



CHAPTER 4

GROSS MORPHOLOGY OF THE TONGUE



4.1 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 utilised 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 specialised for collecting food, eating, swallowing, taste and touch, and nest building.

Due to their commercial importance, the tongue and associated hyobranchial apparatus of domestic poultry have been described in detail (Hodges, 1974; McLelland, 1975; Gargiulo *et al.*, 1991; Nickel *et al.*, 1977; Homberger and Meyers, 1989; see Calhoun, 1954 for a review of the earlier literature).

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; MacAlister, 1864; Gadow, 1879; Owen, 1879; Pycraft, 1900; Göppert, 1903; Duerden, 1912; Faraggiana, 1933; Roach, 1952; Feder, 1972; McCann, 1973; Cho *et al.*, 1984; Fowler, 1991; Bonga Tomlinson, 2000; Gussekloo and Bout, 2005; Porchescu, 2007; Crole and Soley, 2008; Jackowiak and 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 and



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 description is that of Faraggiana (1933) who studied a single excised specimen of the tongue and laryngeal mound. Crole and 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 chapter presents the first definitive morphological description of the emu tongue and reviews, consolidates and compares the scattered information on the morphological features 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 utilised for more meaningful future comparative studies of the ratite tongue.

4.2 MATERIALS AND METHODS

The heads of 23 sub-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% buffered formalin. The heads were allowed to fix for approximately four hours while being transported to the laboratory, after which they were immersed in fresh fixative for a minimum period of 48 hours. Care was taken to exclude air from the oropharynx by wedging a small block of wood in the beak.

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. 4.1). The length (from the apex to the caudal edge of the caudal papillae) and width (between the tips of the last lateral papillae) (Fig. 4.2) 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 28-135mm lens and a Canon Macro 100mm lens for higher magnification photographs.

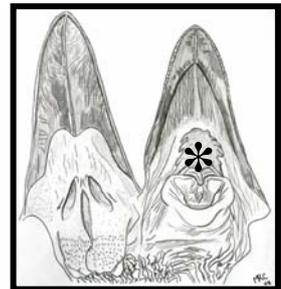
Three tongues were removed from the heads by lifting the organ from the floor of the oropharynx and cutting through the frenulum as well as the paired *ceratobranchiale* and *urohyale* of the hyobranchial apparatus. The mucosa was stripped from the tongues to expose the intraglossal elements (Figs. 4.7, 4.8) of the hyobranchial apparatus.

The terminology used is that of Nomina Anatomica Avium (Baumel *et al.*, 1993).

4.3. RESULTS

4.3.1 Topography

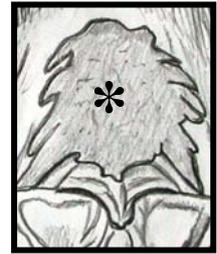
The tongue of the emu consisted of a rostral pigmented body and a caudal, variably pigmented root, both of which lay within the confines of the non-pigmented regions of the roof and floor of the oropharynx (Fig. 4.1). The tongue body occupied the middle third of the floor of the oropharynx and was a triangular structure with the apex pointing rostrally. The tongue root (Figs. 4.1, 4.4) extended from the caudal lingual papillae to the glottis and was flanked by, but did not extend to, the paired *ceratobranchiale* of the hyobranchial apparatus. In the closed gape, the caudal margin of the tongue body lay beneath and in contact with the rostral border of the choana, whereas the triangular tongue root fitted snugly into the rostral aspect of the choana. In some tongues the apex was observed, in the closed gape, to make contact with the base of the median palatine ridge which originated at the border of the pigmented and non-pigmented regions of the oropharyngeal roof.





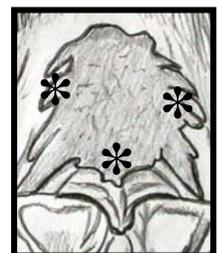
4.3.2 Tongue body (*Corpus linguae*)

