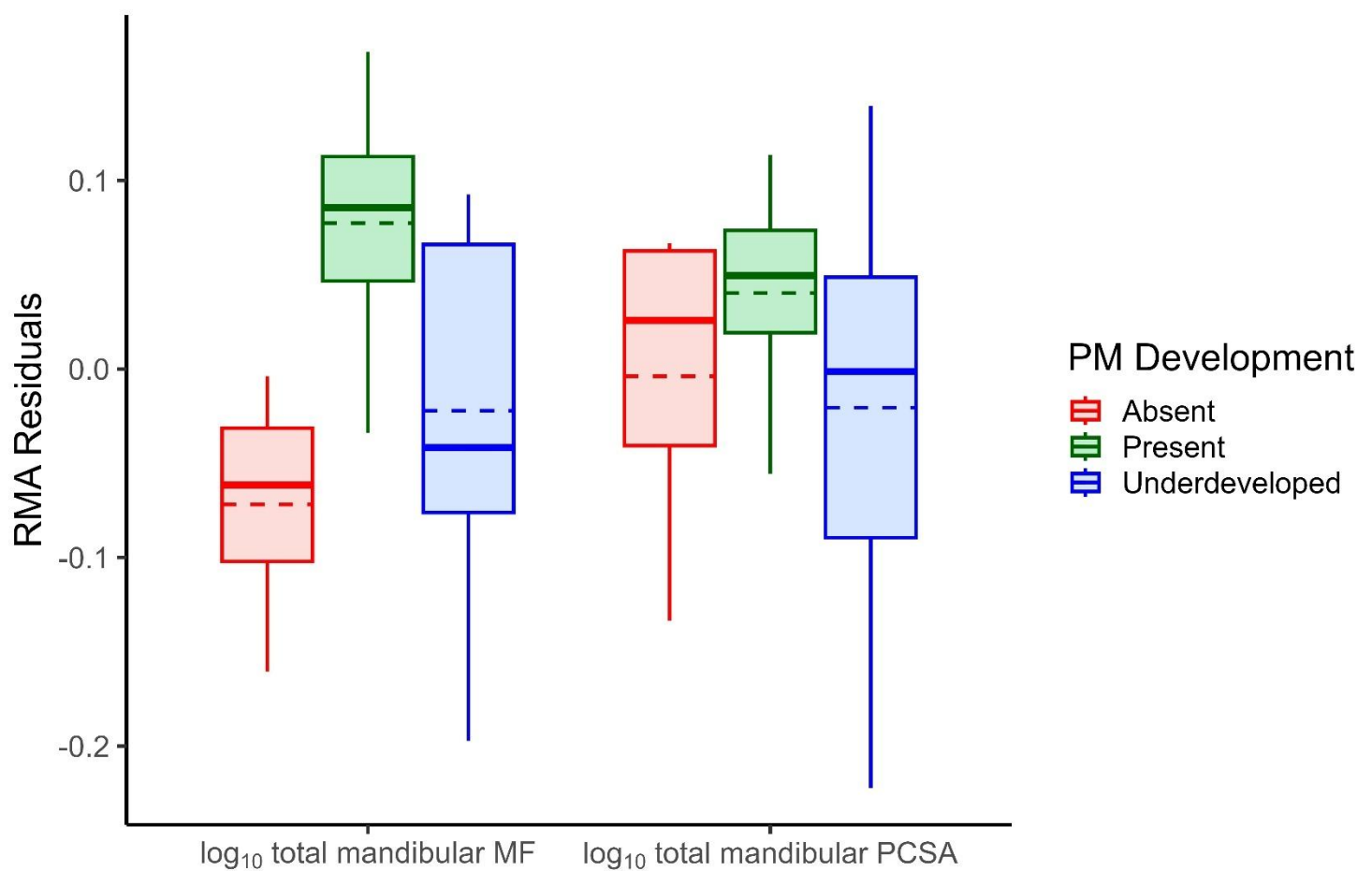


Figure 3 – Boxplot demonstrating data dispersion of muscle force (MF) and PCSA of mandibular adductors against development levels of *m. pseudomasseter* (PM).

