An Interactive Three Dimensional approach to Anatomical Description – The jaw musculature of the Australian Laughing Kookaburra (*Dacelo novaeguineae*)

The investigation of form-function relationships requires a detailed understanding of anatomical systems. Here we document the 3-dimensional morphology of the cranial musculoskeletal anatomy in the Australian Laughing Kookaburra *Dacelo novaeguineae*, with a focus upon the geometry and attachments of the jaw muscles in this species. The head of a deceased specimen was CT scanned, and an accurate 3D representation of the skull and jaw muscles was generated through manual segmentation of the CT scan images, and augmented by dissection of the specimen. We identified 14 major jaw muscles: 6 in the temporal group (*M. adductor mandibulae* and *M. pseudotemporalis*), 7 in the pterygoid group (*M. pterygoideus dorsalis* and *M. pterygoideus ventralis*), and the single jaw abductor *M. depressor mandibulae*. Previous descriptions of avian jaw musculature are hindered by limited visual representation and inconsistency in the nomenclature. To address these issues, we: (1) present the 3D model produced from the segmentation process as a digital, fully interactive model in the form of an embedded 3D image, which can viewed from any angle, and within which major components can be set as opaque, transparent, or hidden, allowing the anatomy to be visualised as required to provide a detailed understanding of the jaw anatomy; (2) provide a summary of the nomenclature used throughout the avian jaw muscle literature. The approach presented here provides considerable advantages for the documentation and communication of detailed anatomical structures in a wide range of taxa.

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8 **Introduction**

9 The relationship between form and function is a central concept in biology (Lauder et al., 1995;
10 Russell 1916; Thompson 1916); it determines the extent to which the anatomy of an organism
11 permits specific behaviours and ecology. Investigating form-function relationships requires a
12 detailed understanding of anatomical systems, i.e. the discipline of anatomy and morphology. For
13 functional questions concerning feeding ecology, the relevant anatomical system is the feeding
14 apparatus; for the majority of vertebrates, this consists of the jaws. The jaw is a functional unit,
15 consisting of a rigid framework – the skull bones of the cranium and mandible, operated by a
16 system of jaw muscles. The skull bones must be able to withstand the forces of catching a
17 struggling prey item, whilst transferring the bite force generated from the jaw muscles to hold,
18 kill and process the prey without sustaining fracture. Fundamentally, the mechanical limits of the
19 jaw's ability to bite the prey item determines the type and size of prey that can be taken (Ferrara
20 et al., 2011; Herrel et al., 2002; Wroe et al., 2005).

22 Form-function relationships can be investigated using mechanistic techniques, such as
23 computational biomechanics, and/or quantitative approaches, such as statistics and
24 morphometrics. For biomechanical modelling, the jaw musculature is an important component of
25 the loads that act upon the skull during feeding and other behaviours. During biting, **isotonic**
26 contraction of the adductor musculature imposes reaction forces on the prey (or other item),
27 whilst shaking or twisting of the food requires **isometric** contraction of the jaw muscles to firmly
28 hold the prey. During each of these activities, the activation of the jaw musculature imposes
29 tensile forces to attachment areas which can result in loads at least as high as the loads being
30 applied to the prey (Herring et al., 2001). Therefore, to simulate the jaw as closely to the actual
31 system as possible it is important to include an accurate representation of the jaw musculature in
32 the model.

33

34 The following description of the jaw musculature of the Australian laughing kookaburra (*Dacelo*
35 *novaeguineae*) was stimulated by the need to incorporate detailed anatomical data into high
36 resolution 3D finite element models as part of an analysis of skull biomechanics in 8 species of
37 kingfisher (Alcedines) (Quayle 2011; Quayle et al., in prep.).

38 **Avian and kingfisher cranial anatomy**

39 A review of the literature indicates that descriptions of avian jaw anatomy are limited, with
40 studies of only a few species, use of two-dimensional drawings, and complicated written
41 descriptions. A major obstacle is the use of differing terminology (Holliday & Witmer 2007).
42 Papers that incorporate higher levels of detail include Holliday and Witmer's description and
43 illustration of the albatross jaw musculature (2007), Elzanowski's description of the tinamous jaw
44 (1987), Zusi and Storer's pied-billed grebe jaw study (1969), Richards and Bock's comparison
45 of Hawaiian honeycreeper feeding apparatus (1973), and Zweers' description of mallard
46 myography (1974). From these descriptions it is evident that avian jaw muscle anatomy differs in
47 relative and absolute size of the various muscles, and in the position and extent of attachments.
48 Consequently, we determined that the jaw musculature in kingfishers should not be reconstructed
49 on the basis of anatomical descriptions of other families.

50

51 The jaw muscles of several species of kingfisher (though not *Dacelo novaeguineae*) have been
52 described by Burton (1984); however his illustrations are difficult to interpret, with little
53 information identifying which part of the skull he is referring to in the figures. Burton's
54 description did, however, reveal several variations in muscle origin and insertion areas between
55 the kingfisher species he studied. This observation reinforced the need to document the
56 kookaburra anatomy independently.

57

58 The lack of detailed published data on the kookaburra jaw musculature meant that firsthand
59 anatomical information was required to accurately model the jaw system. This information was
60 obtained through the dissection of the head of an adult laughing kookaburra (*Dacelo
61 novaeguineae*). The kookaburra was CT scanned prior to dissection, and this scan data was used
62 in conjunction with the dissection information to create a three-dimensional computer model of
63 the skull and jaw muscles of *D. novaeguineae*.

64 **A 3D approach to anatomical description**

65 Anatomy is inherently three-dimensional, but traditional descriptions of anatomy use a
66 combination of text and 2D picture modes. New technologies in data collection, assembly,
67 visualisation and communication, are offering significant new opportunities for improving the
68 study, documentation and publication of anatomy, particularly given the proliferation of 3D
69 imaging capabilities.

70 The following description adopts and exemplifies a three-dimensional approach to displaying
71 anatomical systems through the use of (1) three-dimensional Adobe Portable Document Format
72 (3D PDF) figures, and (2) 3D-enabled web pages. The 3D PDF medium allows an interactive 3D
73 model to be inserted into an electronic document in PDF format, meaning that specialised
74 software is not required to view the model other than the freely available Adobe Reader (desktop
75 version), and permanently embedding the figure directly in the document file. This method of
76 interactive visualisation is becoming increasingly popular, with publications in biomedical

77 science (Kumar et al., 2009; Selvam et al., 2009), astrophysics (Barnes & Fluke 2008),
78 invertebrate (Baeumler et al., 2008; Neusser et al., 2009; Ziegler et al., 2008) and vertebrate
79 anatomy (de Bakker et al., 2012; Holliday et al., 2013; Ruthensteiner & Heß 2008) and
80 paleontology (Knoll et al., 2012; Lautenschlager 2013). In addition, free, open source software
81 that provides a pathway for the generation of 3D PDF figures, especially for use in science, is
82 now available (Barnes et al., 2013).