The tongue body was dorso-ventrally flattened (Fig. 4.5) with the dorsum slightly raised in the centre and sloping towards the margins. The body varied in length between 21-27 mm (average of 23.6 mm), and in width between 20-29 mm (average of 25.9 mm) (Fig. 4.2). The apex (*Apex linguae*) was rudimentary and varied in shape from a sharp point (Fig. 4.1), to a blunt or rounded tip. In some instances the apex was invaginated by a shallow groove forming two smaller points (Fig. 4.2). The dorsal surface (*Dorsum linguae*) was pigmented giving it an ash-grey/brown colour in formalin-fixed specimens (Figs. 4.1, 4.2). However, in the specimens used for scanning electron microscopy, the tongues were of variable pigmentation, ranging from pigmented papillae only, to pigment mainly associated with the dorsal blood vessels, to no pigmentation at all. The ventral surface (*Ventrum linguae*) (Fig. 4.6) was lighter in colour than the dorsal surface with the epithelium appearing glass-like (transparent). The rostro-medial region of the tongue ventrum was slightly concave. A conspicuous, light-coloured, finger-like line extended along the midline from the tip of the frenulum to end bluntly caudal to the apex (Fig. 4.6). This line represented the rostral projection of the *basihyale* (see below) (Fig. 4.8). From the rostro-lateral surfaces of the frenulum two raised bands (*crura*) (Fig. 4.6), were directed and tapered towards the apex. Numerous pale doughnut-shaped structures with a darker centre were clearly visible beneath both the dorsal and ventral surfaces of the tongue body (Figs. 4.2, 4.3, 4.6). Light microscopy confirmed that each of these structures constituted a glandular unit with a central lumen/duct opening onto the lingual surface (Crole and Soley, 2008; see Chapter 5). In some tongues, these structures were obscured due to a darker colouration of the dorsum and only the openings, resembling pits, were visible (Fig. 4.4).



4.3.3 Margins (*Margo linguae*)

The three margins of the tongue body displayed two sets of lingual papillae (Figs. 4.1, 4.2), the left and right lateral lingual papillae (*Papillae linguae laterales*) and the caudal lingual papillae (*Papillae linguae caudales*).



The first lateral papillae originated on either side of and just caudal to the apex. These were the smallest of the lateral papillae and were directed laterally or caudo-laterally. The rest of the papillae progressively pointed more caudo-laterally and became longer and more



slender. The last papillae were the longest and most caudally directed, and in some specimens exhibited a pale tip. In some instances individual papillae emanated from the base of adjacent papillae (Fig. 4.2) and not directly from the lingual margin. The number of papillae present on the lateral lingual margins was variable and not necessarily equal on both sides. Although the left and right lateral margins demonstrated a similar range of papillae (3-8 on the left side and 5-8 on the right side), there appeared 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 totalled 11.2. The doughnut-shaped structures seen below the surface (Fig. 4.3) ended abruptly just beyond the root of the lingual papillae, although in the last lateral and caudal papillae they extended to the papillae tips.

The caudal lingual papillae (Figs. 4.1, 4.2, 4.4) were rudimentary and poorly defined compared to the lateral papillae and demarcated the caudal boundary of the tongue body. In some instances (n=4) the caudal papillae appeared as a fused, centrally positioned structure with variable incisures and small projections (Fig. 4.4). In other specimens (n=4) the fused component was flanked on either side by a single, more typical papilla. In a number of tongues (n=8) the fused component displayed a shallow median groove resulting in the formation of two median papillae which were accompanied by a variable number (0-2) of adjacent papillae (Fig. 4.2). The caudal papillae varied in number between 1-4 (average 2.5). In one specimen, a structure similar in appearance to a lingual papilla was observed to project dorsally from the mucosa covering the left *ceratohyale*, just caudal to the last lateral papilla.

4.3.4 Tongue root (*Radix linguae*)

The tongue root (Figs. 4.1, 4.4) was a fleshy triangular structure, which in most specimens was non-pigmented. The caudal extremity of the root ended as a rounded raised bulbous structure (pigmented in some specimens) that extended into the rostral aspect of the laryngeal fissure (glottis). The mucosa of the tongue root was continuous with the rest of the mucosa covering the oropharyngeal floor and formed a shallow groove where it abutted the paired *ceratobranchiale* and the raised margins of the laryngeal fissure (Fig. 4.4). The surface of the root displayed the same doughnut-shaped structures seen on the tongue body, particularly in the midline. A shallow retrolingual recess existed between the ventral aspect of the caudal lingual papillae and the tongue root.





4.3.5 Frenulum (*Frenulum linguae*)

The frenulum (Figs. 4.5, 4.6) was a fleshy non-pigmented structure attaching the caudal half of the tongue body to the oropharyngeal floor. It was 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 was thrown into longitudinal folds. These folds were obliterated when the tongue body was lifted dorsally from the oropharyngeal floor (Fig. 4.5). The rostral point of the frenulum housed the body of the *basihyale* while the two lateral edges enclosed the rostral parts of the paired *ceratobranchiale* which merged rostrally with the body of the *basihyale* (Fig. 4.6). Extending caudally from the body of the *basihyale*, along the midline, was the *urohyale*, also housed within the frenulum (Fig. 4.6) (see also Fig. 4.8).

