

## Morphology of the tongue of the emu (*Dromaius novaehollandiae*). I. Gross anatomical features and topography

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### ABSTRACT

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Despite numerous papers addressing the topic, the gross morphology of the ratite tongue and more specifically that of the emu, has been superficially or poorly described. This paper presents the first definitive macroscopic description of the emu tongue and reviews, consolidates and compares the scattered information on the gross morphology of the ratite tongue available in the literature. Twenty-three heads obtained from birds at slaughter were used for this study. Specimens were fixed in 10 % neutral buffered formalin, rinsed and the gross anatomy described. The emu tongue is divided into a body and a root. The body is triangular, dorsoventrally flattened, pigmented and displays caudally directed lingual papillae on both the lateral and caudal margins. The root, a more conspicuous structure in comparison to other ratites, is triangular, with a raised bulbous component folding over the rostral part of the laryngeal fissure. Following the general trend in ratites, the emu tongue is greatly reduced in comparison to the bill length and is specifically adapted for swallowing during the cranioinertial method of feeding employed by palaeognaths. This study revealed that it is not only the shape of the tongue that differs between ratites, as previously reported, but also its colour, appearance of its margins and root, and its length in comparison to the bill, and the shape of the *paraglossum*.

**Keywords:** *Dromaius novaehollandiae*, emu, gross morphology, ratite, tongue

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### INTRODUCTION

The gross morphological features of the avian tongue have been described in numerous species (see McLelland 1979 for a review of the earlier literature) and the structural adaptations of this organ linked to diet and mode of feeding (Gardner 1926, 1927). Many of these studies, particularly the earlier works, presented comparative information on the macroscopic features of the tongue with a view to providing taxonomic data (Lucas 1896, 1897; Gardner 1926, 1927; Harrison 1964). This information

was subsequently used to classify the tongue of birds into various categories. Gardner (1926, 1927), for example, recognised eight categories based on the function and adaptations of this organ. Harrison (1964), on the other hand, proposed the classification of avian tongues into five functional groups, namely tongues specialized for collecting food, eating, swallowing, taste and touch, and nest building.

Echoing the suggestion by Gardner (1926, 1927) that microscopic data would enhance the understanding of macroscopic features, recent studies have generally supplied more comprehensive information on the structure of the avian tongue by using both light and electron microscopy in addition to macroscopic descriptions (Kobayashi, Kumakura,

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Yoshimura, Inatomi & Asami 1998; Jackowiak & Godynicki 2005; Jackowiak & Ludwig 2008; Tivane 2008).

Due to their commercial importance, the tongue and associated hyobranchial apparatus of domestic poultry have been described in detail (see Calhoun 1954 for a review of the earlier literature; Hodges 1974; McLelland 1975; Nickel, Schummer & Seiferle 1977; Homberger & Meyers 1989).

During the past 180 years numerous publications on the ratite tongue have appeared in the form of sketches, descriptions and comparisons (Meckel 1829; Cuvier 1836; Gadow 1879; Owen 1879; Pycraft 1900; Göppert 1903; Duerden 1912; Faraggiana 1933; Roach 1952; Feder 1972; McCann 1973; Cho, Brown & Anderson 1984; Fowler 1991; Bonga Tomlinson 2000; Gussekloo & Bout 2005; Porchescu 2007; Crole & Soley 2008; Jackowiak & Ludwig 2008; Tivane 2008). Many of these studies, however, provide incomplete and sometimes misleading information on the macroscopic features of this organ. This situation is exacerbated by the fact that some descriptions are based on limited numbers of specimens ranging from embryos to fully mature birds, resulting in conflicting information that is difficult to interpret. The most comprehensive studies of a ratite tongue are those of Jackowiak & Ludwig (2008) and Tivane (2008) on the ostrich, although the former authors neglected to reference any of the earlier literature on this topic.

To date there have only been four reports on the gross morphology of the emu tongue. The most complete gross morphological description is that of Faraggiana (1933) who studied a single excised specimen of the tongue and laryngeal mound. Crole & Soley (2008) described the basic features of the emu tongue. In a study of feeding in palaeognathous birds, Bonga Tomlinson (2000) depicts the outline of the emu tongue in relation to the hyobranchial apparatus and surrounding mandibular rami, and briefly describes the presence of lingual papillae. Cho *et al.* (1984) simply note that "the emu tongue has a serrated edge".

This paper presents the first definitive macroscopic description of the emu tongue and reviews, consolidates and compares the scattered information on the gross morphology of the ratite tongue available in the literature. This study not only contributes to a better understanding of the upper digestive tract of the emu but also provides data that can be used for more meaningful future comparative studies of the ratite tongue.

## MATERIALS AND METHODS

### Specimen collection

The heads of 23 adult (14–15 months) emus of either sex were obtained from a local abattoir (Oryx Abattoir, Krugersdorp, Gauteng Province, South Africa) immediately after slaughter of the birds. The heads were rinsed in running tap water to remove traces of blood and then immersed in plastic buckets containing 10% neutral buffered formalin. They were allowed to fix for approximately 4 h while being transported to the laboratory, after which they were immersed in fresh fixative for a minimum period of 48 h. Care was taken to exclude air from the oropharynx by wedging a small block of wood in the beak.

### Specimen preparation and recording

The specimens were rinsed in running tap water and each preserved head was used to provide information on the gross anatomical features of the tongue and its topographical relationships within the oropharyngeal cavity. This was achieved by incising the right commissure of the beak, disarticulating the quadratomandibular joint and reflecting the mandible laterally to openly display the roof and floor of the oropharynx (Fig. 1). The length (from the apex to the caudal edge of the caudal papillae) and width (between the tips of the last lateral papillae) (Fig. 2) of 16 tongues were measured and the lateral and caudal lingual papillae counted. The bill length was measured on the mandibular rhamphotheca from the commissure to the rostral bill tip. Relevant anatomical features were described and recorded using a Canon 5D digital camera with a 28–135 mm lens and a Canon Macro 100 mm lens for higher magnification photographs.

Three tongues were removed from the heads by lifting the organ from the floor of the oropharynx and cutting through the frenulum as well as the paired *ceratobranchiale* and *urohyale* of the hyobranchial apparatus. The mucosa was stripped from the tongues to expose the intraglossal elements (Fig. 7 and 8) of the hyobranchial apparatus. All specimens were studied and described at the Department of Anatomy and Physiology, Faculty of Veterinary Science, University of Pretoria, South Africa. This study was approved by the research committee of the Faculty of Veterinary Science (Protocol no. V040/08) and complied with the regulations regarding the ethical use of animals. The terminology used in this study was that of Nomina Anatomica Avium (Baumel, King, Breazile, Evans & Vanden Berge 1993).