83 The 3D meshes produced for the 3D PDF were also used to generate a model available for
84 viewing in web pages. Web-based 3D visualisation is becoming more common with the growing
85 number of browsers supporting accelerated 2D and 3D graphics, especially via the WebGL
86 standard (http://www.khronos.org/webgl); recent examples include applications in bioinformatics
87 (Pettit & Marioni 2013), neuroinformatics (Ginsburg et al., 2011), and surgical teaching (Birr et
88 al., 2013). Like 3D PDF, web-based 3D visualisation enables the interactive manipulation of a 3D
89 model without requiring specialised software other than a modern web browser.

90 Here we present a detailed description of the 3D osteology and jaw musculature of *D.*
91 *novaeguineae,* and provide a summary of the avian jaw muscle synonymies. We aimed to
92 demonstrate and exploit the potential of 3D viewing technology in the anatomical sciences by
93 producing a 3D model that shows the position of the kookaburra jaw muscles on the skull relative
94 to one another; the model can be rotated and superficial muscles hidden or made transparent to
95 allow better visualisation of the deeper anatomy. While the 3D model allows for a detailed
96 descriptive model in a single figure-frame, it is only available for viewing in digital format. For
97 this reason, still images suitable for 2D print media are also included.

98 **Materials & Methods**

99 **Specimen**
100 A fresh, deceased adult laughing kookaburra (*Dacelo novaeguineae*), obtained from Australia
101 Museum's Ornithological collection (specimen no. AM BF2162) was used in the following
102 description. This specimen had died in the care of wildlife rescuers as a result of an infection on
103 the right elbow, although the head and skull did not show any obvious pathologies and thus were
104 deemed to illustrate normative anatomy.

105 **Data acquisition and processing**
106 The kookaburra was scanned in a clinical computed tomography (CT) scanner (Toshiba Aquilion
107 64) at the Newcastle Calvary Mater Hospital, at 120kV, 75mA and using a slice thickness of
108 0.5mm. The resulting DICOM images were imported into MIMICS v11 (MATERIALISE,
109 Belgium) segmentation software, wherein the skull of the kookaburra was digitally separated
110 from the soft tissue by combining a scalar threshold with manual selection tools; the high density
111 of the bone compared to the surrounding soft tissue allowed for quick and simple segmentation of
112 the skull by applying a threshold based on the grey scale pixel values representative of the bone.

113   A 3D model of the cranium and mandible was then created from this segmentation. This digital
114   skull model provided a scaffold to illustrate the muscle attachment points and muscle geometry
115   determined in the dissection (Fig. 1).

116

117   Segmentation of the jaw muscles proved more difficult due to the small size of the muscles, the
118   low resolution of the scanner and the use of CT (without staining for contrast) rather than MRI.
119   While the soft tissue making up the kookaburra jaw muscles was visible in the CT scan data, and
120   the bellies of the larger muscles could be differentiated and separated using MIMICS
121   segmentation tools, the resolution of the scan was too low to accurately identify the smaller jaw
122   muscles and the muscle attachment sites. For this reason, the soft tissue CT scan data was used
123   alongside the dissection information to identify placement of the jaw muscles (Fig. 1 & Fig. 2).

124

125   The jaw muscles were dissected out beginning with the superficial layer. Each individual muscle
126   was described using drawings, photographs and notes to illustrate its position, direction and
127   attachment sites. Muscles of the hyoid and eye were not required for the biomechanical analysis
128   and were not included in this study. The completed notes on kookaburra muscle anatomy were
129   compared with previously published data on avian jaw musculature (Baumel 1993; Burton 1984;
130   Elzanowski 1987; Holliday & Witmer 2007; Zusi & Storer 1969) to determine the individual
131   names of the jaw muscles observed. Muscle nomenclature used was based on Holliday and
132   Witmer (2007) and Burton (1984). Osteological nomenclature (Fig. 3) was based on Baumel
133   (1993), Zusi and Storer (1969)and Ghetie et al., (1976).

134

135   In conjunction with the CT scan data of the specimen, the illustrated dissection notes were used
136   to digitally recreate a three dimensional representation of the kookaburra jaw musculature on the
137   specimen's skull model (Fig. 2). This model was created using the CT editing software MIMICS
138   to manually select areas of the CT image slices where the muscles were determined to occur. The
139   CT slices were then joined in MIMICS to create a 3D model of each muscle which were
140   individually exported as stereolithography (STL) format files.

141   **3D image production**
142   **PDF**
143   A total of 16 segmented surfaces (meshes) – the cranium, mandible, and 14 muscles – comprise
144   the segmented jaw anatomy. The cranium was the largest and most detailed surface, and was
145   remeshed and simplified in MeshLab version 1.3.2 (Visual Computing Lab – ISTI – CNR;
146   http://meshlab.sourceforge.net) using a "Quadric Edge Collapse Decimation" to reduce its facet
147   count from ~635,000 to ~100,000; this reduced the total model size without significant visible
148   degradation. The meshes were converted (using MeshLab) to the widely-used Alias Wavefront
149   ".OBJ" format and listed in a text file, one per line, with colon-separated fields for the part
150   (anatomical) name, a group code, the filename, and the desired part colour expressed as an (r,g,b)
151   triplet. The group code is used to assign parts to named components in a two-level hierarchy. The
152   text file describing the model was read by a small, custom 3D visualisation program written using
153   S2PLOT (Barnes et al., 2006), and the surfaces were loaded, coloured and displayed for

154   inspection. Names were applied to the different meshes, and the export capability in the recent
155   S2PLOT release version 3.2.1 (Barnes et al., 2013) was used to save the complete 3-d model to a
156   Product Representation Compact (PRC) format file.

157   Additional lines in the model description file were used to: define standard views of the anatomy
158   (left lateral, right lateral, anterior, posterior, dorsal and ventral); to select a basic lighting
159   environment (a headlamp) and background colour; and to define the component group names.
160   From the model description file, a custom views file suitable for PDF embedding was generated,
161   and JavaScript fragments to toggle the various component groups were generated. Following the
162   workflow in Barnes et al., (2013), the PRC model was embedded in a LaTeX-format document
163   (Lamport, *LaTeX: A Document Preparation System (2ⁿᵈ Edition)*, 1994) and compiled into a PDF
164   file with embedded 3D figure, incorporating the custom views file and JavaScript fragments and
165   the standard 3D JavaScript code, included with S2PLOT version 3.2.1, which implements
166   standard keystrokes such as cursor keys to rotate the model and the letter 'a' to toggle autospin
167   mode.