4.3.6 Lingual skeleton

The lingual skeleton consisted of the *paraglossum* and the rostral projection of the *basihyale*, both of which were imbedded within the tongue body (Figs. 4.7, 4.8). The *paraglossum* was a broad, thin, teardrop-shaped cartilaginous plate imbedded within the lingual parenchyma. The rostral tip was pointed while the base varied from gently rounded, to scalloped. The *paraglossum* was situated dorsal to the rostral projection of the *basihyale*, to which it was attached by loose connective tissue. The *basihyale* ran almost the full length of the *paraglossum*, ending near its rostral tip. The edges of the *paraglossum* did not extend to the apex or lingual margins or into any of the lingual papillae.





4.4 DISCUSSION

4.4.1 Topography

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; Porchescu, 2007; Jackowiak and Ludwig, 2008; Tivane, 2008), greater rhea (Gadow, 1979; Pycraft, 1900; Faraggiana, 1933; Gussekloo and Bout, 2005), cassowary (P. Johnston, personal communication) and kiwi (Owen, 1879; McCann, 1973).

The general shape of the tongue in birds usually mimics that of the bill (Bradley, 1915; McLeod, 1939; 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 and Farner, 1972; McLelland, 1979; Bailey *et al.*, 1997; Bonga Tomlinson, 2000; Gussekloo and Bout, 2005; Jackowiak and Godynicki, 2005; Jackowiak and Ludwig, 2008), a feature also noted in the emu (see Table 4.1). 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 recognised, namely, the occurrence of caudally directed lingual papillae (Harrison, 1964; McLelland, 1979; King and 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). 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 and McLelland, 1984) as well as non-protrusable (King and 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 method (Bonga Tomlinson, 2000).

4.4.2 Shape

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 whereas the tongue body appeared broader than that depicted in the earlier study.

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 4.1 and indicate that the tongues of the emu and cassowary (P. Johnston, personal communication) 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 4.1).

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).

**Table 4.1 Comparative features of the ratite tongue**

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

⁺ These are approximate measurements. * Extrapolated from the measurements in Roach (1952) (Species not mentioned); [#] Own measurements; (Underlined names indicate a sketch is supplied, bold indicates photographs.)

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





4.4.3 Lingual papillae

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 and McLelland, 1984; Bailey *et al.*, 1997; Kobayashi *et al.*, 1998; McLelland, 1990) including domestic poultry (Calhoun, 1954; Ziswiler and Farner, 1972; McLelland, 1975; Nickel *et al.*, 1977; King and McLelland, 1984; McLelland, 1990). However, it would appear that lingual papillae are not a common or well-developed feature in ratites (Table 4.1), a characteristic also noted by Bonga Tomlinson (2000). Apart from the lateral papillae of the emu 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 were 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 numbers of papillae display 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 4.1). However, in the ostrich and greater rhea (Table 4.1) the caudo-lateral 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 and 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).





4.4.4 Tongue root

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 and 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 and Godynicki, 2005; Jackowiak and 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 (Moore and Elliott, 1946; Gentle, 1971; Nickel *et al.*, 1977; Bailey *et al.*, 1997). Some authors appear to use the term ‘tongue base’ synonymously with ‘tongue root’ (Nickel *et al.*, 1977; Gussekloo and Bout, 2005). In some studies the caudal aspect of the tongue body has been termed the tongue base (Warner *et al.*, 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 and 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 (Homberger and Meyers, 1989; Liman *et al.*, 2001).

The importance of clarity in correctly identifying and naming the various components of the tongue has been pointed out by Moore and 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 and Elliott, 1946; Gentle, 1971; Nickel *et al.*, 1977; Bacha and Bacha, 2000; Al-Mansour and 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 4.1). The structure of the tongue root in kiwi species (McCann, 1973) is unclear. The extension of the tongue root into the rostral aspect of the laryngeal entrance (Faraggiana, 1933; present study) represented an interesting modification not observed or illustrated in other ratites (ostrich and greater rhea) (Göppert, 1903; Faraggiana, 1933; Gussekloo





and Bout, 2005; Porchescu, 2007; Jackowiak and 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 and 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. 4.1) 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.