Table 6 – Analysis of variance of development levels of *m. pseudomasseter* (PM) with the residuals for each biomechanical models' bite force (BF), mandibular muscle force (MF) and mandibular PCSA against body mass (BM).

| y-variable                                                           | ANOVA          |    |              |         |
|----------------------------------------------------------------------|----------------|----|--------------|---------|
|                                                                      | Treatment      | DF | DF Residuals | p value |
| Residuals Log BF-ALL <sup>1/2</sup> ~ Log BM <sup>1/3</sup>          | PM development | 2  | 24           | 0,3482  |
| Residuals Log BF-MA <sup>1/2</sup> ~ Log BM <sup>1/3</sup>           |                | 2  | 24           | 0,1290  |
| Residuals Log BF-MX <sup>1/2</sup> ~ Log BM <sup>1/3</sup>           |                | 2  | 24           | 0,5707  |
| Residuals Log Mandibular MF <sup>1/2</sup> ~ Log BM <sup>1/3</sup>   |                | 2  | 24           | 0,0053  |
| Residuals Log Mandibular PCSA <sup>1/2</sup> ~ Log BM <sup>1/3</sup> |                | 2  | 24           | 0,0120  |

|                                                                      |  |  | Tukey-Kramer Test      |         |                    |                  |
|----------------------------------------------------------------------|--|--|------------------------|---------|--------------------|------------------|
| y-variable                                                           |  |  | Group                  | Diff    | Diff IC            | p value adjusted |
| Residuals Log Mandibular MF <sup>1/2</sup> ~ Log BM                  |  |  | Present-Absent         | 0,1492  | (0,0330 -0,2655)   | 0,0102           |
|                                                                      |  |  | Underdeveloped-Absent  | 0,0497  | (-0,0571 -0,1565)  | 0,4863           |
|                                                                      |  |  | Underdeveloped-Present | -0,0995 | (-0,1826 --0,0164) | 0,0168           |
| Residuals Log Mandibular PCSA <sup>1/2</sup> ~ Log BM <sup>1/3</sup> |  |  | Present-Absent         | 0,1382  | (0,0190 -0,2574)   | 0,0209           |
|                                                                      |  |  | Underdeveloped-Absent  | 0,0463  | (-0,0632 -0,1559)  | 0,5496           |
|                                                                      |  |  | Underdeveloped-Present | -0,0919 | (-0,1771 --0,0066) | 0,0329           |

### 3.2. Dietary mechanical properties

Analyses of RMA residuals of maxillary MM against BM showed significant interaction for mechanical property (MP), with Tukey-Kramer HSD test demonstrating a significant difference between the “Soft” and “Hard” categories (Table 7). For further analysis, a “simplified MP” was created that combined “Mixed” and “Hard” categories as “Other”, with “Soft” unchanged. To test Hypothesis 3, we regressed average FL of muscles related to maximum gape (i.e. DMS, DMS and PPQ) against BM, and analyzed the residuals of this RMA against a simplified MP. It showed statistical significance ( $p < 0,05$ ) and, upon further exploratory analysis using ANOVA and Tukey test, it showed that average fascicle length of maximum gape muscles for soft food consuming birds was significantly higher, supporting Hypothesis 3 (Table 7).

Table 7 – Analysis of variance for mechanical properties of residuals with maxillary muscle mass (MM), mandibular fascicle length (FL) and max gape\* FL against body mass (BM).

|                                                                   |  |  | ANOVA                            |        |                   |                  |
|-------------------------------------------------------------------|--|--|----------------------------------|--------|-------------------|------------------|
| y-variable                                                        |  |  | Treatment                        | DF     | DF Residuals      | p value          |
| Residuals Log Maxillary MM <sup>1/3</sup> ~ Log BM <sup>1/3</sup> |  |  | Mechanical Properties            | 2      | 24                | 0,017            |
| Residuals Log Mandibular average FL ~ Log BM <sup>1/3</sup>       |  |  | Simplified Mechanical Properties | 1      | 25                | 0,0399           |
| Residuals Log Max Gape average FL ~ Log BM <sup>1/3</sup>         |  |  | Properties                       | 1      | 25                | 0,0464           |
|                                                                   |  |  | Tukey-Kramer Test                |        |                   |                  |
| y-variable                                                        |  |  | Group                            | Diff   | Diff IC           | p value adjusted |
| Residuals Log Maxillary MM <sup>1/3</sup> ~ Log BM <sup>1/3</sup> |  |  | Mixed-Hard                       | 0,0418 | (-0,0142 -0,0978) | 0,1714           |
|                                                                   |  |  | Soft-Hard                        | 0,0700 | (0,0109 -0,1291)  | 0,0181           |
|                                                                   |  |  | Soft-Mixed                       | 0,0282 | (-0,0392 -0,0955) | 0,5567           |