168   **Web-based Figure**
169   Our web-based figure is based on the JavaScript *three.js* (http://threejs.org), public domain
170   extensions to *three.js* (via http://learningthreejs.com), and E. Graether's *TrackballControls.js*
171   (http://egraether.com). *Three.js* provides a simple entry point to visualisation of 3D scientific data
172   on the Web by supporting the loading of several common 3D model data formats, and rendering
173   the 3D model using WebGL (http://khronos.org/webgl) where available, and otherwise the 2D
174   Javascript canvas API for devices with no WebGL support. The OBJLoader.js module provides a
175   ready-made importer for the ubiquitous Alias Wavefront OBJ format. Using these components,
176   we developed a custom JavaScript-based web page that reads the identical model description file
177   used for assembling the 3D PDF figure, and constructs a web-based 3D visualisation, coloured as
178   for the 3D PDF version, and offering the same capability to interactively rotate and zoom the
179   model, and to toggle the model components.

180   **Results**

181   **Musculoskeletal anatomy**

182   **Depressor Muscles:**
183   1. *M. depressor mandibulae* (mDM) has a fleshy origin on the squamosal region on the back of
184   the braincase, just posterior to the opening of the ear. It becomes thicker as it extends around the
185   jaw joint to insert over most of the posterior surface of the mandible articular bone (Fig. 4 g,h).
186
187   **Temporal Muscles:**
188   The external adductor complex – *M. adductor mandibulae externus* (mAME) – has three parts:

189 2. M. *adductor mandibulae externus profundus* (mAMEp) originates along the length of the
190 temporal fossa; the attachment extends from the sagittal midline of the cranium (Fig. 4 g,h,) to
191 the region just dorsal to the zygomatic process and along the posterior edge of the post orbital
192 process. *M. adductor mandibulae externus profundus* inserts onto the coronoid process of the
193 mandible posterior to the insertion of *M. pseudotemporalis superficialis* (Fig. 4 a,b,j).

194 3. *M. adductor mandibulae externus superficialis* (mAMEs) has a narrow origin located on the
195 lateral side of the zygomatic process. It extends down around the medial side of the jugal where it
196 fans out to insert widely and thinly over the dorso-lateral surface of the mandibular ramus (Fig. 4
197 a,b,j).

198

199 4. *M. adductor mandibulae externus rostralis temporalis post-orbital lobe* (mAMErt): This
200 muscle is thought to be a member of the adductor mandibulae externus group. Burton (Burton
201 1984) labels it '*M. adductor mandibulae externus rostralis post-orbital slip*' or '*lobe*' in his
202 illustrations but only briefly mentions it in the text. We can find no other literature that uses this
203 term, but we retain its use here in lieu of further information on its possible homology. This
204 muscle was found to have a fleshy origin on the anterior/medial side of the post-orbital process. It
205 inserts onto the coronid process of the manidble, anterior to the insertion of *M. adductor*
206 *mandibulae externus profundus* (Fig. 4 a,b,j). It is clearly separate to the other parts of the
207 external adductor complex (mAME).

208 5. *M. adductor mandibulae posterior* (mAMP) originates along the orbital process of the
209 quadrate and the quadrate body (Fig. 4 a,c,i,j). It inserts onto the dorsal side of the mandible,
210 immediately antero-medial to the jaw joint.

211 **Pseudotemporalis (mPST) Muscles:**
212 6. *M. pseudotemporalis superficialis* (mPSTs) has two sections (displayed here as one muscle).
213 The medial part originates on the laterosphenoid process on the posterior wall of the orbit (Fig. 4
214 a,c,i). The lateral part originates slightly higher in the depression lateral to the process. Both
215 sections insert onto the medial side of the mandible where they fan out to cover most of medial
216 fossa of the mandible, dorsal to the insertion of M. *pseudotemporalis profundus* (Fig. 4 i,j).

217 7. *M. pseudotemporalis profundus* (mPSTp) originates from the medial point of the quadrate
218 orbital process (Fig. 4, a, i). The medial section of the muscle is thick and fleshy, while that
219 lateral side consists of a thin sheet fanning out as it inserts over a large area on the ventral edge of
220 the medial fossa of the mandible (Figure 4 i, j).

221

222 **Pterygoid (PT) Muscles:**
223 8. *M. pterygoideus dorsalis medialis anterior* (mPTDma) originates along the entire length of the
224 medial ridge of the palatine and onto the lateral edge of the pterygoid bone. It inserts onto the
225 anterior end of the mandible's medial process (Fig. 4 d,e,f,n,).

226   9. *M. pterygoideus dorsalis medialis posterior* (mPTDmp) takes its origin along the medial side
227   of the pterygoid bone, beginning from the joint of the palatine and pterygoid and inserting onto
228   the anterior edge of the medial mandibular process (Fig. 4 d,e,n).

229   10. *M. pterygoideus dorsalis lateralis* (mPTDl) has a fleshy origin on the anterior-most portion of
230   the palatine and down onto the dorsal lateral surface of the palatine. This large muscle wraps
231   down and around to insert onto the ventral/medial side of the mandible (Fig. 4 d,e,f,k,m,n).

232   11. *M. pterygoideus ventralis medialis* (mPTVm) originates along the entire ventral surface of the
233   palatine. It extends over the ventral side of the pterygoid bone to insert onto the anterior surface
234   of the tip of the medial mandibular process (Figure 4 k,l,m).
235
236   The *M. pterygoidus ventralis lateralis* (mPTVl) muscle is formed from three parts:

237   12. *M. pterygoideus ventralis lateralis Part 1* (mPTVl pt1) is a large, flat, superficial muscle
238   lying most ventral to all others. It originates along the lateral ventral ridge of the palatine and
239   along the lateral side of the crest where the palatine meets the vomer by an aponeurotic sheet
240   extending anteriorly until it merges with the skin of the palate. Posteriorly this muscle becomes
241   thicker as it extends over the posterior end of the mandible to wrap around and insert onto the
242   lateral side of the mandible, posterior to the attachment of *M. adductor mandibulae externus*
243   *superficialis* (Fig. 4 a,b,j,k,l).
244
245   13. *M. pterygoideus ventralis lateralis Part 2* (mPTVl pt2) – this muscle and *M. pterygoideus*
246   *ventralis lateralis part 3* occur closely together and it is possible that they are different heads of
247   the same muscle. Part 2 attaches to the lateral point of the palatine. It then extends back to fan out
248   and attach over a reasonably large area on the ventral side of the entire medial mandibular
249   process (Fig. 4 k,l,m).

250   14. *M. pterygoideus ventralis lateralis Part 3* (mPTVl pt3) runs laterally adjacent to Part 2. It
251   originates along the dorsal edge of the palatine, lateral to the palatine attachment of *M.*
252   *pterygoideus dorsalis lateralis.* This muscle attaches to the ventral crest of the medial mandibular
253   process (Fig. 4 f,k,m).

254   **3D visualisation**
255   An interactive, 3D model of the jaw muscles described above is available as Figure 5 in the
256   Appendix.

