# Persistence of Meckel's cartilage in sub-adult *Struthio camelus* and *Dromaius novaehollandiae*

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## Abstract

This study describes the persistence of an embryonal structure through to sub-adulthood in the ostrich and emu. Mandibles from sub-adult ostrich and emu were subjected to special staining, light microscopy and dissected to reveal and describe Meckel's cartilage. Meckel's cartilage, composed of hyaline cartilage, was present within the neurovascular canal of both species. The persistence through to sub-adulthood of Meckel's cartilage in the ostrich and emu is a feature not previously reported in any other avian species. The proximal end of Meckel's cartilage was ossified in the region of the articular bone and the distal end was ossified in some specimens. Although this structure may ossify at a much later stage in life, the function in young and sub-adult birds may be to dampen shockwaves along the intramandibular nerve that result from the action of pecking. In the ostrich, the *M. pseudotemporalis superficialis* tendon inserted onto the supra-angular bone and Meckel's cartilage. In the emu, a small portion of the tendon was attached to the supra-angular bone and the main part to Meckel's cartilage. The persistence of Meckel's cartilage in adult lepidosaurs, crocodilians and ratites represents an unusual shared trait between the extant members of the above groups.

KEYWORDS: emu, mandible, Meckel's cartilage, ostrich, ratite

## 1. INTRODUCTION

The bony structures of the cranium and mandible of ratite species have been widely studied (Bock, 1963; Dzerzhinsky, 1999; Gussekloo & Bout, 2002, 2005; Johnston, 2011; Maxwell, 2009; Müller, 1963; Parker, 1866, 1891; Rayfield, 2011; Webb, 1957). More recently, the bill tip of ratite species has received particular attention, initially in the Apterygidae where a bill tip organ was described in five extant kiwi species (Cunningham et al., 2013; Cunningham, Castro, & Alley, 2007). Subsequently, aspects of the rostral bill tips have been studied in the ostrich (*Struthio camelus*) and emu (*Dromaius novaehollandiae*) with regards to the bony bill tip (Crole & Soley, 2017), the branches of the trigeminal nerve supplying this region (Crole & Soley, 2016) and the distribution (Crole & Soley, 2014) and structure (Crole, du Plessis, & Soley, 2015) of Herbst corpuscles.

A cartilaginous rod present in the mandibular neurovascular canal has been described in the ostrich and emu and is closely associated with the *N. intramandibularis* (Crole & Soley, 2016). Although the birds investigated in the study were sub-adult specimens, the cartilage was present in the same location as Meckel's cartilage described in ostrich (Webb, 1957) and greater rhea (*Rhea americana*) (Müller, 1963) embryo's. Meckel's cartilage forms from a condensation of mesenchymal cells in the mandibular arch (pharyngeal arch I), which later

differentiate to form hyaline cartilage (Parada & Chai, 2015). The proximal and distal ends of Meckel's cartilage form various structures such as the mandibular symphysis, the primordia of the malleus and incus bones, and the sphenomandibular ligament (see Parada & Chai, 2015) whereas the middle portion degrades in mammals. In the ostrich (Webb, 1957), kiwi (Parker, 1891) and greater rhea (Müller, 1963), Meckel's cartilage appears during early embryonic development and is essentially responsible for the framework (the dermal bones form around the *Collumela* of the cartilage (Parker, 1891)) and ensuing development of the mandible. Meckel's cartilage and its relationship to the intramandibular nerve has been described and depicted in the ostrich embryo; however, it was noted that this structure does not persist and is resorbed in the adult (Webb, 1957). Although the various bones forming the mandible and the timing of their fusion has been described in the chicken (from hatching to 182 days), Meckel's cartilage was not mentioned as being part of the adult mandible (Hogg, 1983). The literature is scant (Bühler, 1981) on the persistence of Meckel's cartilage within the mandibular neurovascular canal of birds beyond the embryonal stage, and there is no reference to a cartilage within the mandibular canal of adult mammals. However, Meckel's cartilage is present in adult lepidosaurs (Holliday, Gardner, Paesani, Douthitt, & Ratliff, 2010) including the adult Texas blindsnake (*Leptotyphlops dulcis*) (Kley, 2006) and Andean lizard (*Stenocercus guentheri*) (Torres-Carvajal, 2003), and in crocodilians such as the broad-snouted caiman (*Caiman latirostris*) (Bona & Desojo, 2011).

This study describes the persistence of the embryonal Meckel's cartilage in the sub-adult ostrich and emu and represents a novel observation in avian species beyond the embryonal stage.