## RESULTS

### Topography

The tongue of the emu consists of a rostral pigmented body and a caudal, variably pigmented root, both of which lie within the confines of the non-pigmented regions of the roof and floor of the oropharynx (Fig. 1). The tongue body occupies the middle third of the floor of the oropharynx and is a triangular structure with the apex pointing rostrally. The tongue root (Fig. 1 and 4) extends from the caudal lingual papillae to the glottis and is flanked by, but does not extend to, the paired *ceratobranchiale* of the hyobranchial apparatus. In the closed gape, the caudal margin of the tongue body lies beneath and in contact with the rostral border of the choana, whereas the triangular tongue root fits snugly into the rostral aspect of the choana. In some tongues the apex is observed, in the closed gape, to make contact with the base of the median palatine ridge which originates at the border of the pigmented and non-pigmented regions of the palate.

### Tongue body (*Corpus linguae*)

The tongue body is dorsoventrally flattened (Fig. 5) with the dorsum being slightly raised in the centre and sloping towards the margins. It varies in length between 21–27 mm (average of 23.6 mm), and in width between 20–29 mm (average of 25.9 mm) (Fig. 2). The apex (*Apex linguae*) is rudimentary and varies in shape from a sharp point (Fig. 1), to a blunt or rounded tip. In some instances the apex is invaginated by a shallow groove forming two smaller points (Fig. 2). The dorsal surface (*Dorsum linguae*) is pigmented giving it an ash-grey/brown colour in formalin-fixed specimens (Fig. 1 and 2). The ventral surface (*Ventrum linguae*) (Fig. 6) is lighter in colour than the dorsal surface with the epithelium appearing glass-like (transparent). The rostromedial region of the ventrum is slightly concave. A conspicuous, light-coloured, finger-like projection extends along the midline from the tip of the frenulum to end bluntly caudal to the apex (Fig. 6). This line represents the rostral projection of the *basihyale* (see below) (Fig. 8). From the rostromedial surfaces of the frenulum two raised bands (*crura*) (Fig. 6), are directed and taper towards the apex. Numerous pale doughnut-shaped structures with a darker centre are clearly visible beneath both the dorsal and ventral surfaces of the tongue body (Fig. 2 and 3). Light microscopy confirmed that each of these structures constitutes a glandular unit with a central lumen/duct opening onto the lingual surface (Crole & Soley 2008), which grouped together form the lin-

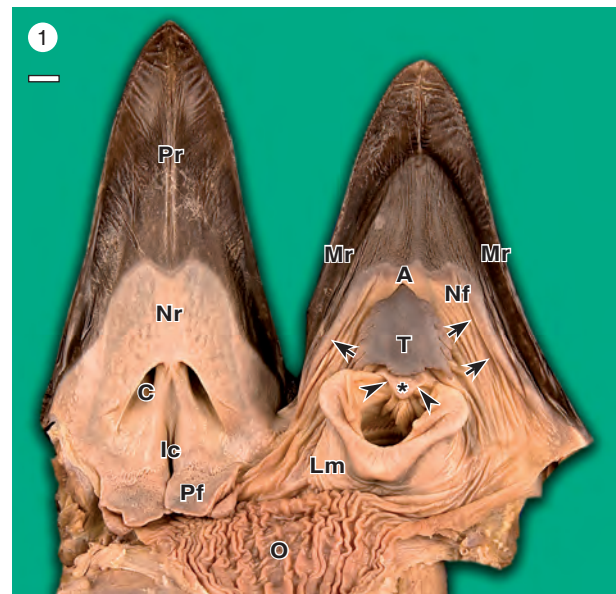


FIG. 1 Emu head opened along the right commissure to reveal the positioning of the tongue within the oropharynx. The body of the tongue (T) lies within the non-pigmented region of both the roof (Nr) and floor (Nf) of the oropharynx, and the small tongue root (\*) extends from the base of the tongue body to the rostral tip of the glottis (arrowheads). The apex (A) of the tongue lies close to the border of the pigmented and non-pigmented regions. Other noticeable features of the oropharynx include the broad mandibular rhamphotheca (Mr), the interramal region of the non-pigmented floor with its numerous folds (arrows), the laryngeal mound (Lm), the median palatine ridge (Pr), the choana (C), infundibular cleft (Ic), pharyngeal folds (Pf) and proximal oesophagus (O). Bar = 5 mm

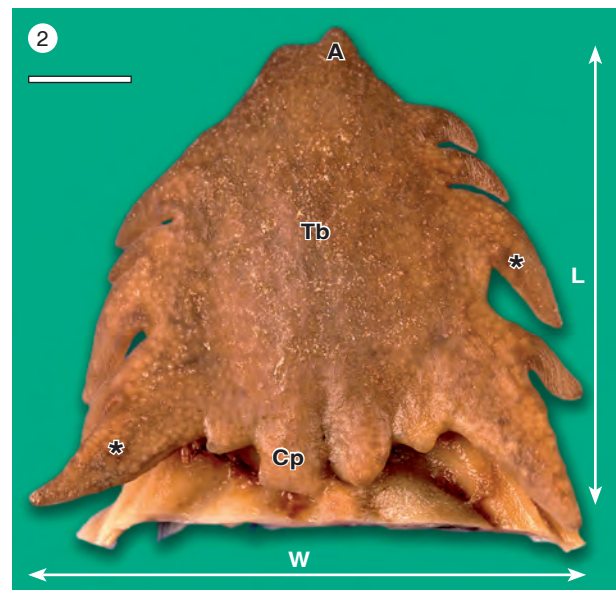


FIG. 2 Dorsal view of the tongue body (Tb) showing the apex (A), lateral lingual papillae (\*) and caudal lingual papillae (Cp). Tongue body length (L) was measured from the apex to the caudal papillae. The width (W) was measured between the tips of the last lateral papillae. Bar = 5 mm

gual glands (*Gll. linguales*) (McLelland 1993). In some tongues, these structures are obscured due to a darker colouration of the dorsum and only the openings, resembling pits, are visible (Fig. 4).

### Margins (*Margo linguae*)

The three margins of the tongue body display two sets of lingual papillae (Fig. 1 and 2), the left and right lateral lingual papillae (*Papillae linguae laterales*) and the caudal lingual papillae (*Papillae linguae caudales*).

The first lateral papillae originate on either side of and just caudal to the apex. These are the smallest of the lateral papillae and are directed laterally or caudolaterally. The rest of the papillae progressively point more caudolaterally and become longer and more slender. The last papillae are the longest and most caudally directed, and in some specimens exhibit a pale tip. In some instances individual papillae emanate from the base of adjacent papillae (Fig. 2) and not directly from the lingual margin. The number of papillae present on the lateral lingual margins is variable and not necessarily equal on both sides. Although the left and right lateral margins demonstrate a similar range of papillae (three to eight on the left side and five to eight on the right side), there appears to be a consistently higher number of papillae on the right margin than compared to the left. The average number of lateral papillae on the tongues studied is 11.2. The doughnut-shaped structures seen below the surface (Fig. 3) end abruptly just beyond the root of the lingual papillae, although in the last lateral and caudal papillae they extend to the papillae tips.