4.4.5 Frenulum

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 movement. 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 and 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 and 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 rostro-caudal (though





unable to protrude) and dorso-ventral planes by virtue of the relatively large, folded frenulum and the association of the hyobranchial apparatus with the tongue body and frenulum.

4.4.6 Lingual skeleton

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 above author.

The *paraglossum* of the emu was teardrop-shaped with a pointed rostral tip and a rounded base, while, 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 (see Chapter 5). 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 ventro-lateral to it (Bonga Tomlinson, 2000; Tivane, 2008). This arrangement differs radically from that of the emu and the other ratites, where the rostral projection of the *basihyale* lies ventral to the *paraglossum*, and has led to some authors not recognising or misinterpreting the narrow, paired structure (Meckel, 1829; Parker, 1866; Webb, 1957; Jackowiak and Ludwig, 2008).

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 and 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 and McLelland, 1984; Bonga Tomlinson, 2000).

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4.6 FIGURES

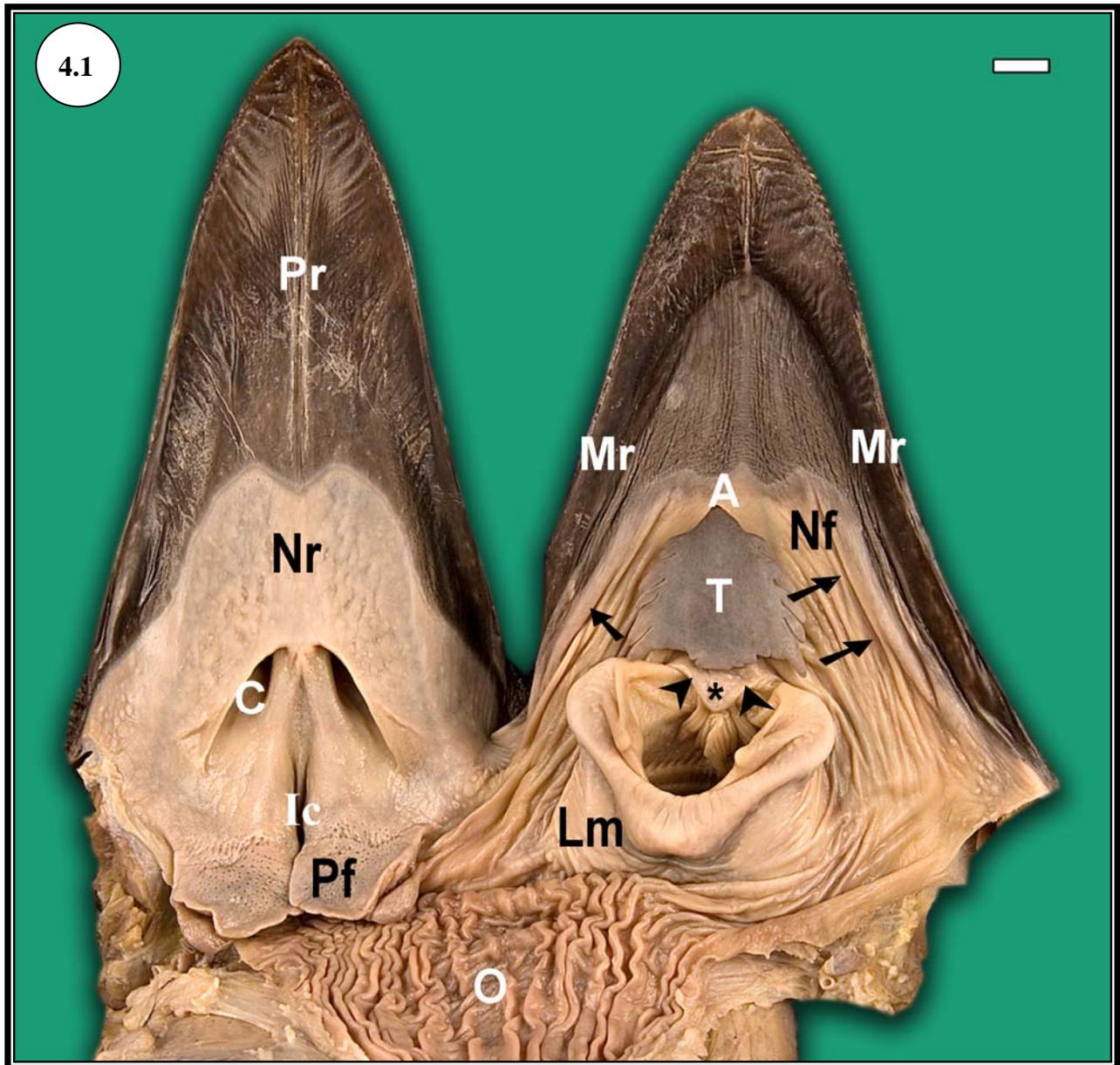


Figure 4.1: Emu head opened along the right commissure to reveal the positioning of the tongue within the oropharynx. The body of the tongue (T) lies within the non-pigmented region of both the roof (Nr) and floor (Nf) of the oropharynx, and the small tongue root (*) extends from the base of the tongue 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 = 5mm.

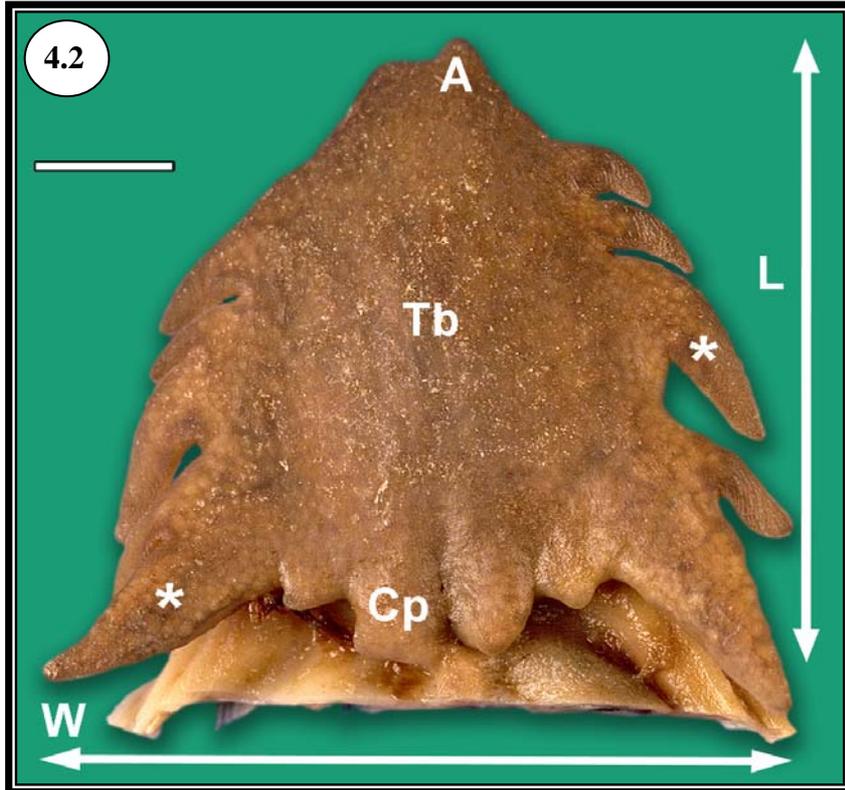


Figure 4.2: Dorsal view of the tongue body (Tb) showing the apex (A), lateral lingual papillae (*) and caudal lingual papillae (Cp). Tongue body length (L) was measured from the apex to the caudal papillae. The width (W) was measured between the tips of the last lateral papillae. Bar = 5mm.