|                                    |     |            |              |        |                  |        |
|------------------------------------|-----|------------|--------------|--------|------------------|--------|
| Residuals                          | Log | Mandibular |              | 0,0730 | (0,0037 -0,1424) | 0,0399 |
| average FL ~ Log BM <sup>1/3</sup> |     |            | Soft - Other |        |                  |        |
| Residuals                          | Log | Max        | Gape         | 0,0886 | (0,0015 -0,1756) | 0,0464 |
| average FL ~ Log BM <sup>1/3</sup> |     |            |              |        |                  |        |

\*max gape is a result of the total average FL for DMD, DMS and PPQ.

Analyses of RMA residuals for all estimated BF for MP showed no statistical significance, rejecting Hypothesis 4.

### 3.3. Biomechanical models

Regression analysis of estimated BF against BM demonstrated positive allometry (Figure 4). Estimated BF for each biomechanical model was tested using ANOVA, showing statistical significance between all models' interactions (Table 8). After applying for the Tukey-Kramer HSD test, BF-MA had the smallest BF estimates and was statistically different from the other two. This supports Hypothesis 6.

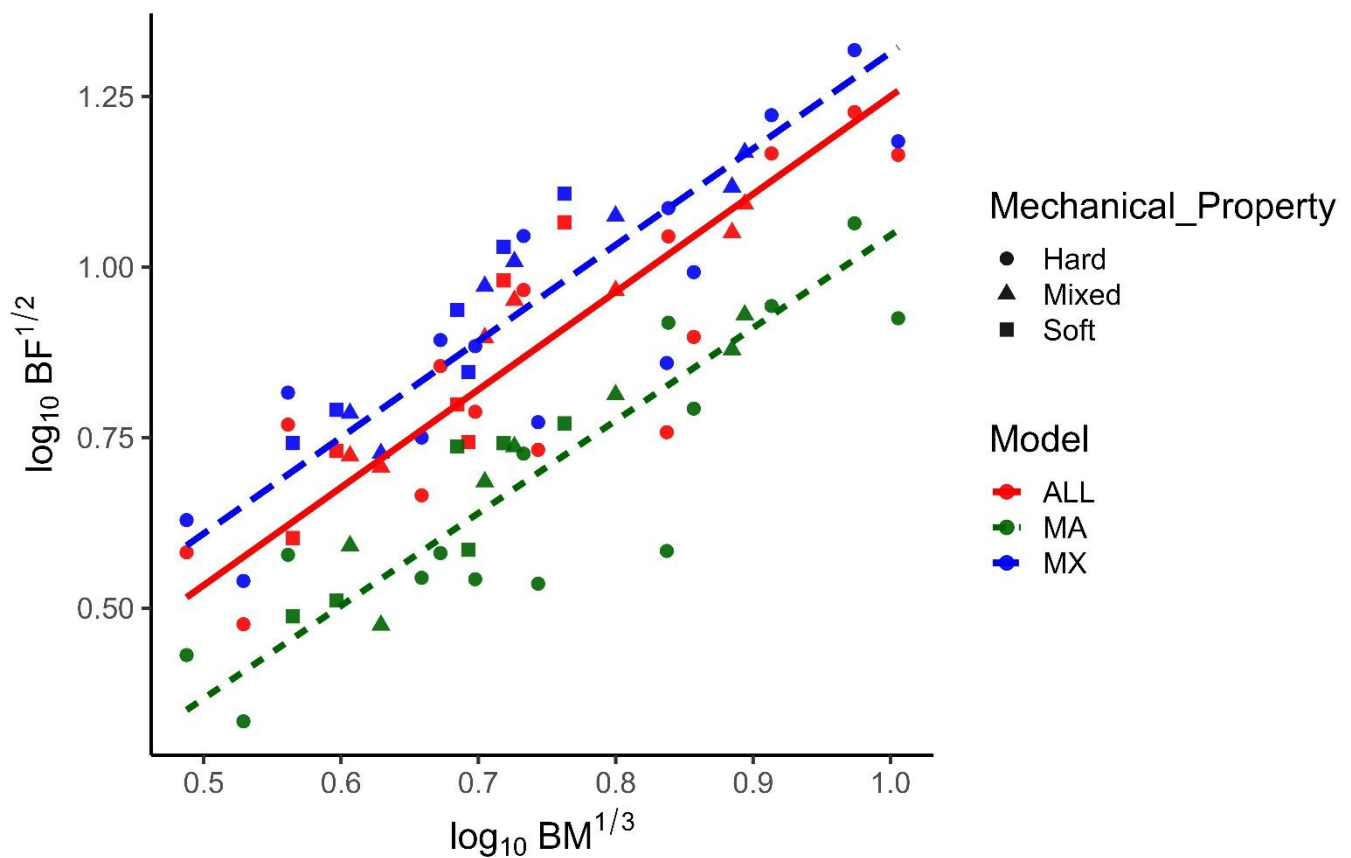


Figure 4 – Graphical representation of reduced major axis of estimated bite force (BF) for all three biomechanical models against body mass (BM).

Table 8 – Analysis of variance and Tukey-Kramer test of total bite force (BF) against all three biomechanical models (MA, MX, ALL).

| y-variable   | ANOVA             |         |                   |                  |
|--------------|-------------------|---------|-------------------|------------------|
|              | Treatment         | DF      | DF Residuals      | p value          |
| Log total BF | BF model          | 2       | 78                | 0                |
| y-variable   | Tukey-Kramer Test |         |                   |                  |
|              | Group             | Diff    | Diff IC           | p adjusted value |
| Log total BF | MA-ALL            | -0,1836 | (-0,3070 -0,0601) | 0,0019           |
|              | MX-ALL            | 0,0704  | (-0,0530 -0,1938) | 0,3656           |
|              | MX-MA             | 0,2539  | (0,1305 -0,3773)  | 0,0000           |

The fulcrum used to calculate maxillary depressor MF greatly influenced results, with the quadratomandibular joint (QMJ) estimates being lower than the ones resulting from the nasofrontal hinge (NFH). Maxillary MF estimated at QMJ were even lower than the mandibular MF estimates at QMJ, suggesting that the maxillary muscles are less strong than mandibular adductors when using the same fulcrum for biomechanical analysis (Figure 5).