257   **Discussion**

Methodological issues

258 With the increasing use of CT as a primary means of collecting anatomical data for use in 3D
259 modelling, it is important to note the limitations of this imaging modality. Whilst it is possible to
260 collect the data required for the 3D modelling of the bones from CT alone, our experience with
261 the specimen used in this study is that incorporating detailed muscle anatomy into a 3D model
262 requires a combination of CT imaging and dissection. In CT, contrast between bone and soft
263 tissue is high, which maximises the accuracy of segmentation protocols (both automatic
264 algorithms and manual image processing) for segmenting bones. However, in the absence of
265 fixing protocols (eg. iodine potassium iodide – 'Lugol's iodine'), contrast between muscles and
266 other soft tissues is low and it is difficult to identify individual muscle bellies on the basis of CT
267 data alone; both the perimysium and intermuscular septa are inconsistently visible. An additional
268 limitation is the comparatively low resolution of medical CT in imaging small animals; for the
269 scans used in this study, maximum pixel resolution in each slice was 0.337 mm, which is a
270 relatively large proportion of the maximum cranial diameter (44 mm), even for a large kingfisher
271 species such as the kookaburra. Without the opportunity to use dissection to augment the 3D
272 imaging of muscle anatomy we could not have produced the level of anatomical data presented
273 here.

275 Whilst small-animal CT scanners (maximum field of view ~100 mm) or micro-CT (~20 mm) can
276 deliver significantly higher resolution than clinical CT, these scanners are not as readily available
277 as clinical CT scanners and we were not able to utilise one at the time of this study. These higher
278 resolution CT scanners also cannot produce images that clearly differentiate muscle bellies
279 without first preparing the specimen with an iodine stain, and require much longer scan times
280 than a clinical CT.

281 It is possible that magnetic resonance imaging (MRI) can provide an alternative to dissection by
282 producing high resolution images of the soft tissue, however MRI is not able to image bone well.
283 A specimen can be both CT and MRI scanned and the resulting images co-registered to fit to the
284 same 3D space co-ordinates, so that CT can be used to model the skeletal elements, while MRI
285 can provide muscle detail. At the time of this study an MRI scanner and co-registration code was
286 not available to us.

Nomenclature

288 Determining the correct names of particular muscles identified in the kookaburra based on
289 previous avian jaw anatomy literature was a complicated process. For many taxonomic groups,
290 anatomical descriptions have ranged across decades, languages, and authors; the issues we
291 discovered with respect to non-standard nomenclature are not restricted to kingfishers. Muscle
292 groups, particularly the *M. adductor mandibulae externus* and *M. pterygoideus dorsalis* muscles
293 were separated into several sections in some studies (Burton 1984; Richards & Bock 1973), or
294 treated as a whole in others (Holliday & Witmer 2007). Within this study, questions remain
295 regarding the extent to which some muscle bellies should be regarded as individual muscles, or
296 be considered as a part of a larger muscle. Specifically, is *M. adductor mandibulae externus*

297 *rostralis temporalis post-orbital* lobe part of one of the other *M. adductor mandibulae externus*
298 muscles (with the only reference found of a separate muscle in this area recorded by Burton
299 (1984); and should *M. pterygoideus ventralis lateralis Part 2* and *Part 3* be considered as
300 separate muscles to *M. pterygoideus ventralis lateralis Part 1*?
301
302 Nomenclature used in this study was based mainly on Burton's (1984) study as it includes
303 kingfisher anatomy and uses similar terminology to Baumel's Nomina Anatomica Avium (1993).
304 However, temporal muscle nomenclature was based upon Holliday and Witmer (2007). Baumel
305 (1993) and Burton (1984) each separate *M. adductor mandibulae externus* into three parts of
306 mAME rostralis, mAME ventralis and mAME caudalis, but we found no clear evidence of 5
307 separate heads for this muscle in *D. novaeguineae*. Holliday and Witmer's nomenclature for the
308 external adductor complex was more similar to the anatomy visible in our specimen.
309
310 There is a lack of consistency in the way in which muscle names are written and abbreviated in
311 text of previous literature. In an attempt to develop a standardised format for writing muscle
312 names and abbreviations, we use the following format:
313   1. When writing the muscle name in text, we use an uppercase 'M.' (contraction for
314   Musculus) at the start of the name, following Baumel's Nomina Anatomica Avium (1993).
315   2. When writing the muscle name in full within text, we italicise the name; hence, *M.*
316   *pseudotemporalis superficialis*. The muscle name is more easily distinguished visually
317   from the surrounding text, making the text easier to read.
318   3. When abbreviating the muscle (e.g. for figure labels), we use lower case for the 'm' and
319   upper case for the abbreviation of the muscle name; hence, mPST. This format visually
320   highlights the informative part of the label.
321   4. Parts of the muscle are written in lower case, hence mPSTs and mPSTp. This makes it
322   easier to identify the muscle under discussion, avoiding the potential confusion that can
323   arise between muscles in the external adductor complex if the abbreviation for the part is
324   written in upper case – Holliday and Witmer (2007) use mAMEP and mAMP for the *M.*
325   *adductor mandibulae externus profundus* and the *M. adductor externus posterior*
326   respectively. We abbreviate these muscles as mAMEp and mAMP.

327 Table 1 lists the avian jaw muscle nomenclature that we have used in this paper, the respective
328 abbreviations for use in labels, and the synonymies in selected literature. Note that some of these
329 published nomenclatures were presented as anatomical illustrations rather than written
330 descriptions, making it difficult to accurately determine exact muscle synonymy.

331 **The role of 3D images in communicating anatomical information**
332 Descriptive anatomy is the foundation for understanding functional anatomy. The recent surge in
333 biomechanical studies of form-function questions in a range of taxa means descriptive anatomy
334 remains as relevant as ever (Holliday et al., 2013). The current emphasis on 3D modelling
335 approaches indicates that anatomical data should be collated and communicated in 3D, as much
336 as is practically possible. It is certainly possible to communicate anatomical information to the

337 level required for 3D models using text or 2D diagrams; the issue is simply that a great deal of
338 text and/or a large number of 2D images are required. Conversely, a single 3D PDF figure or web
339 visualisation can communicate an equivalent level of information with the user being able to
340 interact with the model to gain finer understanding of structure.

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Figure 1

Segmentation of the CT data

The CT scan data for the *Dacelo novaeguineae* head was imported into the segmentation software MIMICS (MATERIALISE, Belgium) (a). The skull was segmented out using thresholding tools to select the regions of bone from the scan images, while the muscles were manually segmented. Segmentation is indicated by the coloured regions on the CT image. The segmented regions on each CT image slice were then joined using Mimics modelling tools to create a 3D model of the *D. novaeguineae* skull and jaw muscles (b). The red line through the skull in (b) indicates the location of the CT slice in (a). Jaw muscles shown in this model are 1. *M. depressor mandibulae*, 2. *M. adductor mandibulae externus profundus*, 3. *M. adductor mandibulae externus superficialis*, 4. *M. adductor mandibulae externus rostralis temporalis post-orbital lobe*, 5. *M. adductor mandibulae posterior*, 6. *M. pseudotemporalis superficialis*, 7. *M. pseudotemporalis profundus*, 8. *M. pterygoideus dorsalis medialis anterior*, 9. *M. pterygoideus dorsalis medialis posterior*, 10. *M. pterygoideus dorsalis lateralis*, 11. *M. pterygoideus ventralis medialis*, 12. *M. pterygoideus ventralis lateralis Part 1*, 13. *M. pterygoideus ventralis lateralis Part 2* and 14. *M. pterygoideus ventralis lateralis Part 3*.