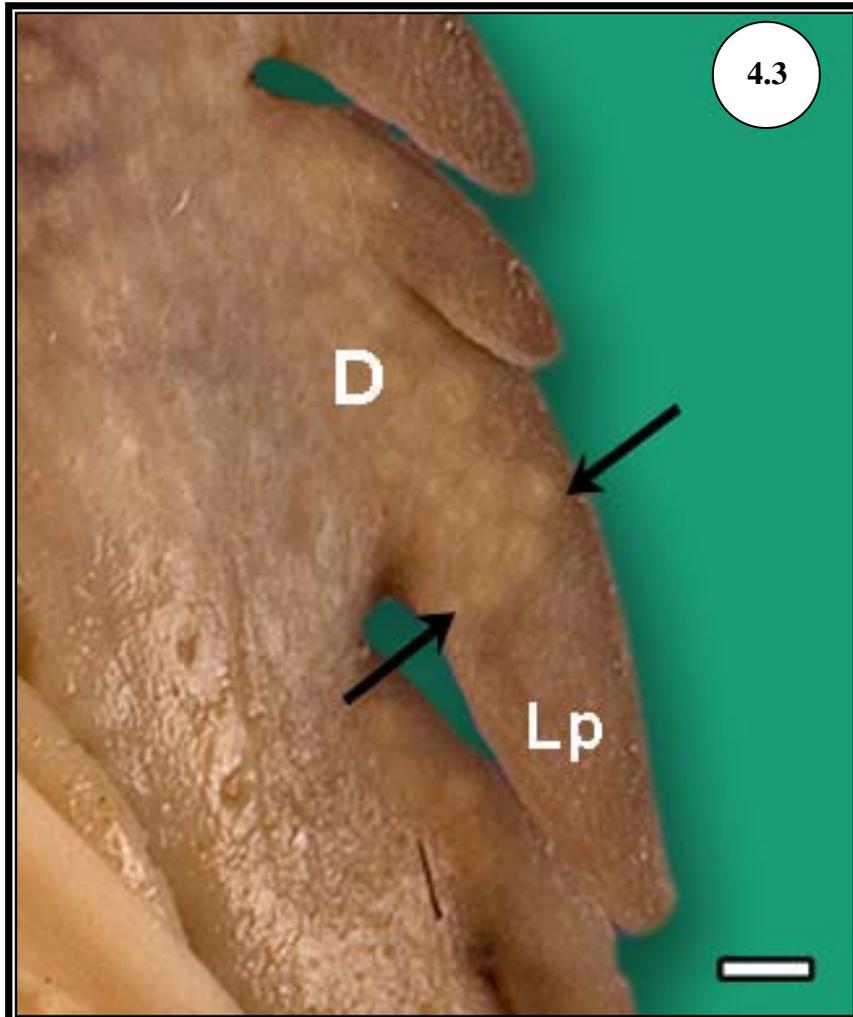


Figure 4.3: Ventral view of the lateral lingual papillae showing the abrupt transition (arrows) between the presence of doughnut-shaped structures (D) and the unelaborated surface of the papillae (Lp). Bar = 1mm.

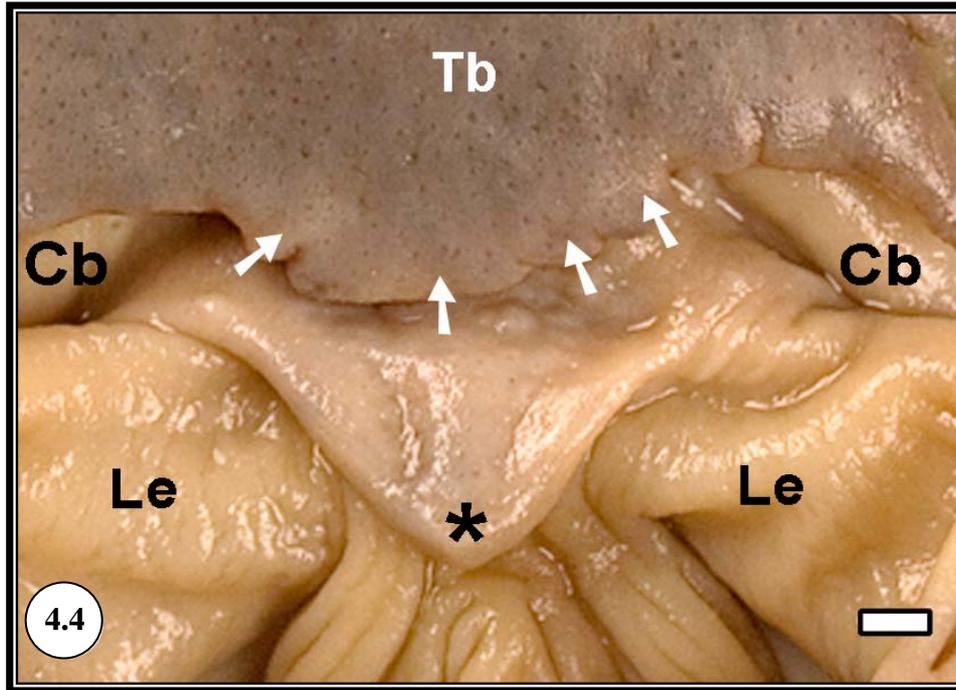


Figure 4.4: Dorsal view of the triangular tongue root, showing the tongue root tip (*) folding over the laryngeal entrance (Le). In this specimen, the caudal lingual papillae (arrows) of the tongue body (Tb) appear fused with variable incisures and small projections being apparent. The rostral parts 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 = 1mm.