The caudal lingual papillae (Fig. 1, 2 and 4) are rudimentary and poorly defined compared to the lateral papillae and demarcate the caudal boundary of the tongue body. In some instances ( $n = 4$ ) the caudal papillae appear as a fused, centrally positioned structure with variable incisures and small projections (Fig. 4). In other specimens ( $n = 4$ ) the fused component is flanked on either side by a single, more typical papilla. In a number of tongues ( $n = 8$ ) the fused component displays a shallow median groove resulting in the formation of two median papillae which are accompanied by a variable number (zero to two) of adjacent papillae (Fig. 2). The caudal papillae vary in number between one to four (average two and a half). In one specimen, a structure similar in appearance to a lingual papilla was observed to project dorsally from the mucosa covering the left *ceratobranchiale*, just caudal to the last lateral papilla.

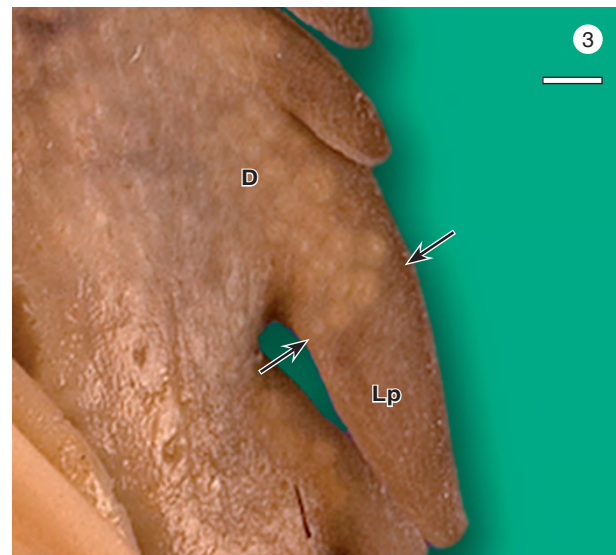


FIG. 3 Ventral view of the lateral lingual papillae showing the abrupt transition (arrows) between the presence of doughnut-shaped structures (D) and the unelaborated surface of the papillae (Lp). Bar = 1 mm

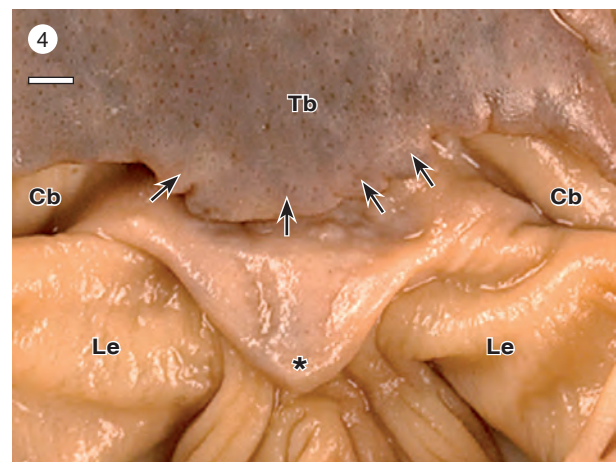


FIG. 4 Dorsal view of the triangular tongue root, showing the caudal extremity of the tongue root (\*) folding over the laryngeal entrance (Le). In this specimen, the caudal lingual papillae (arrows) of the tongue body (Tb) appear fused with variable incisures and small projections being apparent. The rostral parts of the paired *ceratobranchiale* (Cb) are seen bordering the tongue root. Note the pitted surface of the tongue body, representing the openings of the large underlying glands. Bar = 1 mm

### Tongue root (*Radix linguae*)

The tongue root (Fig. 1 and 4) is a fleshy triangular structure, which in most specimens, is non-pigmented. The caudal extremity of the root ends as a rounded, raised bulbous structure (pigmented in some specimens) that extends into the rostral aspect of the laryngeal fissure (glottis). The mucosa of the tongue root is continuous with the rest of the

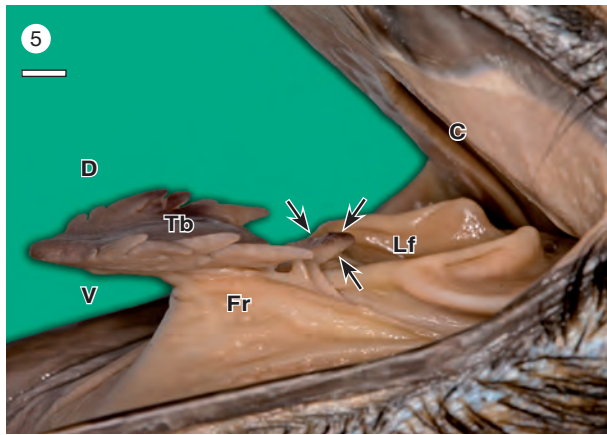


FIG. 5 The dorsoventrally flattened tongue body (Tb) shown in lateral profile. The folds of the frenulum (Fr) are not visible as the tongue body is in the raised position. Dorsum (D), ventrum (V), tongue root tip (arrows), laryngeal fissure (Lf), choana (C). Bar = 5 mm

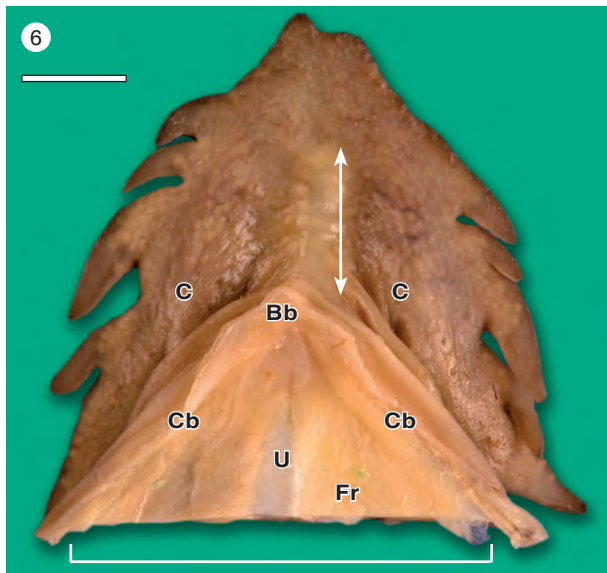


FIG. 6 The tongue body and frenulum in ventral view. Note the extent of the rostral projection of the *basihyale* (double-headed arrow). The position of the body of the *basihyale* (Bb), rostral parts of the paired *ceratobranchiale* (Cb) and the *urohyale* (U) are indicated and occur in triangular formation running within the frenulum (Fr). The doughnut-shaped structures can be clearly seen below the surface. Crura (C). Bar = 5 mm

mucosa covering the oropharyngeal floor and forms a shallow groove where it abuts the paired *ceratobranchiale* and the raised margins of the laryngeal fissure (Fig. 4). The surface of the root displays the same doughnut-shaped structures seen on the tongue body, particularly in the midline. A shallow retrolingual recess exists between the ventral aspect of the caudal lingual papillae and the tongue root.