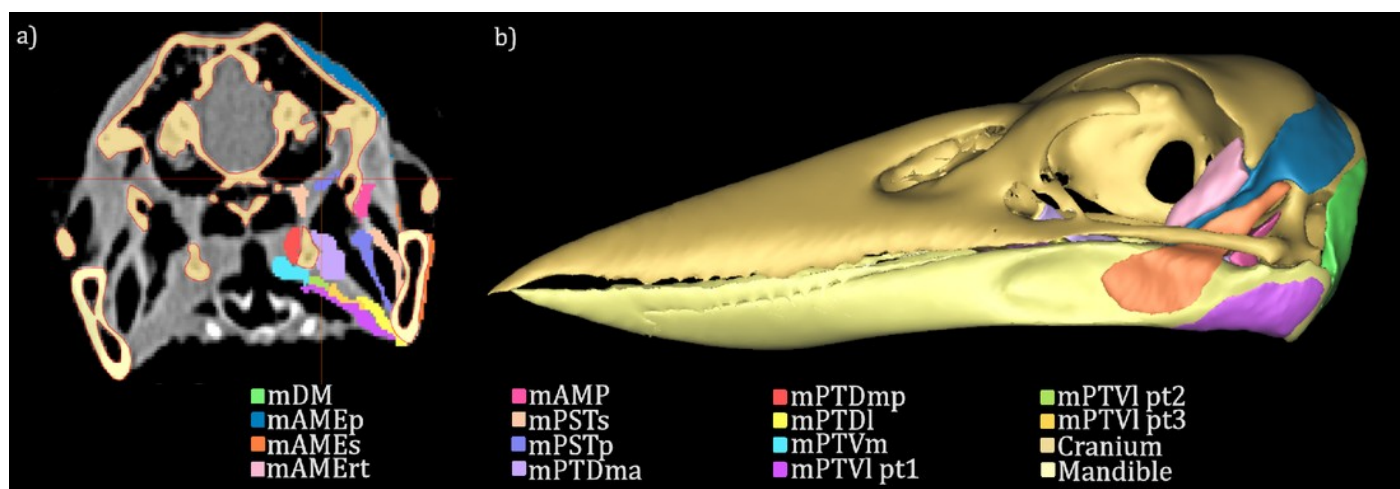



Figure 2

Comparing the dissection to the digital model

Each of the jaw muscles of the laughing kookaburra (*Dacelo novaeguineae*) were individually described and removed during the dissection (a). Notes, drawings and photographs from the dissection were used to identify the jaw muscles on the CT scan so that they could be digitally segmented and modelled (b). This diagram shows the placement of the muscles in the dissected specimen (a) and their digital representation (b). Muscle shown here are 1. *M. depressor mandibulae*, 2. *M. adductor mandibulae externus profundus*, 3. *M. adductor mandibulae externus superficialis*, 4. *M. adductor mandibulae externus rostralis temporalis post-orbital lobe* and 12. *M. pterygoideus ventralis lateralis part 1* (removed in dissection photo).

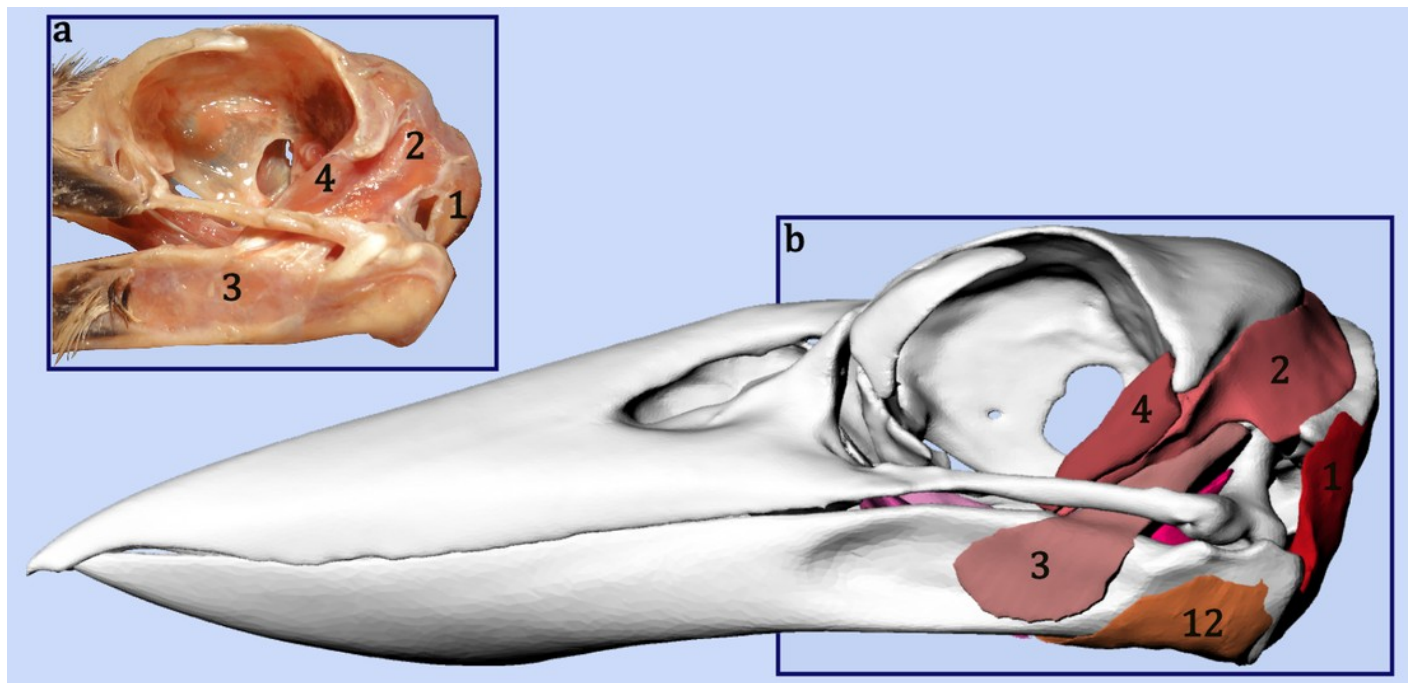



Figure 3

Osteology of the avian skull

Illustrating the bones and features of the avian skull on *Dacelo novaeguineae* in a) anterior, b) posterior, c) lateral, d) dorsal and e) ventral views. f) shows the features of the mandible in dorso-lateral view. Due to the fused nature of avian skull bones, the separation between the bones is not defined. Adapted from (Baumel 1993; Ghetie et al. 1976; Zusi & Storer 1969)