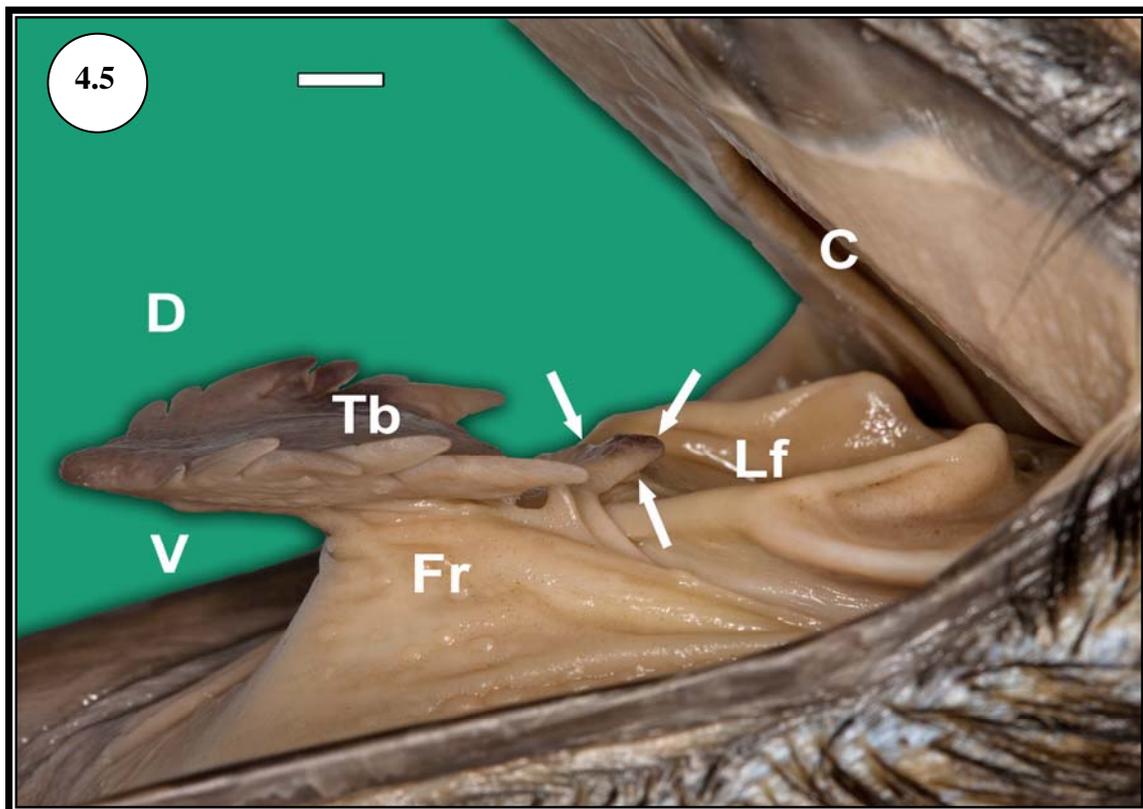


Figure 4.5: The dorso-ventrally flattened tongue body (Tb) shown in lateral profile. The folds of the frenulum (Fr) are not visible as the tongue body is in the raised position. Dorsum (D), ventrum (V), tongue root tip (arrows), Laryngeal fissure (Lf), choana (C). Bar = 5mm.