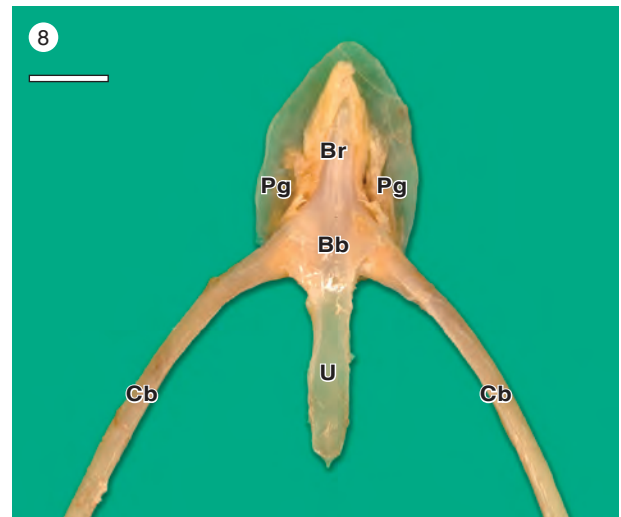
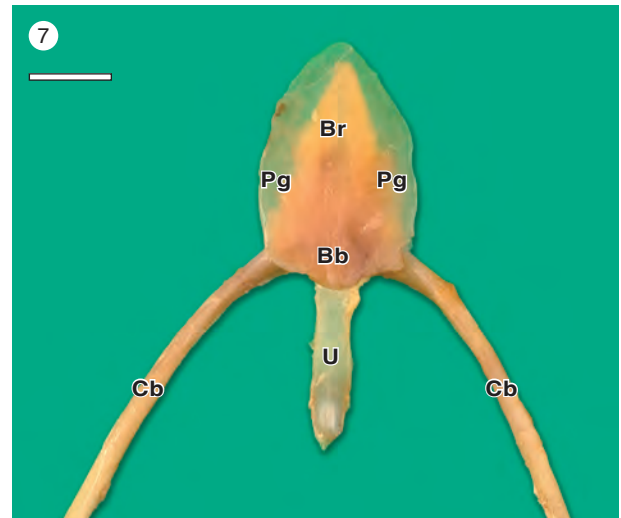


FIG. 7 and 8 The lingual skeleton shown in dorsal (7) and ventral (8) view

The broad *paraglossum* (Pg) lies dorsal to the rostral projection of the *basihyale* (Br) within the tongue body. The body of the *basihyale* (Bb), the rostral parts of the paired *ceratobranchiale* (Cb) and the *urohyale* (U) are all imbedded within the frenulum (see Fig. 6). Bar = 5 mm

### Frenulum (*Frenulum linguae*)

The frenulum (Fig. 5 and 6) is a fleshy non-pigmented structure which attaches the caudal half of the tongue body to the oropharyngeal floor. It is triangular in shape, with the rostral attachment to the ventrum of the tongue forming the point of the triangle. The mucosa along the lateral edges is thrown into longitudinal folds. These folds are obliterated when

the tongue body is lifted dorsally from the oropharyngeal floor (Fig. 5). The rostral point of the frenulum houses the body of the *basihyale* while the two lateral edges enclose the rostral parts of the paired *ceratobranchiale* which merge rostrally with the body of the *basihyale* (Fig. 6). Extending caudally from the body of the *basihyale*, along the midline, is the *urohyale*, also housed within the frenulum (Fig. 6) (see also Fig. 8).

### Lingual skeleton

The lingual skeleton consists of the *paraglossum* and the rostral projection of the *basihyale* (Fig. 7 and 8), both of which are imbedded in the tongue body. The *paraglossum* is a broad, thin, teardrop-shaped cartilaginous plate imbedded within the lingual parenchyma. The rostral tip is pointed while the base varies from gently rounded, to scalloped. The *paraglossum* is situated dorsal to the rostral projection of the *basihyale*, to which it is attached by loose connective tissue. The *basihyale* runs almost the full length of the *paraglossum*, ending near its rostral tip. The edges of the *paraglossum* do not extend to the apex or lingual margins, nor into any of the lingual papillae.

### DISCUSSION

There is no definitive information in the literature on the topography of the emu tongue within the oropharynx. The sketch by Faraggiana (1933) shows the tongue in relation only to the laryngeal mound whereas Bonga Tomlinson (2000) simply depicts the outline of the emu tongue body in relation to the hyobranchial apparatus and mandibular rami. From the specimens examined in the current study it was observed that the apex of the tongue did not extend further than half the distance from the commissure to the rostral bill tip. This contrasts with the positioning of the tongue body indicated by Bonga Tomlinson (2000), which shows it to occupy a far more rostral position relative to the surrounding structures. However, despite differences in the appearance of the various ratite tongues, the topographical relationships of this organ in the emu are generally similar to those illustrated in the ostrich (Göppert 1903; Faraggiana 1933; Bonga Tomlinson 2000; Jackowiak & Ludwig 2008; Tivane 2008), greater rhea (Gadow 1879; Pycraft 1900; Faraggiana 1933; Gussekloo & Bout 2005), cassowary (P. Johnston, personal communication 2008) and kiwi (McCann 1973).

The general shape of the tongue in birds usually mimics that of the bill (Bradley 1915; Harrison 1964;

Koch 1973; Hodges 1974; Nickel *et al.* 1977) or the palate (McLelland 1979). However, in comparison to other bird families, the ratite tongue is greatly reduced in length relative to the bill (Faraggiana 1933; Ziswiler & Farner 1972; McLelland 1979; Bailey, Mensah-Brown, Samour, Naldo, Lawrence & Garner 1997; Bonga Tomlinson 2000; Gussekloo & Bout 2005; Jackowiak & Godynicki 2005; Jackowiak & Ludwig 2008), a feature also noted in the emu (see Table 1). Tongue structure in birds is highly variable and closely related to feeding (McLelland 1979), with the ratite tongue being described as a rudimentary or vestigial organ adapted for rapid swallowing of large food items (Gadow 1879; Pycraft 1900; McLelland 1979; Bonga Tomlinson 2000). Two specific adaptations of the avian tongue for swallowing have been recognized, namely, the occurrence of caudally directed lingual papillae (Harrison 1964; McLelland 1979; King & McLelland 1984) and/or a reduction in tongue size (McLelland 1979). The emu tongue body displays both of the above mentioned adaptations, as does that of the cassowary (P. Johnston, personal communication 2008). Two reasons for tongue reduction in ratites can be advanced. In birds that swallow food whole (Harrison 1964; McLelland 1979) the tongue is unnecessary and therefore rudimentary (Harrison 1964; King & McLelland 1984) as well as non-protrusible (King & McLelland 1984). It is also suggested that because of the cranioinertial feeding method employed by ratites, a longer tongue extending to the bill tip would be injured due to the rapid bill closure involved in this feeding technique (Bonga Tomlinson 2000).