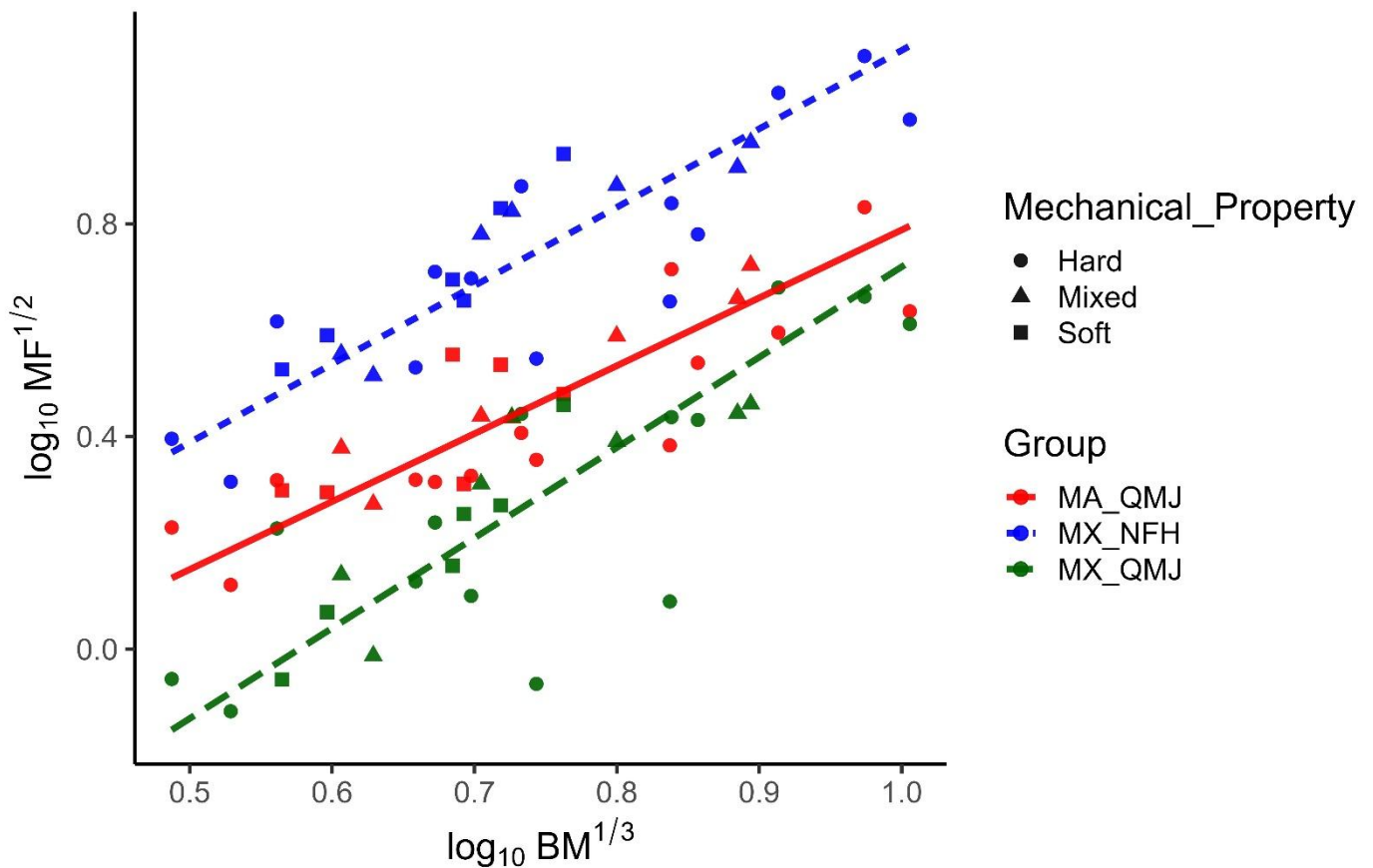


Figure 5 - Graphical representation of reduced major axis of muscle force (MF) using two different fulcrums, against body mass (BM). MA-QMJ: mandibular adductors muscles MF with QMJ; MX-NFH: maxillary depressors MF with NFH; MX-QMJ: maxillary depressors MF with QMJ.

## 4. Discussion

### 4.1. Myological variables inferences

Bite force (BF) and total muscle mass (MM) scaled positively with body mass (BM) in the parrots studied, in accordance with recent literature (Harrison et al., 2022; Harrison et al., 2024). Total physiological cross-sectional area (PCSA) also scaled positively with BM. This demonstrates that, as these muscles become more massive, their impacts on PCSA and total BF increase accordingly. However, average fascicle length (FL) showed no such relation to BM (Table 1, Figure 2). In jaw muscles, longer fascicles allow for increased maximum gape and, consequently, faster contraction, whilst shorter fascicles are linked to higher force (Herrel et al., 2012). This lack of relation between FL and BM may reflect a high specialization in parrots' jaw muscles, where some muscle groups are more tuned to velocity, while others in maximizing force (Corbin et al., 2015).

In other avian groups, the scaling patterns of these variables with BM between passerines and non-passerines is inconsistent (Deeming et al., 2022). Some passerine species, like finches, demonstrated positive allometry when comparing BF and BM, while others such as estrildids showed isometry (van der Meij and Bout, 2004; van der Meij and Bout, 2008). Jaw muscle mass, however, was isometric with BF in the aforementioned passerines and in diurnal raptors (Sustaita, 2008). Such heterogeneity reinforces masticatory muscles as important morphological characters that reflect adaptive traits among avians.

The *m. pseudomasseter* (PM) is only found in parrots and has commonly been hypothesized to increase total BF due to its rostralateral position in the cranium (Hofer, 1950; Carril et al., 2015). However, this muscle is not consistent within this group, with species such as cockatoos having a large, well-developed belly, many neotropical and Australasian species having only a thin belly with scarce fibers, to finally being absent in birds like *Ara* (Hofer, 1950, 1953). We have found that, while a well-developed PM significantly influences mandibular adductors' muscle force and PCSA estimates (Figure 3, Table 6), it does not contribute significantly to total bite force. This suggests that PM might have a functional relevance, rather than purely to increase bite force. Functionally, the PM allows for greater shearing (rostral) movement of the mandible, while weak or absent PM allows for a more caudal movement of the mandible (scraping motion) (Homerger, 2003). This is also supported by the fact that species that have no PM, such as *Ara*, can still generate high bite forces (Carril et al., 2015).