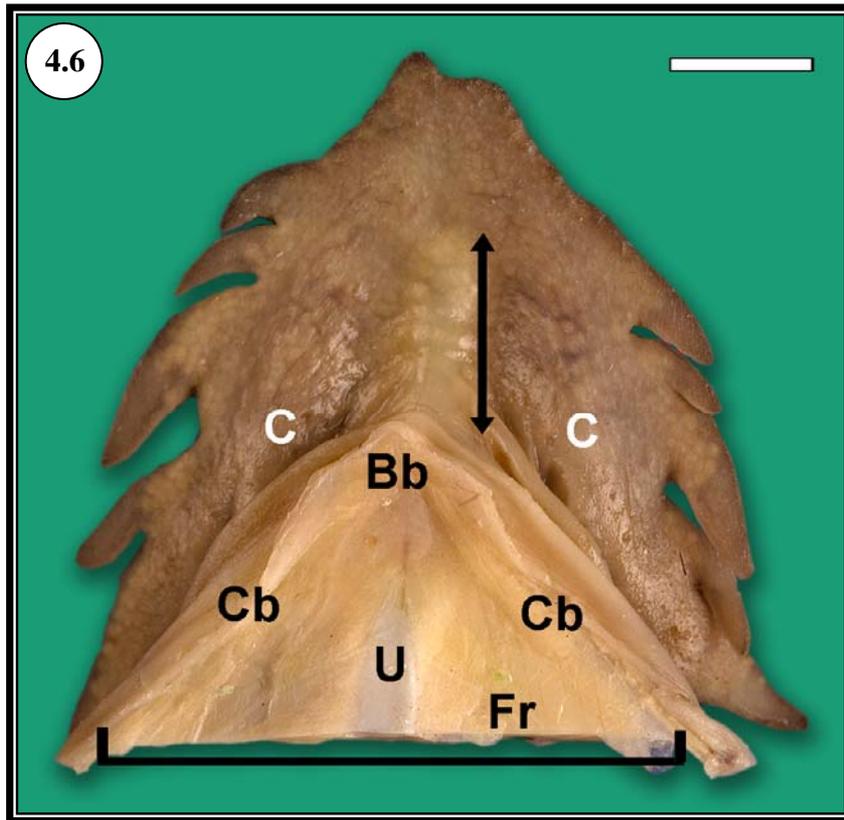
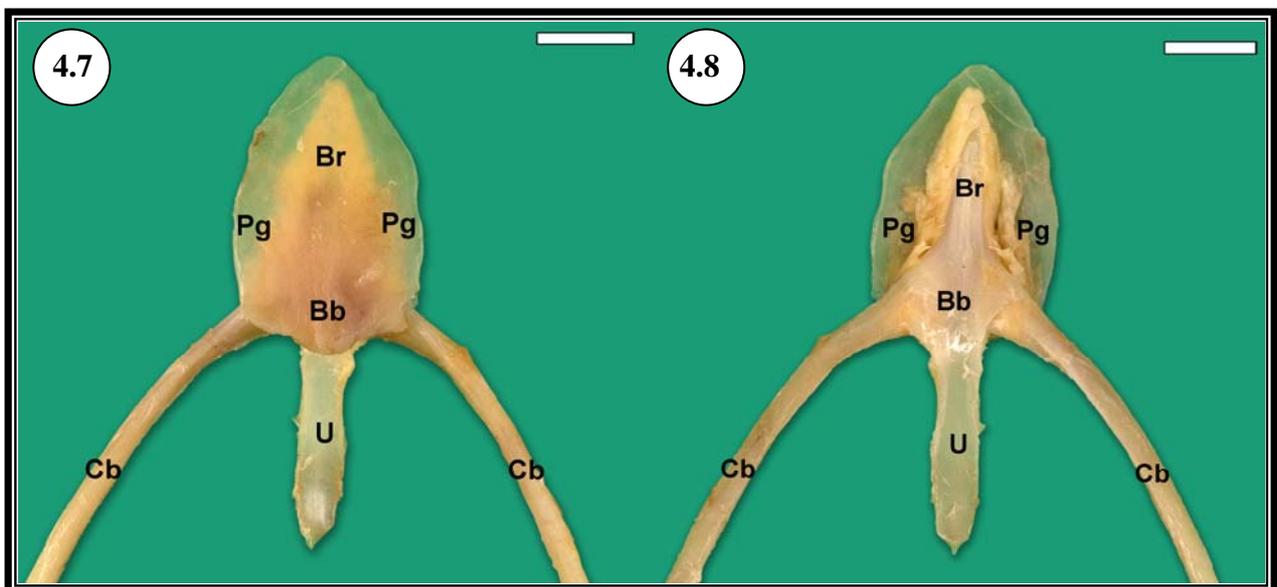


Figure 4.6: The tongue body and frenulum in ventral view. Note the extent of the rostral projection of the *basihyale* (double-headed arrow). The position of the body of the *basihyale* (Bb), rostral parts of the paired *ceratobranchiale* (Cb) and the *urohyale* (U) are indicated and occur in triangular formation running within the frenulum (Fr). The doughnut-shaped structures can be clearly seen below the surface. Crura (C). Bar = 5mm.



Figures 4.7 and 4.8: The lingual skeleton shown in dorsal (4.7) and ventral (4.8) 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. 4.6). Bar = 5mm.