There are surprisingly few accounts documenting the general appearance of the emu tongue, with both Fowler (1991) and Sales (2006, 2007) simply quoting the observation of Cho *et al.* (1984) that "the tongue of the emu has a serrated edge". The fringed appearance of the emu tongue body is also illustrated by Bonga Tomlinson (2000). The most comprehensive description of the general shape of the emu tongue is that of Faraggiana (1933) who described the basic features noted in this study. However, as this author was limited to a single specimen, some differences were apparent. In addition to the rounded apex described by Faraggiana (1933), pointed or split apices were observed in the present study, whereas the tongue body appeared broader than that depicted in the earlier work.

It is clear from previous studies that the shape of the tongue body differs between ratites (Cho *et al.* 1984). These differences in tongue shape are compared in Table 1 and indicate that the tongues of the emu and cassowary (P. Johnston, personal communica-

TABLE 1 Comparative features of the ratite tongue

Species	Body shape	Root shape	Pigmentation	Body margins	Tongue length compared to lower bill length (%) <sup>+</sup>
Emu ( <i>Dromaius novaehollandiae</i> )	Triangular <sup>15,20</sup>	Triangular <sup>15,20</sup>	<u>Body</u> : Yes <sup>15,20</sup> <u>Root</u> : Variable <sup>20</sup>	Serrated <sup>9,13,14,15,20</sup> Lateral <sup>9,14,15,20</sup> and caudal papillae <sup>9,15,20</sup>	20.8 <sup>#</sup> –23.8 <sup>#</sup>
Ostrich ( <i>Struthio camelus</i> )	Triangular or ∩-shaped <sup>4,6,13,14,17,18</sup> Short and/or blunt <sup>3,4,6,8,13,14,17,18</sup> Caudal “lingual pocket” <sup>1,2,9,14,16,17,18</sup>	Flat <sup>17,18,21</sup>	<u>Body</u> : No <sup>18</sup> <u>Root</u> : No <sup>18,21</sup>	Smooth <sup>18</sup> Two caudolateral projections (lingual horns) <sup>1,2,7,9,17,18</sup>	20 <sup>9</sup> –21.4 <sup>#</sup> 25 <sup>17</sup>
Greater rhea ( <i>Rhea americana</i> )	Triangular with rounded apex <sup>9,21</sup>	Flat <sup>21</sup>	<u>Body</u> : Yes <sup>9,11</sup> Lingual horns not <sup>9,21</sup> <u>Root</u> : No <sup>21</sup>	Smooth <sup>9,14</sup> Two globose, bilateral caudolateral papillae <sup>14</sup> Two caudal lingual horns/ projections <sup>9,21</sup>	19 <sup>#</sup> –20.9 <sup>#</sup>
Darwin’s rhea ( <i>Pterocnemia pennata</i> )	V-shaped with pointed apex <sup>13</sup>	–	–	Smooth <sup>13</sup>	–
Cassowary ( <i>Casuarus casuaris</i> )	Triangular, longer than wide <sup>4</sup> Rostral rounded apex free of papillae, no caudal papillae <sup>19</sup>	Flat <sup>19</sup>	<u>Body</u> : No <sup>19</sup> <u>Root</u> : No <sup>19</sup>	Backward pointing tips <sup>4</sup> Denticulate <sup>6</sup> Similar to the emu but a different pattern <sup>19</sup>	13 <sup>19</sup>
Kiwi ( <i>Apteryx australis mantelli</i> ) ( <i>Apteryx haastii</i> ) ( <i>Apteryx oweni</i> )	Triangular long-pyrriform; tip obtuse, retuse or truncate <sup>12</sup> Oblong, constriction below transverse midline; apex truncate or retuse <sup>12</sup> Similar to <i>A. haastii</i> , with larger constriction <sup>12</sup>	(Depicted, but not labeled) <sup>12</sup>	No <sup>5,12</sup> No <sup>12</sup> No <sup>12</sup>	Smooth <sup>5,12</sup> Blunt <sup>12</sup> Folded <sup>12</sup>	9.5*–14.2*

<sup>+</sup> These are approximate measurements

<sup>\*</sup> Extrapolated from the measurements (species not mentioned) in Roach (1952)

<sup>#</sup> Own measurements

Underlined names indicate a sketch is supplied, bold indicates photographs:

<sup>1</sup>Meckel (1829) <sup>2</sup>Cuvier (1836), <sup>3</sup>MacAlister (1864), <sup>4</sup>Gadow (1879), <sup>5</sup>Owen (1879), <sup>6</sup>Pyraffi (1900), <sup>7</sup>Göppert (1903), <sup>8</sup>Duerden (1912), <sup>9</sup>Faraggiana (1933), <sup>10</sup>Roach (1952), <sup>11</sup>Feder (1972), <sup>12</sup>McCann (1973), <sup>13</sup>Cho et al. (1984), <sup>14</sup>Bonga Tomlinson (2000), <sup>15</sup>Crole & Soley (2008), <sup>16</sup>Porchescu (2007), <sup>17</sup>Jackowiak & Ludwig (2008), <sup>18</sup>Tivane (2008), <sup>19</sup>Johnston (Personal communication), <sup>20</sup>Present study, <sup>21</sup>Personal observation

tion 2008) share similar gross morphological features. It should be noted, however, that it is not only tongue shape that differs between ratites. The appearance of the tongue body margins, tongue root, the prevalence of pigmentation, tongue size relative to the length of the bill, the occurrence of special features (for example, the lingual pocket in the ostrich), and the shape and composition of the *paraglossum* all define differences in ratite tongue structure and appearance (see Table 1).

It is also noteworthy that in birds with an omnivorous diet the tongue conforms to a generalised pattern described as triangular with a pointed apex, with the chief adaptive feature being that of caudally pointing spines (papillae) on the caudal margin (Gardner 1927). This statement would certainly be true for the emu, which also enjoys a varied diet (Davies 1978).

Lingual papillae (dorsal, lateral and caudal) are a common feature of the avian tongue and have been described in numerous species (Gardner 1926, 1927; McLelland 1979; King & McLelland 1984; Bailey *et al.* 1997; Kobayashi *et al.* 1998; McLelland 1990) including domestic poultry (Calhoun 1954; Ziswiler & Farner 1972; McLelland 1975; Nickel *et al.* 1977; King & McLelland 1984; McLelland 1990). However, it would appear that lingual papillae are not a common or well-developed feature in ratites (Table 1), a characteristic also noted by Bonga Tomlinson (2000). Apart from the lateral papillae of the emu (Table 1) and cassowary (Gadow 1879; Pycraft 1900), the rest of the ratites documented display smooth lateral tongue margins. In the little spotted kiwi (McCann 1973) the lateral tongue margins are narrowly infolded, but show no papillae.