### 4.2. Diet and bite force correlations

Finches (Frigilidae) are known for having a high BF that tightly correlates to their diet and which is mainly comprised of hard seeds (van der Meij and Bout, 2004; van der Meij and Bout, 2008). Similarly, psittaciformes produce high BFs and consume large quantities of seed and nuts and were therefore thought to have similar correlations to feeding ecology, however, we found limited data related to this.

Maxillary depressors' MM and PCSA were consistently higher than other muscle functional groups in all families within our sample (Figure 2). This suggests that upper beak adduction is of significant value for this group of birds, and it can be either related to dietary needs or other behavioral factors. For example, we found that the maxillary depressors MM was highest in birds that consume mostly soft food (Table 7), albeit many of the nectivorous and highly frugivorous species in our sample were ethanol fixed specimens which may have influenced the total MM, even though a correction factor was applied to mitigate the resulting changes in MM (Leonard et al., 2022a; Leonard et al., 2022b). It has also been experimentally demonstrated that parrots use the upper beak to stabilize food items and the mandible as the main force component to process such item, while the upper beak is the solely responsible for body propulsion during vertical climbing and parrot beak-gait locomotion (beakiation) (Dickinson et al., 2022; Young et al., 2023; Young et al., 2022).

To consume nectar and pollen, lorries and lorikeets (Loriini) must open their bill and protrude their modified, brush-like tongue to lick food from the flowers (McDonald, 2003). Other small, soft food consuming parrots also require a large gape to better access various fruits and flowers (Matuzak et al., 2008). Upon inspection of average FL of muscles related to maximum gape (i.e. mandibular depressors and protractor of quadrate and pterygoid) in soft food consuming parrots against the other dietary categories, we found that average FL for this group were longer when compared to others (Table 7), which may allow for increased gape and faster bite (Herrel et al., 2012). The less curved, more gracile beak seen in nectivorous and other small, mostly frugivorous species like *Brotoogeris* is another possible adaptation that could facilitate access to their favored food items (Galetti, 1997). This suggests that a high specialization to certain food items may indeed be reflected in the masticatory anatomy of this group.

The parrot's bill is a multifunctional tool responsible for a vast array of ecological and behavioral actions, and evolutionary paths depend on both environmental changes and how organisms adapt to these new conditions (Ramírez-Herranz et al., 2024). It is used by some species to excavate soft earth for food acquisition (Voltura et al., 2024) and for clay consumption in nutrient deprived forests (Lee et al., 2010). Tool use has been recorded in the New Zealand Kea (*Nestor notabilis*), Goffin's Cockatoo (*Cacatua goffini*) and two species of *Ara* (Huber and Gajdon, 2006; O'Hara et al., 2021; O'Neill et al., 2021), requiring precise beak use to fabricate and manipulate makeshift tools. Additionally, over 70% of parrot species nest in tree cavities as secondary nesters, using the beak to adjust the tree hollow size (Renton et al., 2015; Ramírez-Herranz et al., 2024). Almost all members of this taxa are excellent climbers, and the beak plays an important role as a "third member", with the bill alone is strong enough for the parrot to support its own weight (Young et al., 2023; Dickinson et al., 2024). Lastly, due to their high intelligence and social behavior, it has been documented that parrots actively choose harder to access food items, a behavior known as contrafreeloading - favoring working to acquire food possibly as a source of mental stimulation (Beekmans et al., 2023). Diet, along with its

mechanical properties, is simply one of many factors involved in the adaptation of the parrot beak.

#### 4.3. Biomechanical models

Estimated bite force using dissection and PCSA has been validated with *in vivo* data in many mammals (Ginot et al., 2018, 2019), reptiles (Curtis et al., 2010; Groning et al., 2013; Meyers et al., 2018), the cownose ray (Kolmann et al., 2015), and even grasshoppers (Ginot and Blanke, 2024), but few studies have done the same for birds. When comparing estimated with *in vivo* bite and grip force of diurnal birds of prey, Sustaita and Hertel (2010) found that estimated forces were consistently higher than empirical ones, although functional and scaling predictions of PCSA and total force were correlated with measured data.

Bite force assessment through PCSA, mechanical advantage, and lever-arms systems are similarly modeled between birds and reptiles - both consider the mandible as a static third-class lever system and the QMJ as the main fulcrum - with the BF-MA model in this study based on these assumptions. Birds, however, have a much more movable skull (Bout and Zweers, 2001). Parrots' skulls are highly prokinetic and morphologically adapted to biting using both the mandible and maxilla (Homburger, 2003; Dickinson et al., 2022), so a single lever system such as BF-MA has biomechanical limitations.