## 2. MATERIALS AND METHODS

A total of 12 sub-adult (12–14 months) and 1 adult (8 years) ostrich (*Struthio camelus* Linnaeus, 1758) and 13 sub-adult (12–14 months) emu (*Dromaius novaehollandiae* Latham, 1790) heads, from birds of either sex, were collected after slaughter from the Klein Karoo Ostrich abattoir (Oudtshoorn, Western Cape Province, South Africa), Oryx Abattoir (Krugersdorp, Gauteng, South Africa), Emu Ranch (Rustenburg, North-West Province, South Africa) and an emu farm (Krugersdorp, Gauteng, South Africa). All heads were thoroughly rinsed with either distilled water or running tap water to remove mucus, blood and regurgitated food and further processed as outlined below. This research was approved by the Faculty of Veterinary Science Research Committee and the use of the animals in this study was approved by the Animal Use and Care Committee of the University of Pretoria (V066/11). This study was performed from 2011–2013 at the University of Pretoria, Faculty of Veterinary Science, Onderstepoort, South Africa. All specimens are stored at the above-mentioned facility.

### 2.1. Gross anatomy

Five ostrich and five emu heads which had been immersion-fixed in 10% neutral-buffered formalin were dissected to determine the course of the mandibular nerve and expose the mandibular neurovascular canal. The heads were rinsed for at least 48 hr prior to dissection. The skin was removed from the lateral aspect of the skull by sharp dissection and fat and fascia removed to expose the musculature. Muscles of mastication and those associated with the quadratomandibular joint and relevant to Meckel's cartilage were traced to their origins and insertions to allow for identification and description. The course of the mandibular nerve was followed through the musculature into the mandibular neurovascular canal to the point

where it entered the mandibular rostrum. The above-mentioned canal was exposed by removing portions of the bony mandible surrounding it to facilitate description of the topography of the structures within the canal.

### 2.2. Modified differential staining of the mandibles to demonstrate cartilage

The mandibles from three fresh ostrich and three fresh emu heads were disarticulated and the soft interramal region removed. As much rhamphotheca and soft tissue as possible was manually removed from the underlying bone. The mandibles were subsequently fixed in a solution of formalin (40%): glacial acetic acid: ethanol (70%) (1:1:8) for 2 hr. Both sets of specimens were then treated according to the method of Kelly and Bryden (1983). Each step of this technique was followed except that alizarin red S was not applied to stain the bone. The specimens were washed in distilled water for 30 min (three 10 min changes) and then placed in Alcian blue solution (10 mg Alcian blue 8GX, 20 ml glacial acetic acid, 80 ml 95% ethanol) for 48 hr to 2 months (in the emu) to stain the cartilage. The specimens were rehydrated through a decreasing ethanol series (95%, 95%, 75%, 40%, 15%, distilled water [at least 2 hr for each step]). They were then incubated for 72 hr at 37°C in Trypsin enzyme solution (1 g trypsin 883,600; 30 ml disodium tetraborate, 70 ml distilled water) to which five drops of 3% hydrogen peroxide were added to bleach highly pigmented tissues. The specimens were then successively transferred to a 0.5% potassium hydroxide solution and a 3:1, 1:1 and 1:3 0.5% potassium hydroxide:glycerol solution, respectively, for at least 24 hr each. The specimens were finally placed in pure glycerol. Once stained and cleared, these specimens were used to describe the intramandibular cartilage (Meckel's cartilage) running in the mandibular neurovascular canal. The findings were digitally recorded with a Canon EOS 5D digital camera (Canon, Ōita, Japan) equipped with a Canon Macro 100 mm lens and annotated in Corel Draw X5.

### 2.3. Light microscopy

Five ostrich and five emu heads were collected as indicated above, immersion-fixed in 10% neutral-buffered formalin and transported to the Faculty of Veterinary Science, University of Pretoria.

To achieve removal of the mandible, the quadratomandibular joints were disarticulated and the oesophagus and soft tissue incised to separate the upper and lower parts of the head. The soft interramal region was removed from the bony mandible by sharp incision following the inside mandibular edge. The mandibular rostrum and arms were decalcified prior to further processing for light microscopy (see below).

Decalcification of the mandibles took place over a period of 6 weeks in an 8% formic acid solution. The samples were placed in a fresh solution fortnightly. The right half of each mandible was serially sectioned in the transverse plane at about 5 mm intervals from the rostrum to the caudal part of the mandibular ramus correlating with the rictus. All tissue samples were then dehydrated through 70%, 80%, 96% and 2X 100% ethanol and further processed through 50:50 ethanol: xylol, 2X xylol and 2X paraffin wax (60–120 min per step) using a Shandon model 2LE Automatic Tissue Processor (Shandon, Pittsburgh, PA, USA). Tissue samples were then imbedded manually into paraffin wax in plastic moulds. Sections were cut at 4–6 μm and stained with H&E (Bancroft & Gamble, 2002). Histological sections were viewed, features of interest described and digitally recorded using an Olympus BX63

light microscope (Olympus Corporation, Tokyo, Japan) equipped with a DP72 camera and Olympus cellSens imaging software (Olympus Corporation), and annotated.