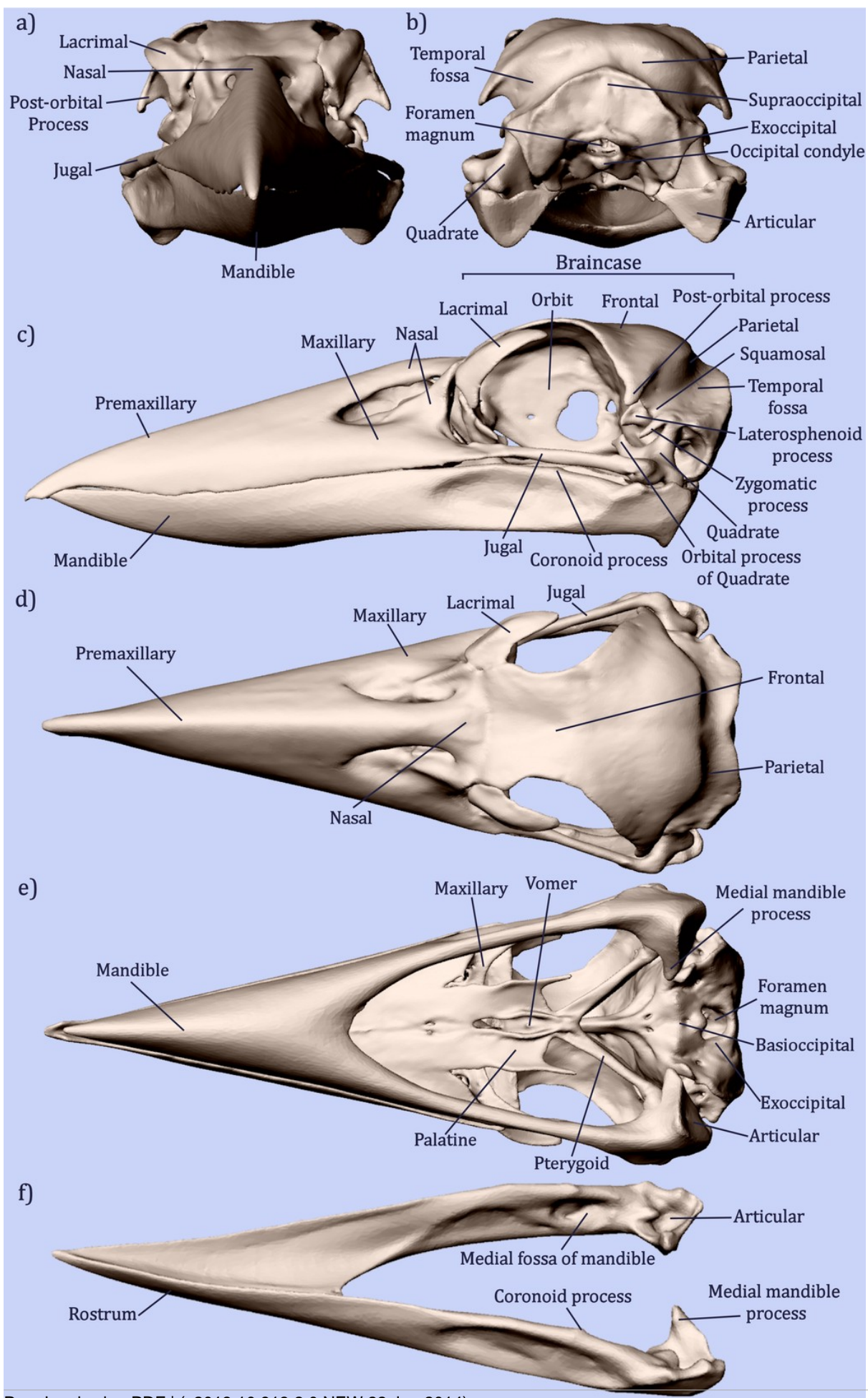
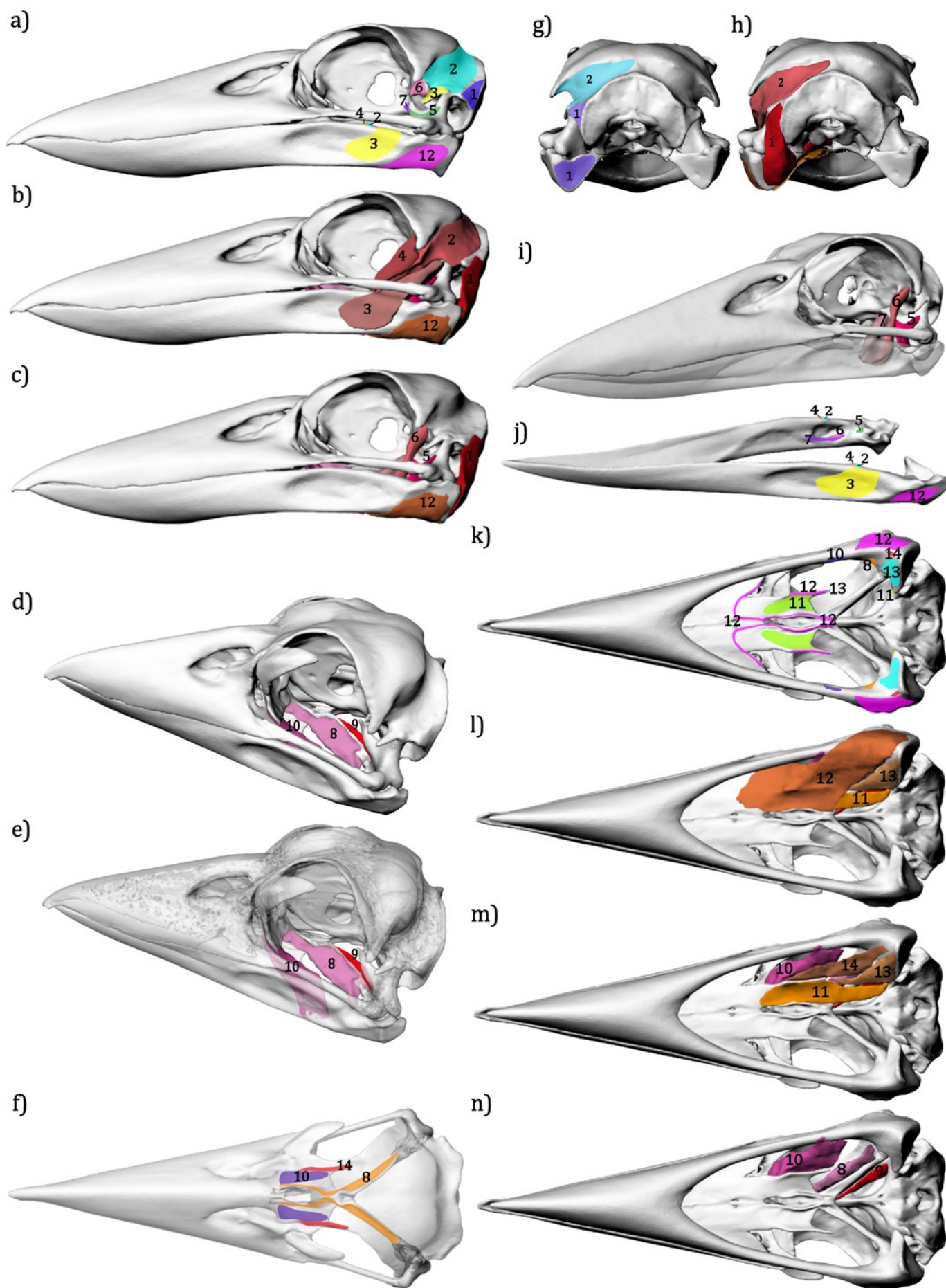