Both BF-MX and BF-ALL models proposed in this study considered maxillary depression as a relevant factor in estimated total bite force. They showed that the pterygoid complex was capable of a much higher force than the mandibular adductors (Figure 4, 5). While all three models had similar scaling patterns with body mass and muscle variables, estimated total bite force was statistically different among themselves, with BF-MX and BF-ALL having significantly similar results (Table 8). Considering that the maxillary depressors were the heaviest muscle group and have the greatest PCSA (Figure 2, Table 5), it is appropriate to expect that it should have greater force than the mandibular adductors. This result, however, is only observed within the models BF-MX and BF-ALL (Figure 5), suggesting that they are more sensible in capturing realistic force generated by the maxillary depressors than the single lever system BF-MA model. More complex models, combining myological input forces with fully kinesthetic models of all mobile cranial bones and joints resolved in three-dimensional digital space, may be beyond the capacity of current modeling software (Granatosky and Dickinson, pers. comm.). As modeling software becomes robust enough to more fully account for more of the complexities of this system, and more *in vivo* data become available, we will be able to anatomically calculate BF with greater precision and validate these estimates.

Unfortunately, only two species in our sample have published *in vivo* bite force, preventing a statistically significant validation for these biomechanical models. Taking that into consideration, total bite force estimated by BF-MX model for *Ara ararauna* was of 234N and 39N by BF-ALL for *Trichoglossus haematodus*, with their *in vivo* values of 259,77N and 52,45N respectively (Table 3) (Harrison et al., 2024). This model also estimated a force of 432N for *Cacatua moluccesis*, while measured *in vivo* bite force for

*Anodorhynchus hyacinthinus*, the largest flying psittaciform, was 538,86N (Harrison et al., 2024). The *Cacatua* has a robust skull and massive jaw muscles, which can proportionally increase its BF despite being much smaller than *Anodorhynchus*. Finally, the *in vivo* value for *Agapornis roseicollis* was 16,83N (Dickinson et al., 2022), a species with similar body size and diet to *Agapornis fischeri*. The BF-MX model estimated a value of 42N, while the BF-MA model estimated 14N.

## 5. Limitations and future directions

Psittaciformes are mostly dietary generalists with few examples of diet specialization, although these species are still observed to have some level of diet plasticity (Renton et al., 2015; Lopes et al., 2016). Publications on the dietary habits of wild parrots are limited, with approximately 44% of 380 species having poor information available (Voltura et al., 2024). Lastly, wild parrots consume mainly native species found in their geographical range, increasing considerably the number and characteristics of mechanical properties of the food items consumed (Benavidez et al., 2018). This makes diet categorization of this group excruciatingly difficult, limiting considerably our analysis on dietary correlates.

While PCSA is a reliable proxy to estimate bite force for interspecies comparison, it has variable significance at the intraspecific level, with individual-level differences influencing final bite force (Ginot et al., 2018). Furthermore, published values of intrinsic muscle strength, a variable needed to calculate PCSA, vary considerably (between 25 Ncm<sup>2</sup> and 40 Ncm<sup>2</sup>), and with no real consensus among available studies on avian bite force estimations (Groning et al., 2013).

## 6. Conclusions

The uniqueness of the parrot beak systems and its dual function was reflected in the jaw muscle's morphology within this sample. Our results suggest that parrots do indeed have high bite force, and that muscle mass, physiological cross-sectional area and bite force scaled positively against body mass. Fascicle length had isometry with body mass. When well-developed, the *m. pseudomasseter* increased the muscle force and PCSA of the mandible adductors but did not significantly contribute to increased bite force estimated in the biomechanical models. Although dietary mechanical properties had no significant correlation to bite force, we found out that nectivorous birds and small, soft food consuming birds have longer fascicles in muscles related to maximum gape (mandibular depressors and protractor of quadrate and pterygoid), an adaptation that allows parrot species to better access to their favored food items. Unfortunately, it was not possible to validate these models due to lack of published *in vivo data*. Lastly, the BF-MX and BF-ALL models showed greater bite force estimates than BF-MA, since they considered the influence of the massive maxillary adductors on total bite force.