The lateral lingual papillae of the emu tongue show a lack of bilateral symmetry which involves differences in both number and shape, with a greater number of papillae usually being observed on the right margin. Faraggiana (1933) also noted that the number of papillae was not the same on each side of the tongue body whereas Bonga Tomlinson (2000) provides a definitive number of five lingual papillae on the lateral margins. In contrast, as noted in this study, the number of papillae displays a normal variation between specimens of 3–8 on the left and 5–8 on the right margins.

The caudal lingual papillae of the emu tongue are rudimentary compared to other bird species and even though identifiable, are often not well-developed. The sketch by Bonga Tomlinson (2000) neglects to depict the caudal lingual papillae in this species. In

comparison to the other ratites, the emu appears to be the only member which possesses structures recognisable as caudal lingual papillae (Table 1). However, in the ostrich and greater rhea (Table 1) the caudolateral aspect of the tongue body displays papillae-like extensions. Whether these structures represent true caudal lingual papillae remains undetermined.

The function of the lingual papillae is reportedly to assist in the aboral transport of food (McLelland 1979; King & McLelland 1984). In the emu the lingual papillae may be instrumental in removing smaller food particles from the roof of the oropharynx in a similar fashion to that proposed by Bonga Tomlinson (2000) for palaeognathous birds (see below).

Some confusion exists in the literature regarding the naming of the caudal extremity of the tongue body (the tongue base) and the tongue root (Moore & Elliott 1946) with both terms being used interchangeably (McLelland 1975). In domestic poultry the tongue is clearly defined into a free rostral tip (apex), a body and a caudal root (McLelland 1993). Descriptions of the tongue using this terminology exist for a number of species (see, for example, Faraggiana 1933; Bailey *et al.* 1997; Jackowiak & Godynicki 2005; Jackowiak & Ludwig 2008). Based on the work of Lillie (1908) and Bradley (1915) it is generally accepted that the border between the tongue body and root is the row of caudal lingual papillae (Botezat 1910; Moore & Elliott 1946; Gentle 1971; Nickel *et al.* 1977; Bailey *et al.* 1997). This border coincides with the boundary between the oral and pharyngeal cavities as described for *Anas* by Zweers *et al.* 1977 (cited by McLelland 1993). Some authors appear to use the term 'tongue base' synonymously with 'tongue root' (Nickel *et al.* 1977; Gussekloo & Bout 2005). In some studies the caudal aspect of the tongue body has been termed the tongue base (Warner, McFarland & Wilson 1967; McLelland 1975; Bhattacharyya 1980; Bonga Tomlinson 2000) or even the tongue root (Koch 1973; McLelland 1979; McLelland 1990; Kobayashi *et al.* 1998) whereas in other publications the term tongue base is used but not defined (Bacha & Bacha 2000; Calhoun 1954). Alternative terminology used for the tongue root includes the posterior part of the tongue (Gentle 1971), the sensory area (Bhattacharyya 1980) and the preglottal part of the tongue (Homburger & Meyers 1989; Liman, Bayram & Koçak 2001).

The importance of clarity in correctly identifying and naming the various components of the tongue has



been pointed out by Moore & Elliott (1946), particularly in regard to the location of taste buds. Failure to recognise the caudal aspect of the tongue (the tongue root) as part of the tongue could lead to invalid conclusions about the presence of taste buds in this organ, as they are reportedly concentrated in this region (Moore & Elliott 1946; Gentle 1971; Nickel *et al.* 1977; Bacha & Bacha 2000; Al-Mansour & Jarrar 2004).

A clearly defined triangular structure represents the tongue root in the emu and is positioned between the caudal margin of the tongue body and the laryngeal entrance. This structure seems to be unique to the emu as in other ratites the tongue root is represented by a featureless stretch of mucosa (Table 1). The structure of the tongue root in kiwi species is unclear (McCann 1973). The extension of the tongue root into the rostral aspect of the laryngeal entrance (Faraggiana 1933; present study) represents an interesting modification not observed or illustrated in other ratites (ostrich and greater rhea) (Göppert 1903; Faraggiana 1933; Gussekloo & Bout 2005; Porchescu 2007; Jackowiak & Ludwig 2008; Tivane 2008). The positioning of the tongue root would also appear to assist in sealing the rostral part of the larynx when the glottis is closed, almost assuming the role of an epiglottis, which is not present in birds (Kaupp 1918; Calhoun 1954; King & McLelland 1984; Nickel *et al.* 1977). This argument regarding the role of the tongue root functioning as an epiglottis in the emu has been proposed by Gadow (1879) but disputed by Faraggiana (1933). The tongue root of the emu also appears to play a special role in assisting to close off of the rostral aspect of the choana in the closed gape. The choana of most birds is divided into a rostral slit-like part (*pars rostralis*) and a caudal triangular part (*pars caudalis*) (King 1993) with the tongue commonly closing off the rostral part of the choana (McLelland 1975, 1979). In the emu, the triangular choana (Fig. 1) is not divided into rostral and caudal parts and therefore the tongue body plays no part in closing off the choana in the closed gape. Instead, the tongue root partially closes off the rostral aspect of the choana in this species.

Little mention is made in the literature of the frenulum in birds. A possible reason for this may be its general lack of remarkable features, serving simply to attach the tongue to the oropharyngeal floor (McLelland 1979). In the emu, the frenulum is a relatively large structure which houses part of the hyobranchial apparatus. The lateral margins are longitudinally folded which would seem to indicate that the tongue is capable of a certain degree of move-

ment. This observation lends further support to the role played by the tongue of palaeognaths in cranioinertial feeding and in drinking. During swallowing in palaeognaths the tongue is lifted and contacts the palate before moving caudally, thereby scraping any food caudal to the tongue into the proximal oesophagus (Bonga Tomlinson 2000). Palaeognaths transport food from their bill tips to the oesophageal entrance via the cranioinertial feeding method (Bonga Tomlinson 2000), also described as the 'catch and throw' method by Gussekloo & Bout (2005). The transport of food into or close to the oesophageal entrance is facilitated by a large gape and marked depression of the tongue. Tongue depression enlarges the 'buccal cavity' (oropharyngeal cavity), which assists in moving food to the caudal oropharynx, while retraction of the tongue assists in the final transport of fluid to the oesophagus during drinking (Gussekloo & Bout 2005). Therefore, despite the emu tongue showing such relatively reduced dimensions and rigidity, it possess a surprisingly large range of movements in both the rostrocaudal (though unable to protrude) and dorsoventral planes by virtue of the relatively large, folded frenulum and the association of the hyobranchial apparatus with the tongue body and frenulum.