## 3. RESULTS

The mandibles of the ostrich and emu were similarly sized; however, in the ostrich it was U-shaped and in the emu V-shaped (Figure 1). The mandible was formed by a number of bones in both species (Figures 2–4). The most rostral component was the dentary bone (*Os dentale*) which formed the mandibular rostrum (*Rostrum mandibulae*) (Figure 1) and distal arm of the mandible (*Ramus mandibulae*) (Figures 2 and 3). The tomial crest (*Crista tomialis*) was situated on the dorso-lateral edge of the dentary bone and continued caudally along the mandibular arm (Figure 1). The mandibular rostrum has been described in detail (Crole & Soley, 2017) and will therefore not be discussed/described here. The splenial bone (*Os spleniale*) was situated immediately caudal to the dentary bone and contributed to the intermediate part (*Pars intermedia*) of the mandibular arm (Figure 2). The dentary and splenial bones were united by the *Sutura dentosplenialis* (Figure 4). The comparative positioning of the remaining bones forming the mandible is indicated in Figures 2 and 3 based on the embryological studies of Webb (1957) and Parker (1866).

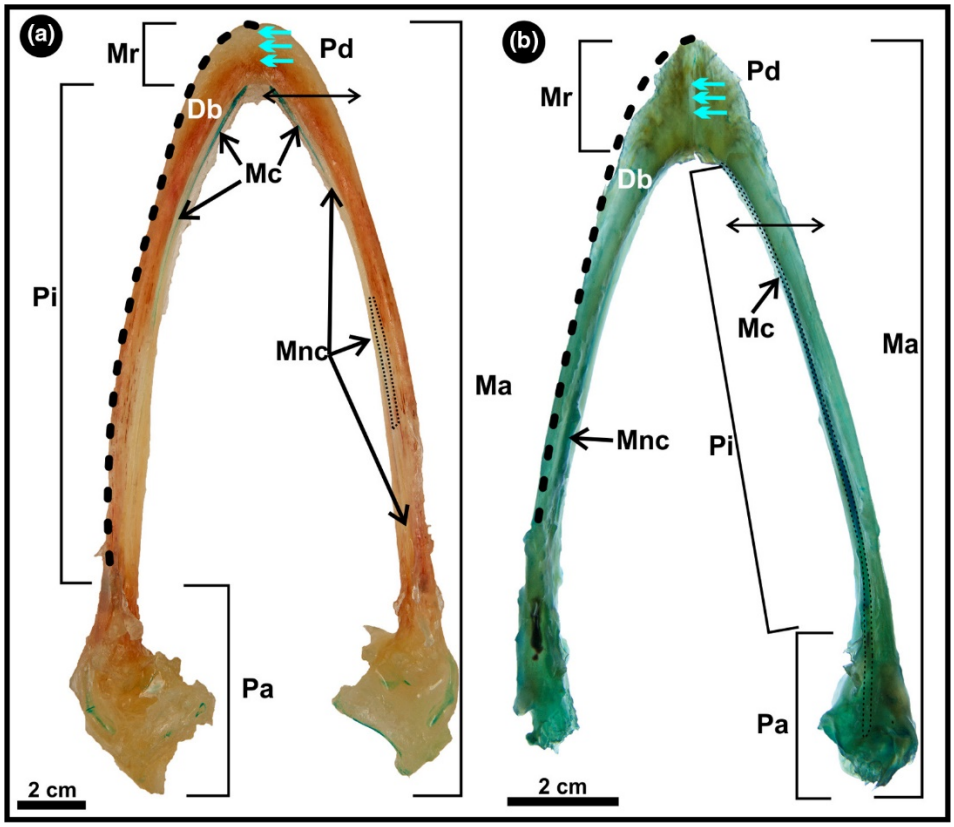
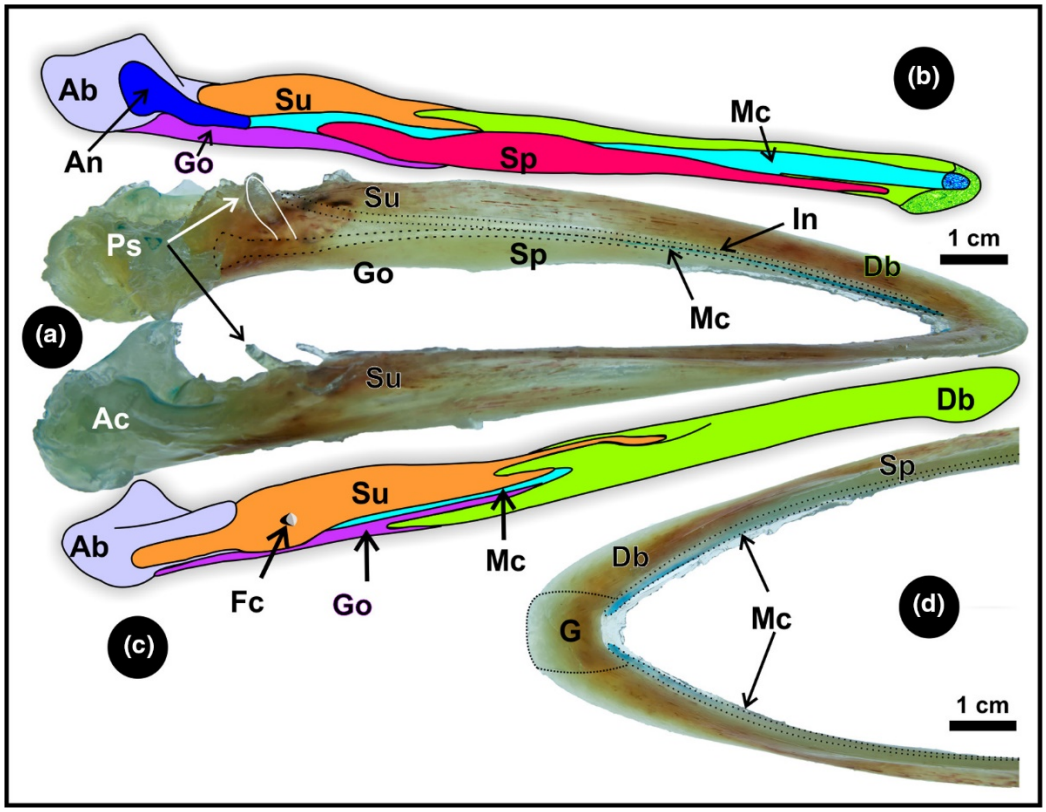