Figure 4

Jaw musculature of the Australian Laughing Kookaburra *Dacelo novaeguineae*

a) Lateral view showing the attachment areas of the jaw muscles, b) the geometry of the jaw muscles and c) deeper muscle geometry with muscle 2,3 and 4 hidden. d) Showing the geometry of the *M. pterygoideus dorsalis* muscles and e) their position in a transparent skull. f) Dorsal view of a transparent skull showing attachment sites of the *M. pterygoideus* muscles to the dorsal side of the palatine and pterygoid bones. g) Attachment sites of muscles on the posterior side of the skull and h) their geometry. i) geometry of the *M. adductor mandibulae externus* and *M. pseudotemporalis* muscles, skull is shown with a transparent mandible to display their medial attachment to the mandible. j) Dorsolateral view of the muscle attachment sites on the mandible. k) Muscle attachment sites on the ventral side of the skull, and the geometry of l) superficial, m) middle and n)deep layers of ventral muscles. 1. *M. depressor mandibulae*, 2. *M. adductor mandibulae externus profundus*, 3. *M. adductor mandibulae externus superficialis*, 4. *M. adductor mandibulae externus rostralis temporalis post-orbital lobe*, 5. *M. adductor mandibulae posterior*, 6. *M. pseudotemporalis superficialis*, 7. *M. pseudotemporalis profundus*, 8. *M. pterygoideus dorsalis medialis anterior*, 9. *M. pterygoideus dorsalis medialis posterior*, 10. *M. pterygoideus dorsalis lateralis*, 11. *M. pterygoideus ventralis medialis*, 12. *M. pterygoideus ventralis lateralis Part 1*, 13. *M. pterygoideus ventralis lateralis Part 2* and 14. *M. pterygoideus ventralis lateralis Part 3*.

Jaw muscle nomenclature

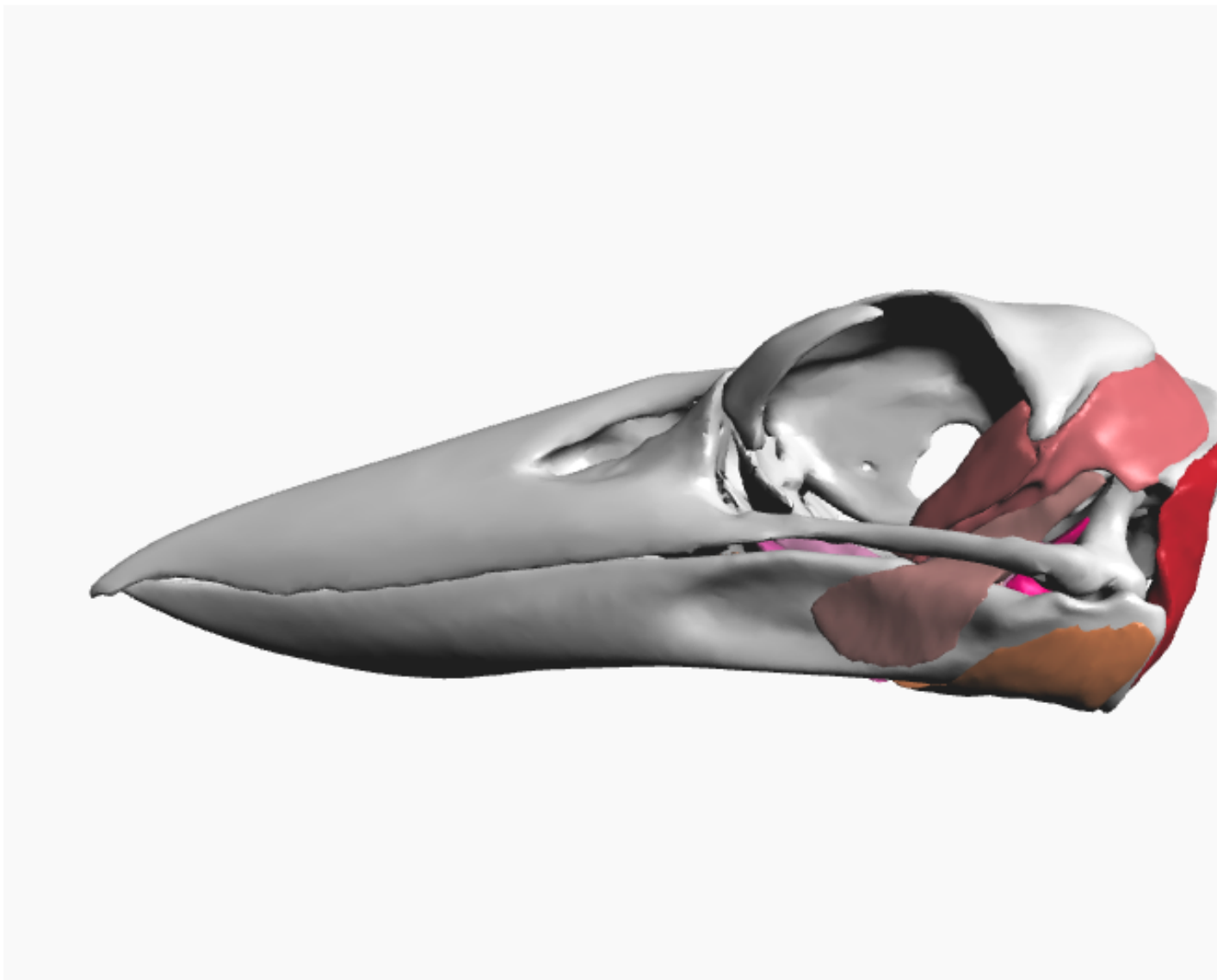
Equivalent avian jaw muscle names used in this study and selected literature. Muscle
equivalents of which we are uncertain are designated by (?).