The lingual skeleton of the emu is formed by the median, unpaired *paraglossum* and the rostral projection of the *basihyale* of the hyobranchial apparatus. The *paraglossum* is related dorsally to the rostral projection of the *basihyale* as also described by Bonga Tomlinson (2000) in the emu and the greater rhea. However, the findings of this study contrasted with those of Bonga Tomlinson (2000) in that the rostral projection of the *basihyale* extended further rostrally, ventral to the *paraglossum*, than that depicted by the author.

The *paraglossum* of the emu was teardrop-shaped with a pointed rostral tip and a rounded base although it is depicted by Parker (1866) in *Dromaius irroratus* as inverted heart-shaped and by Bonga Tomlinson (2000) in *Dromaius novaehollandiae* as arrowhead-shaped. In ratites the *paraglossum* remains cartilaginous and does not ossify in older birds (Bonga Tomlinson 2000), a situation also apparent in the emu. The shape of the *paraglossum* differs between the ratites. The *paraglossum* of the emu (*Dromaius irroratus* and *novaehollandiae*), rhea (*Rhea americana*) and cassowary (*Casuarius bennettii*) are all basically arrowhead-shaped, although individual differences are apparent, particularly regarding the form of the base (Parker 1866; Bonga Tomlinson 2000; present study). The *paraglossum*

of the kiwi (*Apteryx australis*) (Parker 1891) is also a single structure but is much narrower than that of the emu, rhea and cassowary and has a split, elongated base. The ostrich *paraglossum* is divided into two narrow *paraglossalia* which flank the rostral projection of the *basihyale* and are located ventrolateral to it (Bonga Tomlinson 2000; Tivane 2008). This arrangement differs radically from that of the emu, where the rostral projection of the *basihyale* lies ventral to the *paraglossum*, and the other ratites and has lead to some authors not recognising or misinterpreting the narrow, paired structure (Meckel 1829; Parker 1866; Webb 1957; Jackowiak & Ludwig 2008) present in the ostrich tongue.

The tongue of birds is a rigid organ due to the presence of the *paraglossum* (Koch 1973) and, except in parrots, the absence of intrinsic musculature (Ziswiler & Farner 1972; Koch 1973; Nickel *et al.* 1977; McLelland 1990). The rigidity afforded by the *paraglossum* in palaeognathous birds is needed for the swallowing phase in order to push the food into the oesophagus. The rostral projection and body of the *basihyale*, situated ventrally in the tongue body, connects the hyobranchial apparatus with the tongue, and due to its close association, retracts the tongue during swallowing. The great mobility of the hyobranchial apparatus in birds, attributed to the fact that it does not articulate with the skull (McLeod 1939), is the main contributor to the movement of the tongue (King & McLelland 1984; Bonga Tomlinson 2000).

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## REFERENCES

AL-MANSOUR, M.I. & JARRAR, B.M. 2004. Structure and secretions of the lingual salivary glands of the White-Cheeked Bulbul, *Pycnonotus leucogenys* (Pycnonotidae). *Saudi Journal of Biological Sciences*, 11:119–126.

BACHA, W.J. & BACHA, L.M. 2000. Digestive system, in *Color atlas of veterinary histology*, edited by D. Balado. Philadelphia: Lippincott Williams & Wilkins.

BAILEY, T.A., MENSAH-BROWN, E.P., SAMOUR, J.H., NALDO, J., LAWRENCE, P. & GARNER, A. 1997. Comparative morphology of the alimentary tract and its glandular derivatives of captive bustards. *Journal of Anatomy*, 191:387–398.

BAUMEL, J.J., KING, A.S., BREAZILE, J.E., EVANS, H.E. & VANDEN BERGE, J.C. 1993. *Handbook of avian anatomy: Nomina anatomica avium*, 2<sup>nd</sup> ed. Cambridge, Massachusetts: Nuttall Ornithological Club.

BHATTACHARYYA, B.N. 1980. The morphology of the jaw and tongue musculature of the common pigeon, *Columba livia*, in relation to its feeding habit. *Proceedings of the Zoological Society, Calcutta*, 31:95–127.

BONGA TOMLINSON, C.A. 2000. Feeding in paleognathous birds, in *Feeding: form, function, and evolution in tetrapod vertebrates*, edited by K. Schwenk. San Diego: Academic Press.

BOTEZAT, E. 1910. Morphologie, Physiologie und phylogenetische Bedeutung der Geschmacksorgane der Vögel. *Anatomischer Anzeiger*, 36:428–461.

BRADLEY, O.C. 1915. *The structure of the fowl*. London: A. and C. Black, Ltd.

CALHOUN, M.L. 1954. *Microscopic anatomy of the digestive system of the chicken*. Ames, Iowa: Iowa State College Press.

CHO, P., BROWN, B. & ANDERSON, M. 1984. Comparative gross anatomy of ratites. *Zoo Biology*, 3:133–144.

CROLE, M.R. & SOLEY, J.T. 2008. Histological structure of the tongue of the emu (*Dromaius novaehollandiae*). *Proceedings of the Microscopy Society of Southern Africa*, 38:63.

CUVIER, G. 1836. *Leçons d'anatomie comparée*, 3<sup>rd</sup> ed. Vol. 1 & 2, edited by M. Duméril. Bruxelles: Dumont.

DAVIES, S.J.J.F. 1978. The food of emus. *Australian Journal of Ecology*, 3:411–422.

DUERDEN, J.E. 1912. Experiments with ostriches. XVIII. The anatomy and physiology of the ostrich. A. The external characters. *Agricultural Journal of the Union of South Africa*, 3: 1–27.

FARAGGIANA, R. 1933. Sulla morfologia della lingua e del rialzo laringeo di alcune specie di uccelli Ratiti e Carenati non comuni. *Bollettino dei Musei di Zoologia e Anatomia comparata*, 43:313–323.

FEDER, F-H. 1972. Zur mikroskopischen Anatomie des Verdauungsapparates beim Nandu (*Rhea americana*). *Anatomischer Anzeiger*, 132:250–265.

FOWLER, M.E. 1991. Comparative clinical anatomy of ratites. *Journal of Zoo and Wildlife Medicine*, 22:204–227.

GADOW, H. 1879. Versuch einer vergleichenden Anatomie des Verdauungssystems der Vögel. *Jenaische Zeitschrift für Medizin und Naturwissenschaft*, 13:92–171.

GARDNER, L.L. 1926. The adaptive modifications and the taxonomic value of the tongue in birds. *Proceedings of the United States National Museum*, 67: Article 19.

GARDNER, L.L. 1927. On the tongue in birds. *The Ibis*, 3:185–196.

GENTLE, M.J. 1971. The lingual taste buds of *Gallus domesticus*. *British Poultry Science*, 12:245–248.