**Figure 1.** Dorsal view of the ostrich (a) and emu (b) mandible. Double-headed arrows indicate the position and plane of section illustrated in Figure 4. The mandible is formed by left and right mandibular arms (Ma) which unite rostrally at the mandibular symphysis (turquoise arrows). The mandibular arm comprises three components, the *Pars articularis* (Pa), *Pars intermedia* (Pi) and the mandibular rostrum (Mr). Two components of the dentary bone (Db) are visible, namely the *Pars dorsalis* (Pd) and the *Pars symphysialis* (turquoise arrows). The tomial crest (thick, black dotted line) is located dorso-laterally on the mandibular rostrum and intermediate part of the mandible. The mandibular neurovascular canal (Mnc) is situated medially and Meckel's cartilage (Mc, partially outlined in a and outlined in b), stained with alcian blue, runs within the canal. Stained and cleared specimens (Kelly & Bryden, 1983). The specimen appears blue in b as it was left in the alcian blue solution for 2 months to allow the cartilage to stain




**2.** Ostrich mandible. (a) (dorso-lateral view) and (d) (ventral view): specimen of a 12–14 months old ostrich stained with alcian blue for cartilage and the tissues cleared. (b and c) Medial (b) and lateral (c) sketch of the components forming the mandible of a 27-day-old ostrich embryo (adapted from original sketch by Webb (1957)). Meckel's cartilage (Mc, outlined in a and d for clarity) is still clearly visible in this sub-adult ostrich, the rostral ends of which terminate at the bony region underlying the *Gonys* (G), without fusing. The intramandibular nerve (In, outlined for clarity) is closely associated with Meckel's cartilage. Dentary bone (Db); splenial bone (Sp); supra-angular bone (Su); gonial bone (Go); angular bone (An); articular cartilage (Ac); articular bone (Ab); *Fenestra mandibularis caudalis* (Fc) and tendinous insertion of *M. pseudotemporalis superficialis* (Ps) onto the caudo-dorsal aspect of Meckel's cartilage