This study:	This study abbreviation:	Baumel (1993)	Ghetie et al. (1976)	Burton (1984)	Richards & Bock (1973)	Holliday & Witmer (2007)
1. M. depressor mandibulae	mDM	M. depressor mandibulae	M. occipitomandibularis	M. depressor mandibulae	M. depressor mandibulae a,b and c	Not included
2. M. adductor mandibulae externus profundus	mAMEp	M. adductor mandibulae externus rostralis temporalis	M. temporalis	M. adductor mandibulae externus rostralis temporalis	M. adductor mandibulae externus rostralis temporalis	M. adductor mandibulae externus profundus
3. M. adductor mandibulae externus superficialis	mAMEs	M. adductor mandibulae externus rostralis	M. masseter superficialis (?)	M. adductor mandibulae externus rostralis lateralis	M. adductor mandibulae externus rostralis lateralis	M. adductor mandibulae externus superficialis
4. M. adductor mandibulae externus rostralis temporalis post-orbital lobe	mAMErt	Part of M. adductor mandibulae externus rostralis (?)	M. masseter	M. adductor mandibulae externus rostralis temporalis post-orbital lobe	Part of M. adductor mandibulae externus rostralis temporalis (?)	Part of M. pseudotemporalis superficialis or M. adductor mandibulae externus profundus (?)
5. M. adductor mandibulae posterior	mAMP	M. adductor mandibulae externus profundus caudalis	M. quadratomandibularis superficialis	M. adductor mandibulae externus caudalis	M. adductor mandibulae posterior	M. adductor mandibulae posterior
6. M. pseudotemporalis superficialis	mPSTs	M. pseudotemporalis superficialis	M. mandibularis infraorbitalis (?)	M. pseudotemporalis superficialis	M. pseudotemporalis superficialis	M. pseudotemporalis superficialis
7. M. pseudotemporalis profundus	mPSTp	M. pseudotemporalis profundus	M. quadratomandibularis profundus oralis	M. pseudotemporalis profundus	M. pseudotemporalis profundus	M. pseudotemporalis profundus
8. M. pterygoideus dorsalis medialis anterior	mPTDma	M. pterygoideus dorsalis medialis	M. pterygomandibularis (?)	M. pterygoideus dorsalis medialis	M. pterygoideus dorsalis medialis anterior	M. pterygoideus dorsalis
9. M. pterygoideus dorsalis medialis posterior	mPTDmp	M. pterygoideus dorsalis medialis	M. craniopterygoquadratus oralis (?)	M. pterygoideus dorsalis medialis	M. pterygoideus dorsalis medialis posterior	M. pterygoideus dorsalis
10. M.	mPTDl	M.	M.	M.	M.	M.

This study:	This study abbreviation:	Baumel (1993)	Ghetie et al. (1976)	Burton (1984)	Richards & Bock (1973)	Holliday & Witmer (2007)
pterygoideus dorsalis lateralis		pterygoideus dorsalis lateralis	mandibulopalatinus pars lateralis	pterygoideus dorsalis lateralis	pterygoideus dorsalis lateralis	pterygoideus dorsalis
11. M. pterygoideus ventralis medialis	mPTVm	M. pterygoideus ventralis medialis	M. mandibulopalatinus pars medialis	M. pterygoideus ventralis medialis	M. pterygoideus ventralis medialis	M. pterygoideus ventralis
12. M. pterygoideus ventralis lateralis part 1	mPTVl pt1	M. pterygoideus ventralis lateralis	Not determined	M. pterygoideus ventralis lateralis	M. pterygoideus ventralis lateralis	M. pterygoideus ventralis
13. M. pterygoideus ventralis lateralis part 2	mPTVl pt2	M. pterygoideus ventralis lateralis	Part of M. mandibulopalatinus pars medialis (?)	M. pterygoideus ventralis lateralis	M. pterygoideus ventralis medialis fan	M. pterygoideus ventralis
14. M. pterygoideus ventralis lateralis part 3	mPTVl pt3	M. pterygoideus ventralis lateralis	M. entotympanicus (?)	M. pterygoideus ventralis lateralis	Not determined	M. pterygoideus ventralis

3D visualisation of skull bones and jaw musculature in *Dacelo novaeguineae*

This 3D figure is an appendix to Quayle et al., "An Interactive Three Dimensional approach to Anatomical Description - The jaw musculature of the Australian Laughing Kookaburra (*Dacelo novaeguineae*)." If viewing from within Adobe Reader, click on the image to activate the 3D model. To use the model, click to view the label for each structure, left click and drag to free rotate, control left click and drag to pan, use scroll wheel to zoom. Select the "Toggle Model Tree" icon to show/hide individual components of the model. Right click on the component names in the "Model Tree" to make transparent. Muscle labels: 1 mDM *M. depressor mandibulae*, 2 mAMEp *M. adductor mandibulae externus profundus*, 3 mAMEs *M. adductor mandibulae externus supercialis*, 4 mAMErt *M. adductor mandibulae externus rostralis temporalis post-orbital lobe*, 5 mAMP *M. adductor mandibulae posterior*, 6 mPSTs *M. pseudotemporalis supercialis*, 7 mPSTp *M. pseudotemporalis profundus*, 8 mPTDma *M. pterygoideus dorsalis medialis anterior*, 9 mPTDmp *M. pterygoideus dorsalis medialis posterior*, 10 mPTDl *M. pterygoideus dorsalis lateralis*, 11 mPTVm *M. pterygoideus ventralis medialis*, 12 mPTVl pt1 *M. pterygoideus ventralis lateralis Part 1*, 13 mPTVl pt2 *M. pterygoideus ventralis lateralis Part 2* and 14 mPTVl pt3 *M. pterygoideus ventralis lateralis Part 3*.

Figure 5: 3D visualisation of skull bones and jaw musculature in *Dacelo novaeguineae*.

Object:

Toggle: Cranium; Mandible; Depressor muscle; Temporal muscles; Pseudotemporalis muscles; Dorsal Pterygoid muscles; Ventral Pterygoid muscles.

This 3D figure is an appendix to Quayle et al., "An Interactive Three Dimensional approach to Anatomical Description - The jaw musculature of the Australian Laughing Kookaburra (*Dacelo novaeguineae*)." If viewing from within Adobe Reader, click on the image to activate the 3D model. To use the model, click to view the label for each structure, left click and drag to free rotate, control left click and drag to pan, use scroll wheel to zoom. Select the "Toggle Model Tree" icon to show/hide individual components of the model. Right click on the component names in the "Model Tree" to make transparent. Muscle labels: 1 mDM *M. depressor mandibulae*, 2 mAMEp *M. adductor mandibulae externus profundus*, 3 mAMEs *M. adductor mandibulae externus superficialis*, 4 mAMErt *M. adductor mandibulae externus rostralis*, 5 mAMP *M. adductor mandibulae posterior*, 6 mPSTs *M. pseudotemporalis superficialis*, 7 mPSTp *M. pseudotemporalis profundus*, 8 mPTDma *M. pterygoideus dorsalis medialis anterior*, 9 mPTDmp *M. pterygoideus dorsalis medialis posterior*, 10 mPTDl *M. pterygoideus dorsalis lateralis*, 11 mPTVm *M. pterygoideus ventralis medialis*, 12 mPTVl pt1 *M. pterygoideus ventralis lateralis* Part 1, 13 mPTVl pt2 *M. pterygoideus ventralis lateralis* Part 2 and 14 mPTVl pt3 *M. pterygoideus ventralis lateralis* Part 3.