GÖPPERT, E. 1903. Die Bedeutung der Zunge für den sekundären Gaumen und den Ductus nasopharyngeus. *Morphologisches Jahrbuch*, 31:311–359.

- GUSSEKLOO, S.W.S. & BOUT, G.R. 2005. The kinematics of feeding and drinking in palaeognathous birds in relation to cranial morphology. *The Journal of Experimental Biology*, 208:3395–3407.
- HARRISON, J.G. 1964. Tongue, in *A new dictionary of birds*, edited by A.L. Thomson. London: Nelson.
- HODGES, R.D. 1974. The digestive system, in *The histology of the fowl*. London: Academic Press.
- HOMBERGER, D.G. & MEYERS, R. 1989. Morphology of the lingual apparatus of the domestic chicken *Gallus gallus*, with special attention to the structure of the fasciae. *American Journal of Anatomy*, 186:217–257.
- JACKOWIAK, H. & GODYNIKSI, S. 2005. Light and scanning electron microscopic study of the tongue in the white tailed eagle (*Haliaeetus albicilla*, Accipitridae, Aves). *Annals of Anatomy*, 187:251–259.
- JACKOWIAK, H. & LUDWIG, M. 2008. Light and scanning electron microscopic study of the structure of the ostrich (*Struthio camelus*) tongue. *Zoological Science*, 25:188–194.
- KAUPP, M.S. 1918. *The anatomy of the domestic fowl*. Philadelphia: W.B. Saunders Company.
- KING, A.S. 1993. Apparatus respiratorius [Systema respiratorium], in *Handbook of avian anatomy: nomina anatomica avium*, 2<sup>nd</sup> ed., edited by J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans & J.C. Vanden Berge. Cambridge, Massachusetts: Nuttall Ornithological Club.
- KING, A.S. & McLELLAND, J. 1984. Digestive system, in *Birds – their structure and function*, 2<sup>nd</sup> ed. London: Bailliere Tindall.
- KOBAYASHI, K., KUMAKURA, M., YOSHIMURA, K., INATOMI, M. & ASAMI, T. 1998. Fine structure of the tongue and lingual papillae of the penguin. *Archivum Histologicum Cytologicum*, 61:37–46.
- KOCH, T. 1973. Splanchnology, in *Anatomy of the chicken and domestic birds*, edited by B.H. Skold & L. DeVries. Ames, Iowa: The Iowa State University Press.
- LILLIE, F.R. 1908. *The development of the chick*. New York: Henry Holt and Co.
- LIMAN, N., BAYRAM, G. & KOÇAK, M. 2001. Histological and histochemical studies on the lingual, preglottal and laryngeal salivary glands of the Japanese quail (*Coturnix coturnix japonica*) at the post-hatching period. *Anatomia*, 30:367–373.
- LUCAS, F.A. 1896. The taxonomic value of the tongue in birds. *Auk*, 13:109–115.
- LUCAS, F.A. 1897. The tongues of birds. *Reports of the United States National Museum*, 1895:1003–1020.
- MACALISTER, A. 1864. On the anatomy of the ostrich (*Struthio camelus*). *Proceedings of the Royal Irish Academy*, 9:1–24.
- MCCANN, C. 1973. The tongues of kiwis. *Notornis*, 20:123–127.
- McLELLAND, J. 1975. Aves digestive system, in *Sisson and Grossman's The anatomy of the domestic animals*, edited by R. Getty. Philadelphia: W.B. Saunders Company.
- McLELLAND, J. 1979. Digestive system, in *Form and function in birds*, Vol. 1, edited by A.S. King & J. McLelland. London: Academic Press.
- McLELLAND, J. 1990. Digestive system, in *A colour atlas of avian anatomy*. Aylesbury, England: Wolfe Publishing Ltd.
- McLELLAND, J. 1993. Apparatus digestorius [Systema alimentarium], in *Handbook of avian anatomy: Nomina anatomica avium*, 2<sup>nd</sup> ed., edited by J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans & J.C. Vanden Berge. Cambridge, Massachusetts: Nuttall Ornithological Club.
- McLEOD, W.M. 1939. Anatomy of the digestive tract of the domestic fowl. *Veterinary Medicine*, 34:722–727.
- MECKEL, J.F. 1829. *System der vergleichenden Anatomie*. Halle: Der Rehgerschen Buchhandlung.
- MOORE, D.A. & ELLIOTT, R. 1946. Numerical and regional distribution of taste buds on the tongue of the bird. *Journal of Comparative Neurology*, 84:119–131.
- NICKEL, R., SCHUMMER, A. & SEIFERLE, E. 1977. Digestive system, in *Anatomy of the domestic birds*. Berlin: Verlag Paul Parey.
- OWEN, R. 1879. *Memoirs on the extinct and wingless birds of New Zealand; with an appendix of those of England, Australia, Newfoundland, Mauritius and Rodriguez*. Vol. 1. London: John van Voorst.
- PARKER, T.J. 1891. Observations on the anatomy and development of apteryx. *Philosophical Transactions of the Royal Society of London, B.*, 182:25–134.
- PARKER, W.K. 1866. On the structure and development of the skull in the Ostrich Tribe. *Philosophical Transactions of the Royal Society of London*, 156:113–183.
- PORCHESCU, G. 2007. Comparative morphology of the digestive tract of the Black African ostrich, hen and turkey. Ph.D. thesis, Agrarian State University of Moldova.
- PYCRAFT, W.P. 1900. On the morphology and phylogeny of the palaeognathae (*Ratitae and Crypturi*) and neognathae (*Cariatae*). *Transactions of the Zoological Society of London*, 15: 149–290.
- ROACH, R.W. 1952. Notes on the New Zealand kiwis (1). *New Zealand Veterinary Journal*, 1:38–39.
- SALES, J. 2006. Digestive physiology and nutrition of ratites. *Avian and Poultry Biology Reviews*, 17:41–55.
- SALES, J. 2007. The emu (*Dromaius novaehollandiae*): A review of its biology and commercial products. *Avian and Poultry Biology Reviews*, 18:1–20.
- TIVANE, C. 2008. A morphological study of the oropharynx and oesophagus of the ostrich (*Struthio camelus*). M.Sc. thesis, University of Pretoria.
- WARNER, R.L., McFARLAND, L.Z. & WILSON, W.O. 1967. Microanatomy of the upper digestive tract of the Japanese quail. *American Journal of Veterinary Research*, 28:1537–1548.
- WEBB, M. 1957. The ontogeny of the cranial bones, cranial peripheral and cranial parasymphetic nerves, together with a study of the visceral muscles of *Struthio*. *Acta Zoologica*, 38: 81–202.
- ZISWILER, V. & FARNER, D.S. 1972. Digestion and the digestive system, in *Avian biology*, edited by D.S. Farner, J.R. King & K.C. Parkes. New York: Academic Press.