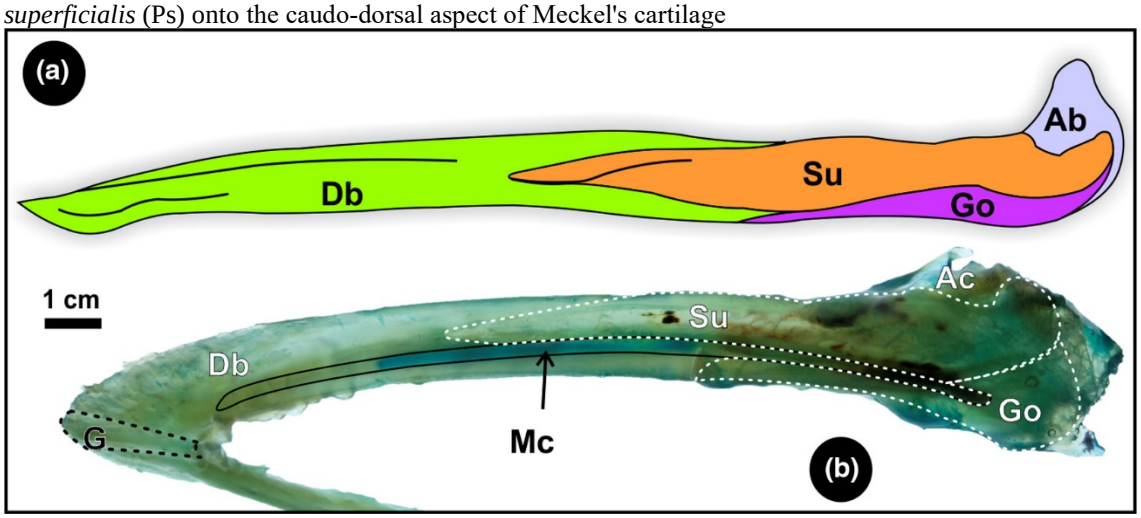



**Figure 3.** Emu mandible. (a) (lateral view) and (b) (ventro-lateral view): specimen stained with alcian blue for cartilage and the tissues cleared. (a) Sketch of the components forming the mandible of a 6-week-old emu chick (adapted from original sketch by Parker (1866)). (b) Meckel's cartilage (Mc, outlined for clarity) is clearly visible in this 12–14 months old emu and in this view obscures the intramandibular nerve. Dentary bone (Db); supra-angular bone (Su); gonial bone (Go); articular cartilage (Ac) overlying the retroarticular process; articular bone (Ab) and *Gonys* (G). The specimen in (b) appears blue as it was left in the alcian blue solution for 2 months to allow the cartilage to stain