## Acknowledgment

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## CONSIDERAÇÕES FINAIS

Os músculos mastigatórios dos psitacídeos se mantiveram relativamente homogêneos nas diferentes espécies estudadas. As principais características relevantes foram o alto grau de variação do músculo pseudomasseter, a ossificação total do arco suborbital (inclusive com fusão deste com o processo zigomático em *Cacatua*, *Nymphicus* e *Melopsittacus*) e a presença do ventre externo da parte lateral do músculo pterigoide ventral, presente em apenas dois gêneros de psitacídeos (*Platycercus*, *Cyanoramphus*).

A força de mordida dos papagaios estimada através de modelos anatômicos de biomecânica foi proporcionalmente elevada relativo ao peso corporal do grupo. Após analisar características de morfologia muscular (massa muscular, comprimento de fibras, PCSA) com força de mordida, dieta e grupos funcionais musculares, concluímos que: (1) a massa muscular e força de mordida se comportam de forma positivamente alométrica com massa corporal dos indivíduos; (2) não houve correlação alta força de mordida e animais que consomem muitas sementes e castanhas, entretanto, houve correlação entre um maior comprimento dos fascículos do músculos depressores de mandíbula e abdutor de maxila com animais nectívoros e com grande consumo de frutas; (3) o músculo pseudomasseter bem desenvolvido influencia na força muscular total e no PCSA dos músculos adutores, porém, não influencia na estimativa total da força de mordida, sendo similar à os seus outros estágios de desenvolvimento.

Apesar de não ter sido possível validar os modelos anatômicos de estimativa de força de mordida pela escassez de valores reais de mordida das espécies estudadas, foi possível concluir que: (1) os dois modelos que consideravam o movimento da maxila como componente da força de mordida final estimaram forças estatisticamente maiores que o modelo que utiliza apenas a mandíbula como alavanca; (2) os mesmos dois modelos estimaram forças estatisticamente maiores para o grupo dos pterigoides, músculos responsáveis pela depressão da maxila, sendo mais condizente com os valores morfológicos (ex. massa muscular) coletados para estes músculos do que o modelo mandibular.

### *Considerações do Programa de Doutorado Sanduíche no Exterior - PDSE*

Este intercâmbio para a Carolina do Norte, EUA, foi fundamental para o meu projeto e me proporcionou enormes aprendizados, não só na parte prática com as dissecações, técnicas de digestão de músculo, biomecânica e nas análises estatísticas, como na parte teórica de revisão bibliográfica, escrita e publicação. Tive oportunidade de conhecer excelentes profissionais e criar contatos para futuras colaborações de pesquisa.

Durante meu período sanduíche fui acolhida pela NCState e pelo professor Adam. No laboratório dedicado à pesquisa de anatomia funcional com foco no aparelho mastigatório de mamíferos, aprendi a uma técnica utilizada para calcular o PCSA dos músculos, que envolve a digestão do tecido conjuntivo dos mesmos por ácido, a fim de individualizar as fibras musculares e então chegar na força muscular que aquele músculo é capaz de gerar. O processamento das minhas amostras se mostrou especialmente desafiador, pois pude

observar muita variação do tempo de processamento dos fascículos dependendo do tipo de amostra (fresca ou fixada), temperatura ambiente e do ácido em si, fatores estes não tão descritos na literatura.

Apesar das ótimas experiências, também houve alguns “perrengues” associados, muitos deles relacionados ao limitado valor da bolsa de pesquisa oferecida pela CAPES. Tal bolsa se encontra a anos sem reajuste, e com o aumento do custo de vida a nível global, acaba se tornando um ponto de vulnerabilidade para qualquer aluno de intercâmbio. Esta oportunidade de realizar o intercâmbio é importantíssima e de extremo valor para o crescimento da pesquisa nacional, e agradeço imensamente à CAPES por ter permitido isso, mas deixo registrado esta urgente necessidade de reajuste no valor da bolsa.

Trouxe estes ensinamentos comigo e consegui replicá-los no laboratório da Faculdade de Saúde da UnB, gerando muitos resultados positivos. Com esta nova opção de coleta e processamento de material anatômico, espero poder contribuir na adição desta linha de pesquisa no laboratório de pesquisa em anatomia de animais silvestres da UnB, junto do meu orientador professor Marcelo. Considero esta linha de pesquisa relativamente ampla, e pode ser utilizada em uma gama de grupos musculares e grupos de animais, sendo que há muito espaço para pesquisa e publicação em anatomia funcional, tanto para animais silvestres e exóticos como para animais domésticos.