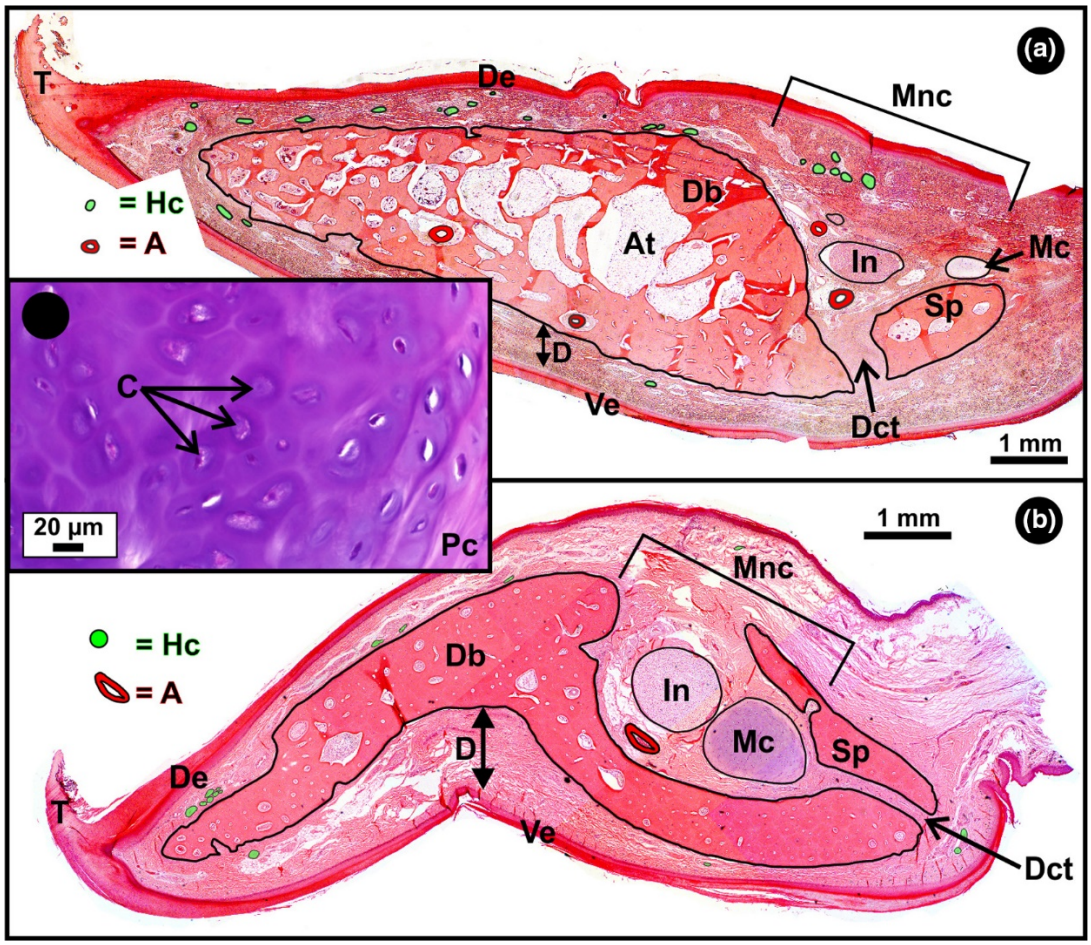



**Figure 4.** Composite micrographs showing a transverse section of the mandible just caudal to the rostrum in the ostrich (a) and of the mandibular arm in the emu (b) (exact locations indicated in Figure 1). Note that Meckel's cartilage (Mc) is situated medial to the intramandibular nerve (In) in the mandibular neurovascular canal (Mnc) and is more robust in the emu. The ventro-medial aspects of the dentary (Db) and splenial (Sp) bones are joined by dense, irregular connective tissue (Dct), the *Sutura dentosplenialis*. The dentary bone in the ostrich at this level still contains small cavities filled mainly with adipose tissue (At). Herbst corpuscles (Hc, green dots); dermis (D); tomium (T); dorsal (De) and ventral (Ve) epithelium and arteries (A). (c) Enlargement of the outer edge of Meckel's cartilage in the ostrich demonstrating typical hyaline cartilage with chondrocytes (C) situated in lacunae and a surrounding perichondrium (Pc)

The intramandibular nerve (Crole & Soley, 2016) entered the mandibular neurovascular canal at the origin of the canal, approximately at the junction of the articular and intermediate parts of the mandibular arm (Figure 2). There was no obvious bony structure indicating the opening of the canal in either of the birds. The mandibular neurovascular canal (*Canalis neurovascularis mandibulae*) was not an entirely closed canal in either the ostrich or emu (Figure 4). The canal was formed by all the bones of the mandible except for the articular bone and was wide caudally and narrowed rostrally. The canal was more open in the ostrich than in the emu and resembled a shallow groove (Figure 4). Located in the canal or groove was a bar of cartilage, which was considered to represent Meckel's cartilage (Figures 1–4). The cartilage (Figure 4c) was typically hyaline in appearance and basophilic in nature. It was surrounded by a prominent perichondrium (Figure 4c) clearly divided into an outer fibrous component and an inner more cellular layer exhibiting appositional growth. The peripherally arranged chondrocytes within lacunae were flattened to oval in shape and relatively small, while the more centrally located cells were round and larger (Figure 4c). Based on transverse sections of the cartilage the concentration of chondrocytes was greatest towards the periphery

and more sparse centrally. Most chondrocytes were individually positioned within the cartilage matrix although pairs of chondrocytes were also a common feature. The matrix revealed regional differences in staining intensity and a clear distinction between the territorial and interterritorial matrix was apparent. Meckel's cartilage (Figure 4c) and its close association with the intramandibular nerve was readily identified in both species (Figures 1–4). This cartilage was positioned deep within the canal/groove and for the caudal two-thirds lay ventro-lateral to the closely associated intramandibular nerve. In the rostral third of the canal, Meckel's cartilage was situated medial to the intramandibular nerve (Figures 2 and 4). The proximal end of Meckel's cartilage was ossified in the region of the articular bone of the mandible. At the point of entry of the mandibular nerve into the mandibular neurovascular canal, in the ostrich, the long, narrow tendon of insertion of *M. pseudotemporalis superficialis* was attached to the medial aspect of the supra-angular bone and the caudo-dorsal aspect of Meckel's cartilage via the perichondrium (Figure 2a). In the emu, a small portion of the tendon was attached to the dorso-medial aspect of the supra-angular bone and the main part to the caudo-dorsal aspect of Meckel's cartilage via the perichondrium, as in the ostrich. The distal end of Meckel's cartilage was ossified in some specimens, and where this occurred, the ossified portion fused with the caudal part of the mandibular rostrum. Meckel's cartilage was more robust in the emu than in the ostrich (Figures 1–4). In one ostrich specimen (at least 8 years old), Meckel's cartilage had ossified and was identifiable as a rod of bone in the same region where Meckel's cartilage was present in the other specimens.

## 4. DISCUSSION

The mandibular rostrum has been described in detail in the ostrich and emu (Crole & Soley, 2017). The origin of the mandibular neurovascular canal in both species was not marked by a *Fossa aditus neurovascularis mandibulae* as described in other birds (Baumel & Witmer, 1993) and it would appear that this bony feature is not present in these species. Another point of difference involving the structure of the mandibular neurovascular canal is that it remained partially open in the ostrich, emu (present study) and greater rhea (Müller, 1963) but is reportedly closed in other birds, such as the chicken (Hogg, 1983). The caudal mandibular fenestra noted in the greater rhea (Müller, 1963) was not present in the ostrich or emu, both of which displayed only one mandibular fenestra, which appeared equivalent to the rostral mandibular fenestra in the greater rhea (Müller, 1963).

A unique observation in this study was the presence and persistence of Meckel's cartilage through to sub-adulthood (12–14 months old birds) in both the ostrich and emu. This cartilage has been described previously as hyaline cartilage (Crole & Soley, 2016). Similar to that reported in some *Accipitres* (Webb, 1957), the rostral portion of Meckel's cartilage ossifies partly in the ostrich and emu. In birds, the *Pars articularis* of Meckel's cartilage ossifies during embryonic development to form the articular bone while the rostral part is either absorbed or ossifies as the mentomandibular bone (Webb, 1957). By Day 34 in the ostrich embryo Meckel's cartilage begins to reduce in size (Webb, 1957) and, as reported by Parker (1866), the rostral two-thirds are resorbed soon after hatching. Webb (1957), based on the findings of Parker (1866) and Parker (1891), states that in the ostrich, rhea, emu and kiwi, only the caudal part of Meckel's cartilage ossifies as the articular bone while the remainder is resorbed. However, it is clear from the present study that Meckel's cartilage persists in the adult bird in both the ostrich and emu and is also present in greater rhea chicks (Müller, 1963). Based on the observation in the present study that Meckel's cartilage was a more robust structure in the emu, Webb's (1957) observation that it diminishes in size in the ostrich embryo may be correct; although it does not finally disappear. Why previous authors (Parker,

1866, 1891; Webb, 1957) failed to observe the presence of Meckel's cartilage and reported it as being resorbed in the embryo can only be speculated on as no reason or evidence was provided for their conclusions. It is possible that this may represent a perpetuation of the initial misinterpretation made by Parker (1866). In one ostrich specimen (at least 8 years old), Meckel's cartilage appears to have ossified. This finding is similar to that of Müller (1963) in the adult rhea (head length of 180 mm) in which a rod of bone was present in the same location as that of Meckel's cartilage in greater rhea chicks. This would appear to indicate that Meckel's cartilage may ossify in ratites as they age. A similar situation has been reported in respect of the hyobranchial apparatus in the ostrich (Soley, Tivane, & Crole, 2015). The ossification of Meckel's cartilage would not lead to the misinterpretation of the structure being absent or resorbed, as a physical rod of bone is still present. On the other hand, with resorption, no presence of a rod would be evident. This strengthens the argument that if Meckel's cartilage persists and is not resorbed in other avian species, it would still be identified as a rod of bone within the mandibular neurovascular canal.

In lepidosaurs, the distal (rostral) aspect of Meckel's cartilage is closely linked to the complex functioning of the mandibular symphysis, which is in turn related to the specific feeding habits of the species (Holliday et al., 2010). For example, in lingual feeders, the distal aspect of Meckel's cartilage serves as an attachment for some of the muscles of the tongue (*M. genioglossus*) (Holliday et al., 2010). However, in the ostrich, emu and greater rhea (Bonga Tomlinson, 2000; Crole & Soley, 2012a, 2012b), although Meckel's cartilage was not described, there was no evidence of hyolingual muscles attaching to the latter, or of the distal ends forming part of the mandibular symphysis (Crole & Soley, 2017). The mandibular rami are completely fused at the symphysis in birds (Bühler, 1981), a situation also apparent in the ostrich and emu, and Meckel's cartilage would thus not play a role in respect of this joint in these two species as it reportedly does in the lepidosaurs (Holliday et al., 2010). Furthermore, the rostral ends of Meckel's cartilage in the ostrich and emu remained unfused, a feature shared by some lepidosaur species including Schneider's Skink (*Eumeces schneideri*), Northern water snake (*Nerodia sipedon*), Ball python (*Python regius*), Sudan plated lizard (*Gerrhosaurus major*), yellow-spotted tropical night lizard (*Lepidophyma flavimaculatum*), gold tegu (*Tupinambis tequixin*), savannah monitor (*Varanus exanthematicus*) and Nile monitor (*Varanus niloticus*) (Holliday et al., 2010). The insertion of the long tendon of *M. pseudotemporalis superficialis* onto the perichondrium of the caudal portion of Meckel's cartilage in the ostrich and emu has not previously been reported. Although Webb (1957) noted that the insertion of the superficial pseudotemporal muscle was on the medial surface of the surangular (supra-angular) bone, there was no mention of a large, firm attachment to Meckel's cartilage. The insertion of this muscle in neognathous birds is on the *Tuberculum pseudotemporale* (Baumel & Witmer, 1993; Vanden Berge & Zweers, 1993), which is situated slightly rostral to the quadratomandibular joint near the base of the medial mandibular process of the mandible (Baumel & Witmer, 1993). The *Tuberculum pseudotemporale* was not identified to be present in the ostrich or emu. In crocodilians, the *M. pseudotemporalis superficialis* attaches to a large, fibrocartilaginous sesamoid cartilage, the *Cartilago transiliens* (Holliday & Witmer, 2007). Thus, in both the crocodylians and the ostrich and emu the *M. pseudotemporalis superficialis* displays an attachment to a cartilaginous structure. Although the ostrich was included in the study by Holliday and Witmer (2007), neither the attachment of the *M. pseudotemporalis superficialis* to Meckel's cartilage, nor Meckel's cartilage itself, were mentioned. This interesting link between muscle attachments to, and the presence of, Meckel's cartilage in the ostrich, emu, lepidosaurs and crocodilians will need to be explored in future comparative studies.

A bill tip organ has been proposed as a shared feature of ratite species (Crole & Soley, 2017) despite their differing eating habits. Similarly, the presence and persistence through to adulthood of Meckel's cartilage would thus appear to be a unique feature of the ostrich and emu (and possibly of other ratite species such as the greater rhea (Müller, 1963)) and may represent an additional shared feature of ratite species which is not present (or reported) in other avian species. The presence of Meckel's cartilage in the ostrich and emu may also be considered a trait that is shared with lepidosaurs and crocodilians. Apart from assisting in the embryological formation of the mandible and serving as an attachment site for *M. pseudotemporalis superficialis*, the persistence of Meckel's cartilage, at least until early adulthood, may indicate additional functions for this structure.

The presence of, and close association between, the *N. intramandibularis* (Crole & Soley, 2016) and Meckel's cartilage within the mandibular neurovascular canal of the ostrich and emu has not been reported in other adult birds, including the chicken (Bubień-Waluszewska, 1981) and mallard (Berkhoudt, 1980). It is unlikely that Meckel's cartilage would add any structural support to the mandible in the sub-adult bird, although it is possible that this cartilage ossifies with advancing age thus fulfilling such a function (see above). A protective function is also not indicated as it is not positioned on the open, medial part of the mandibular neurovascular canal. Excluding the function of Meckel's cartilage acting as an attachment site for *M. pseudotemporalis superficialis*, the persistence through to sub-adulthood is an enigma that has either developmental or functional implications. Developmentally, it may represent a non-functional embryonal remnant carried through to sub-adulthood, and therefore, serves as an example of paedomorphosis. Although earlier authors supported paedomorphosis in ratite species (see Bonga Tomlinson, 2000) it represents an older concept. Alternatively, Meckel's cartilage may be a trait strengthening a closer link between the ostrich and emu (ratites) and the lepidosaurs and crocodilians. Functionally, it may represent a structure that plays a role in absorbing mechanical energy produced by pecking against hard substrates (Crole & Soley, 2016). Meckel's cartilage would possibly prevent nerve fibres within the *N. intramandibularis* (Crole & Soley, 2016) from creating action potentials by direct mechanical stimulation as opposed to transporting action potentials initiated by mechanoreceptors in the bill tip (Crole & Soley, 2014). Gussekloo and Bout (2005) demonstrated that the forces experienced by the bill tip of the greater rhea during pecking were not great and were sufficiently spread over the bony surface area of the bill tip. However, the forces generated would still travel caudally along bone (Dzerzhinsky, 1999). In support of this proposed function, certain bony structures have been demonstrated to redirect forces in the cranium. To protect the braincase of ratites from dangerous concussive forces the bony palate needs to be a solid framework and in the emu “the main trajectory of compression stresses runs from the palatine process of the premaxillary bone to the vomer, then to the pterygoid, the quadrate, and finally via the quadrate's otic process to the braincase” (Dzerzhinsky, 1999). The palatal process of the premaxilla is absent in the ostrich (Crole & Soley, 2017; Dzerzhinsky, 1999; Webb, 1957) and as a result the roof of the oropharynx displays a large gap unsupported by bone (Dzerzhinsky, 1999) while in the emu, the equivalent region is supported by bone, most notably the palatal process of the premaxilla (Crole & Soley, 2017). Thus in the ostrich “compression stresses run from the bill tip through the premaxillary and maxillary bones to the palatine and then almost directly to the apex of the basipterygoid process” (Dzerzhinsky, 1999). The reason for the difference in the structure of the premaxilla in the ostrich and emu has not been determined. However, the absence of the palatal processes in the ostrich may be an adaptation to dissipating concussive forces away from the large, paired *N. ophthalmicus R. medialis* (Crole & Soley, 2016) conveying sensory information from the maxillary rostrum. Cartilage is present along each of the major

nerve trunks carrying impulses from the bill tip, in the form of Meckel's cartilage (present study) and the cartilaginous nasal septum (Crole & Soley, 2016). These structures may provide mechanical isolation by absorbing forces from pecking, thereby preventing direct stimulation of the nerve trunks (Crole & Soley, 2016).

The persistence of Meckel's cartilage in adult lepidosaurs, crocodilians and the ostrich and emu is posited as a functional structure and further investigations as to why these animals share this trait are warranted. Furthermore, now that the awareness has been created, it would be important to establish a database of other avian species that may display Meckel's cartilage beyond the embryonal stage to determine it's significance in adult birds.

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## AUTHOR CONTRIBUTIONS

MRC took the primary lead in the compilation of the manuscript. The concept was the original idea of MRC and elaborated upon by JTS. JTS acted in a supervisory role on all aspects of the work and was responsible for the refinement of the manuscript. Both authors collected the specimens, discussed the results and contributed equally to the manuscript.

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